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PHYTOPLANKTON & BIOTIC INTERACTIONS

Extreme drought favors potential mixotrophic organisms in tropical semi-arid reservoirs

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Abstract Climate change is affecting the global hydrological cycle and is causing drastic changes in the freshwater hydrological regime. Water level (WL) reduction caused by drought tends to increase the concentration of nutrients favoring the dominance of cyanobacteria. We hypothesized that the WL reduction favors the dominance of cyanobacteria at regular dry conditions, but at extremely dry events mixotrophic algae would thrive because of light limitation due to increased resuspension of sediments on the water column. To test our hypothesis, we compared phytoplankton traits and water quality variables between two sets of reservoirs located in two watersheds with contrasting precipitation regimes within the Brazilian semi-arid. The reservoirs were compared in a dry period and in an extremely dry period to evaluate the response of the variables to an extreme drought. Drought intensification decreased the reservoirs' WL and water transparency and increased the total phosphorous. Cyanobacteria dominated in the dry period, and the contribution of mixotrophic algae increased in the extremely dry period. Thus, phytoplankton with mixotrophic potential was favored by the extreme drought. This result suggests that this can be one possible scenario for phytoplankton communities in reservoirs of semi-arid regions if extreme droughts become more frequent because of climate change.

Keywords Climate change · Water level reduction · Water quality · Phytoplankton · Functional traits · Cyanobacteria

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Introduction

Phytoplankton is a widely distributed polyphyletic photosynthetic group that possesses different adaptive strategies for survival, growth, and reproduction influenced by the organism's morphology and physiology (Reynolds, 2006). The phytoplankton community is structured according to morphological, physiological, and ecological characters distributed in three major axes: (i) resource acquisition, (ii) growth, and (iii) avoidance of predators (Litchman & Klausmeier, 2008). Key factors, such as light intensity, water depth, and mixing regime, influence the phytoplankton dynamics, species composition, and dominance (Huisman & Weissing, 1994; Zohary et al., 2010). A method widely used in community ecology is the trait-based approach, which focuses on the relationships of species traits with environmental factors, interspecific interactions, and fitness (McGill et al., 2006).

Functional trait-based approaches were developed to group species with similar morphological, physiological, and ecological properties, indicating optimal ecological strategies to a given environmental condition (Reynolds, 2006; Naselli-Flores & Barone, 2012). The functional approach is a powerful predictor of ecosystem dynamics (Reynolds & Irish, 1997; McGill et al., 2006; Brasil & Huszar, 2011). The trait-based functional approach classifies phytoplankton traits by type (morphological, physiological, behavioral, and life history) and by ecological function (reproduction, resource acquisition, and predators avoidance) (Litchman & Klausmeier, 2008). For each major component of the trait-based approach exists a wide range of traits that imply phytoplankton survival and reproduction (Litchman & Klausmeier, 2008).

Phytoplankton organisms have a wide range of different shapes (e.g., round cells, filaments, ellipsoids, and other complex shapes) (Reynolds, 2006). Morphology is essential for phytoplankton reproduction, predator avoidance, and resource acquisition (Litchman & Klausmeier, 2008). Moreover, species physiology is a key component of resource acquisition. For example, phytoplankton adaptive strategies for high or low light demand reverberate through photosynthesis rates and nitrogen fixation, which may favor the dominance of either cyanobacteria (Huisman & Weissing, 1994) or mixotrophic algae (Rothhaupt, 1996).

Mixotrophy is an important functional trait that combines autotrophy and heterotrophy in the same organism; therefore, these individuals may act as either producer or consumer (Sanders, 1991). Many phytoplankton species are able to phagocyte bacteria and perform mixotrophic metabolism. Some argue that this ability may be a rule rather than an exception both in marine and freshwater ecosystems (Hartmann et al., 2012; Flynn et al., 2013). Studies showed significant contributions of mixotrophic algae to total bacterivory in marine oligotrophic environments (Anderson & Rivkin, 2001; Unrein et al., 2007, 2014; Gast et al., 2014). However, only a few studies demonstrated this importance in freshwater eutrophic systems (Saad et al., 2013, 2016). Phytoplankton species with a potential for mixotrophy were observed in the Brazilian semi-arid region in nutrient-rich and turbid environments (Medeiros et al., 2015; Costa et al., 2016). This finding suggests that mixotrophy may be an important strategy in light-limited aquatic ecosystems because of low water levels and high inorganic turbidity, even if they have high nutrient concentrations.

Precipitation rates lower than evaporation rates lead to water level reduction; consequently, nutrient concentration, turbidity, salinity, and conductivity increase, thus causing severe implications for productivity, species composition, and cyanobacterial bloom persistency (Naselli-Flores & Barone, 2005; Jeppesen et al., 2015). However, in a severe drought scenario, phytoplankton functional traits, such as low light demand and potential to mixotrophy, may be favored (Costa et al., 2016).

Temperature changes, increase in atmospheric carbon dioxide, and increase in frequency and intensity of extreme events, such as droughts and floods, are considered the major stressors associated with climate change (Woodward et al., 2010). According to the Intergovernmental Panel on Climate Change, tropical regions are the most susceptible to global warming (IPCC, 2014) and the effects of global warming on tropical aquatic ecosystems is still under debate (De Senerpont Domis et al., 2013a, 2013b; Sarmento et al., 2013). Furthermore, this scenario will be intensified in tropical semi-arid regions because of the increase in frequency and intensity of droughts (Marengo et al., 2009; Roland et al., 2012*)*.

Given the uncertainties of the effects of climate change on the biota of tropical systems (De Senerpont

Domis et al., 2013a, 2013b; Sarmento et al., 2013), especially in semi-arid regions where these changes are amplified, this study aimed to determine the effects of water level reduction on phytoplankton communities and environmental variables in an understudied tropical semi-arid region involving 16 aquatic systems inside two sub-basins with distinct rainfall levels during a prolonged extreme drought. Recent studies in the Brazilian semi-arid region, reported some signals on an increase on mixotrophs during extreme and prolonged drought (Medeiros et al., 2015; Costa et al., 2016). Therefore, we hypothesized that the water level reduction caused by drought and evaporation would increase nutrients favoring the dominance of cyanobacteria in dry conditions but that mixotrophic algae would thrive as a result of light limitation due to increased sediment resuspension in extremely dry conditions (i.e., with extremely low water level). We used a space-for-time substitution approach in this study to predict the effects of climate change on the phytoplankton community structure in tropical semi-arid systems.

Materials and methods

Study site

The sample units (reservoirs) were all located in the Piranhas-Açu watershed, which is entirely embedded in the semi-arid region of Northeast Brazil. The regional climate is tropical semi-arid (BS'h', Alvares et al., 2013) and is characterized by irregular rainfall, high evapotranspiration rates, and negative water balance during most of the year. The rainy season is concentrated in five months, generally from January to May. The rivers in this region are considered intermittent, and the reservoirs are generally shallow and have multiple uses, such as water supply, fishing, irrigation, and entertainment (Barbosa et al., 2012).

The study was carried out in two sets of reservoirs (n = 16) located in two sub-basins; eight reservoirs are located in the Piancó sub-basin (PB) and eight in the Seridó sub-basin (SB) (Fig. 1). Although both regions are considered semi-arid (BS'h', Alvares et al. 2013), they have contrasting mean annual precipitation values of about 500 mm in SB and 700 mm in PB. Owing to the natural differences in aridity within the same climatic region and between the sampling periods, the study design comprised two sub-basin (PB and SB) and two sampling periods with contrasting levels of aridity: (1) dry (January 2014) and (2) extremely dry (January 2016). This sampling period was characterized by a severe to extreme drought according to Standardized Precipitation Index (SPI) (Brazilian National Institute of Meteorology, 2016), with most of the reservoir storage reaching less than 40% of its maximum capacity and precipitation remaining well below the average.

Sampling and analysis

The samples were collected from the water column with a PVC tube in five sites near the reservoir's dam (deepest point) and integrated in one composite sample for nutrients, chlorophyll-*a,* and phytoplankton community analyses at the end of each campaign. Water temperature, dissolved oxygen, pH, turbidity, and conductivity were measured each meter from the surface to the bottom using a multiparameter probe Horiba (U-22 model). The samples for phytoplankton counting and identification were fixed with acetic solution of lugol.

Water transparency was measured by Secchi disk depth. The euphotic depth (Zeu) was calculated as 2.7 times the Secchi depth (Cole, 1994). Water for chlorophyll-*a* was filtered through glass microfiber filters (GF/C Whatman). Chlorophyll-*a* was extracted with 95% ethanol and measured by spectrophotometry (Jespersen & Christoffersen, 1988). Total phosphorus (TP) was analyzed by the ascorbic acid method after oxidation with potassium persulfate (Valderrama, 1981).

Reservoir water volume and precipitation data were provided by the Agriculture Company from Rio Grande do Norte (EMPARN) and Water Management Executive Agency from Paraiba (AESA).

The δ^2H and δ^{18}O of the water sample were determined using the Multiflow system connected to an Isoprime Mass Spectrometer (Thermo Electron, Waltham Massachusetts, USA). This analysis was performed to give an indirect estimation of the water balance in the reservoirs. The higher the δ2H δ^{18}O values of water is, the lower the inlet water to evaporation ratio (Kosten et al., 2010). All isotopic ratios are expressed in δ units relative to the Vienna mean standard ocean water as follows:

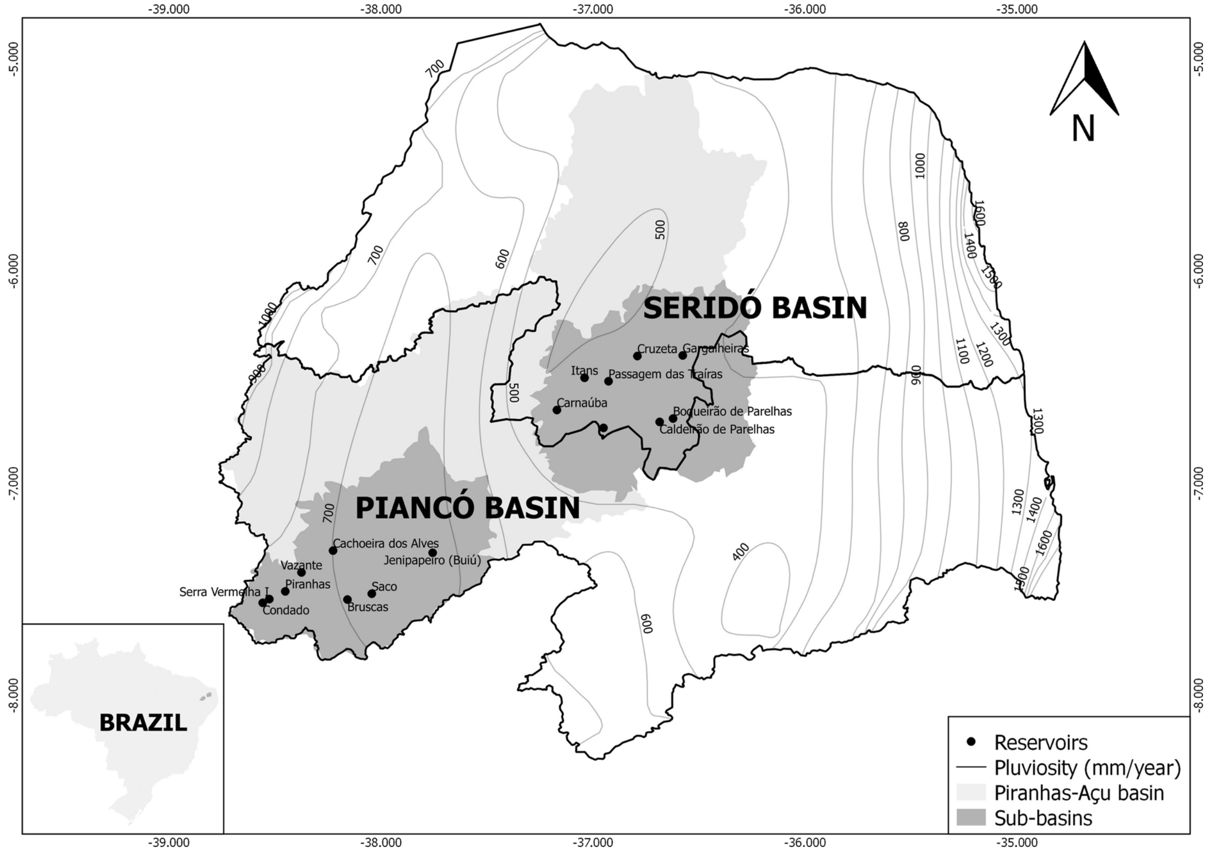

Fig. 1 Study area of the Piranhas-Açu River watershed showing the 16 reservoirs distributed in the two sub-basins, Piancó sub-basin (PB) and Seridó sub-basin (SB). Isohyets show the differences in annual precipitation. The reservoirs in SB are located in the drier region, within the isohyets of 500 mm, and those in PB are located within the isohyets of 700 mm

$$\delta^2H \; or \; \delta^{18}O = \left[\frac{R_{sample}}{R_{std}} - 1\right] \cdot 1000,$$

where R_{sample} and R_{std} are the ^{2}H/H or ^{18}O/^{16}O ratios of the sample and standard, respectively. The precision of analysis is ± 2.0 and ± 0.2% for the δ^2H and δ^{18}O values, respectively.

We derived the inlet water: evaporation ratio using δ^{18}O. The derivation is based on the principle that light isotopes evaporate quicker than heavy isotopes. The heavier the lake water is relative to the incoming water, the more lake water is subjected to evaporation. The inlet water:evaporation ratio was calculated using the Gat–Bowser model (Gat & Bowser, 1991; Rozanski et al., 2001). The input on relative humidity to the model was obtained from the dataset of New et al. (2002). The inlet water δ^{18}O values were approximated by the isotopic composition of the precipitation at the lake location (data obtained from Bowen and Revenaugh (2003)). A smaller inlet water: evaporation ratio (a proxy for water balance) implies that more water is evaporated relative to the net input of water to the reservoirs.

Phytoplankton functional traits

The phytoplankton community was identified whenever possible at the species level. Quantitative analysis was performed with an inverted microscope Leica at 400×magnification according to Utermöhl (1958), and the settling units (cells, colonies, and filaments) were enumerated in random fields (Uehlinger, 1964). Algal biovolume (mm3L-1) was calculated from approximated geometric models (Hillebrand et al., 1999) and the fresh-weight unit was expressed in mass (mg L-1) (Wetzel & Likens, 2000). The phytoplankton functional traits were grouped by summing up the biomass with the same traits and according to the trait-

Table 1 Groups of the phytoplankton functional traits identified in the study

Phytoplankton function traits	
Morphological	Physiological
Unicellular	N fixing
Small round/ovoid	Potential mixotrophy
Large round/ovoid	High light acquisition
Complex shapes	Low light acquisition
Pluricellular	
Filamentous	
Coenobial	
Colonial	

based functional approach (Litchman & Klausmeier, 2008). Phytoplankton species were characterized as morphological trait species with cell shapes as small round or ovoid, large round or ovoid, complex shapes, filamentous, coenobial, and colonial. We considered cell length to determine small (< 10 µm) and large (> 10 µm) size according to Reynolds (2006). The physiological functional traits were characterized by species potentiality: nitrogen fixing, mixotrophic, and high or low light requirement. All species from Nostocales Order were considered as potentially N fixing. According to literature, we considered as potential mixotrophs the species from the groups of Cryptophyceae and Euglenophyceae that occurred during the study. We establish the light requirements (low or high light demands) according to Reynolds (2006). Thus, we obtained 10 functional traits, with six being morphological traits and four being physiological traits (Table 1).

Statistical analysis

A two-way ANOVA was performed to test the isolated and combined effects of the region (sub-basins) and the sampling periods on the biological (phytoplankton species traits) and environmental variables. All phytoplankton abundance data used were based on biomass. Prior to performing the analysis, environmental and biological variables were log transformed (log x + 1) to improve normality except the percentage of maximum volume variable. The Shapiro–Wilk test was performed to check for data normality. A linear regression was performed to assess whether turbidity was a good predictor of mixotrophic algae in the studied reservoirs in the extremely dry period.

A detrended correspondence analysis (DCA) with biological data was used to determine the best-constrained ordination method for our data (Ter Braak & Prentice, 1988). The redundancy analysis (RDA) was used to examine the relationships between the environmental variables and the morphological and physiological functional traits. The environmental matrix in the RDA included pH, temperature (T°), dissolved oxygen (DO), conductivity (Cond), turbidity (Turb), chlorophyll-*a* (Chla), TP, water volume as % of maximum capacity (Vol), and euphotic zone (Zeu). The biological matrix comprised the morphological functional traits (small round/ovoid, large round/ovoid, filamentous, coenobial, complex shapes, and colonies) and the physiological functional traits (nitrogen fixing, potential for mixotrophy, and high or low light requirement). Data were transformed in log (x + 1) to achieve a normal distribution except the percentage of maximum volume and pH variables. To evaluate whether the variation explained by the variables was higher than that by the same number of randomly generated variables, a Monte Carlo test using 999 permutations was performed (Mc Cune & Mefford, 2011).

Results

Reservoirs in the drier basin (SB) had a lower percentage of maximum volume (Fig. 2a), a smaller maximum depth (Fig. 2b), Secchi depth (Fig. 2c), and inlet water:evaporation ratio (Fig. 2d), and a higher concentration of total phosphorus (Fig. 2e) and chlorophyll-*a* (Fig. 2f) than those in the other basin (PB). Moreover, the differences in phosphorus and chlorophyll-*a* concentrations between the two sets of reservoirs were even higher during the extreme dry period (Figs. 2e, f), significant interaction terms).

Phytoplankton biomass estimated from the total biovolume (Fig. 3a) and species richness (Fig. 3b) did not vary during the sampling periods and between regions.

A total of 51 species were identified in the wetter basin (PB), with 33 species found during the dry period and 38 species during the extremely dry period. In the drier basin (SB), 67 species were identified, with

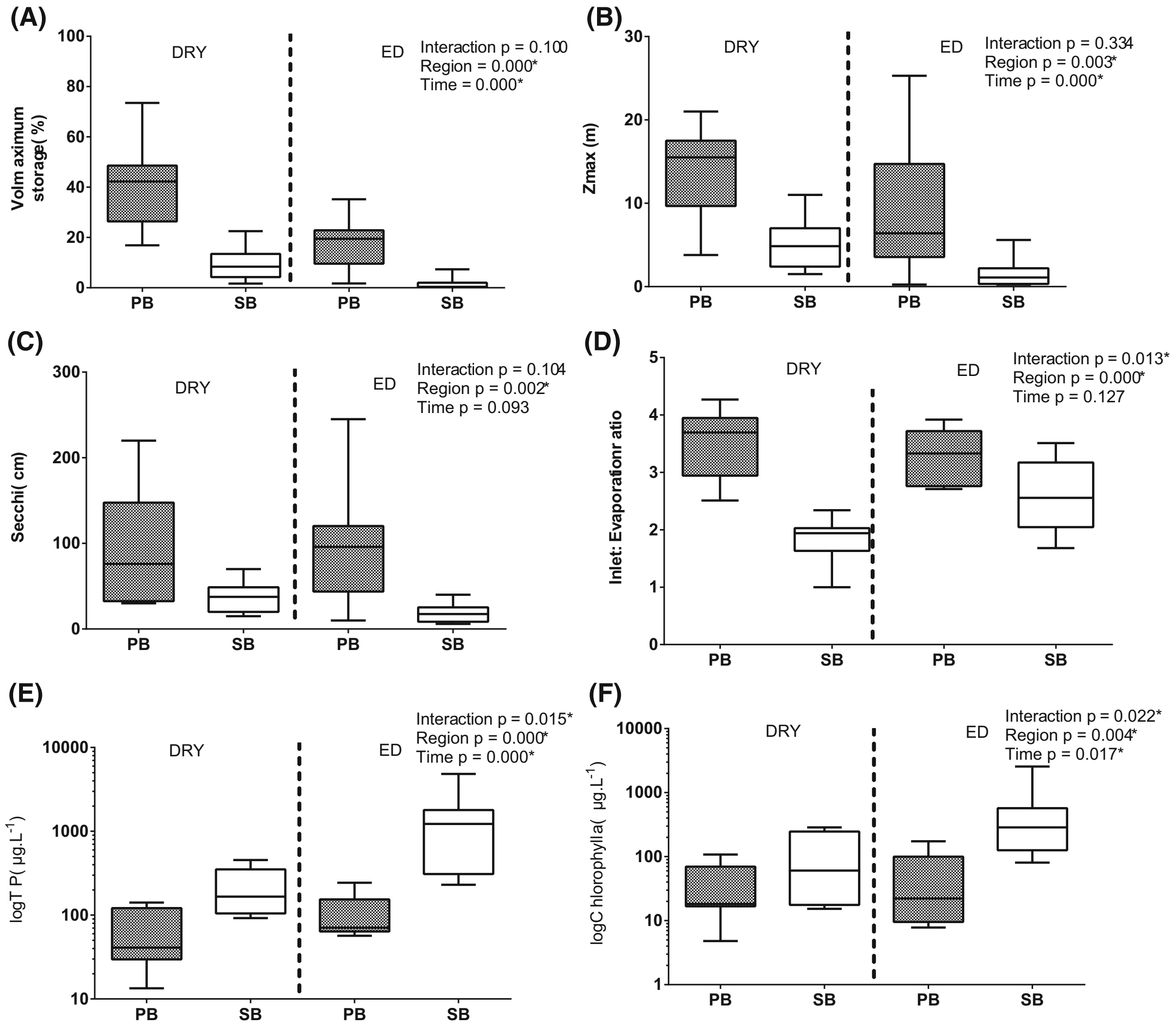

Fig. 2 Box plots of some of the environmental variables **a** maximum volume storage (Vol%), **b** maximum depth (Zmax), **c** Secchi disk depth, **d** water:evaporation ratio, **e** total phosphorous, and **f** chlorophyll-*a* in the two regions (PB and SB) and in the two sampling periods: dry and extremely dry (ED). The dotted lines separate the studied periods. The box plot shows the median, minimum, maximum, first, and third quartiles. The results of the two-way ANOVA are shown for each variable

39 species found during the dry period and 44 species during the extremely dry period.

The relative biomass of phytoplankton functional traits differed between regions and among sampling periods (Fig. 4). For the morphological functional traits, we observed the dominance of filaments (e.g., *Cylindrospermopsis raciborskii* and *Aphanizomenon sp.)* in the PB reservoirs and of colonies (e.g., *Microcystis aeruginosa)* in the SB reservoirs during the dry period. And dominance of colonies (e.g., *Microcystis aeruginosa)* in the PB reservoirs and an increase in biomass of large round/ovoid (e.g., *Cryptomonas sp.)* in the SB reservoirs during the extremely dry period (Fig. 4a).

For the physiological functional traits, we observed the co-dominance of nitrogen fixing and low light acquisition traits (e.g., *C. raciborskii)* in PB reservoirs and a dominance of high light acquisition traits (e.g., *M. aeruginosa)* in SB reservoirs during the dry period, but a dominance of high light acquisition traits in PB reservoirs and a co-dominance of nitrogen fixing and potential mixotrophy (e.g., *Cryptomonas sp.*) in SB reservoirs during the extremely dry period (Fig. 4b). It is noteworthy that during the extremely dry period, the

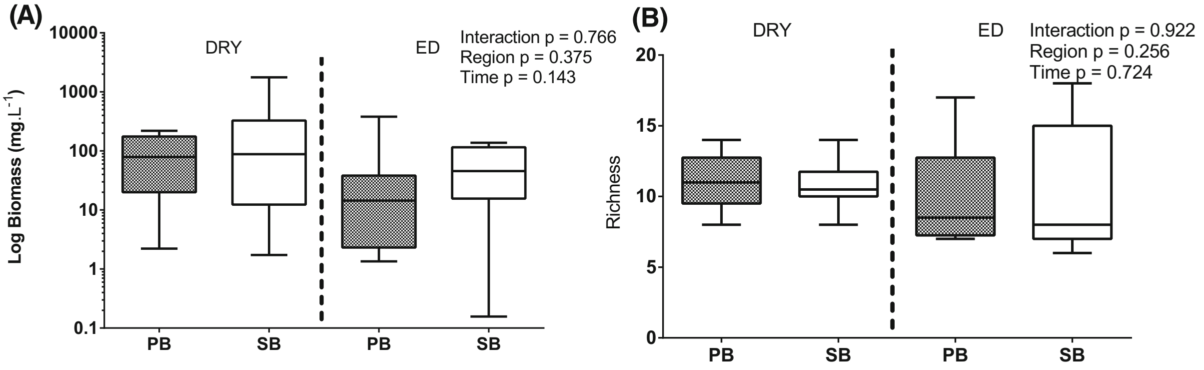

Fig. 3 Box plots of the total phytoplankton biomass in log scale (**a**) and species richness (**b**) in the two regions (PB and SB) and in the two sampling periods: dry and extremely dry (ED). The dotted lines separate the studied periods. The box plot shows the median, minimum, maximum, first, and third quartiles. The results of the two-way ANOVA are shown for each variable

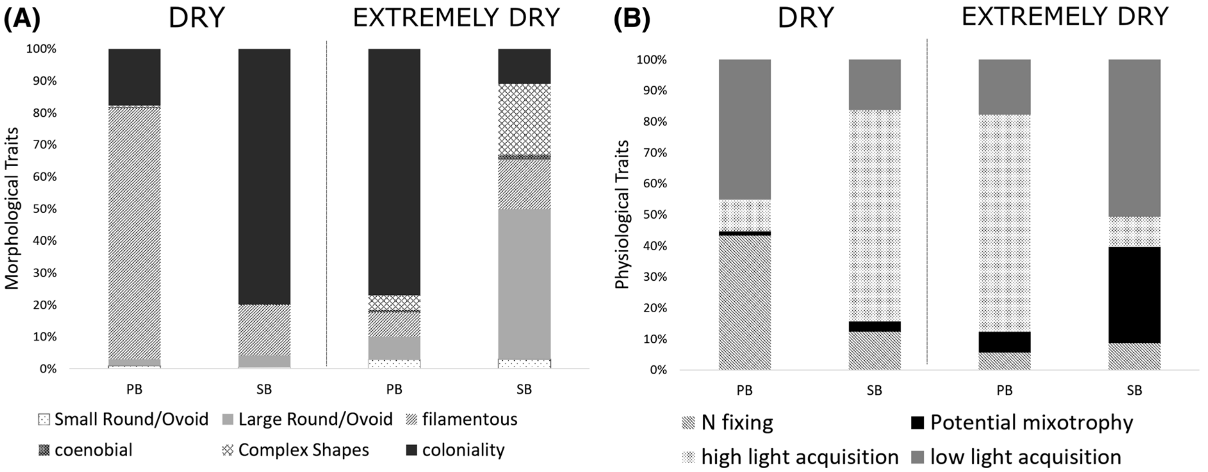

Fig. 4 Relative biomass of the phytoplankton morphological functional traits (**a**) and the physiological functional traits (**b**) between the two regions (PB and SB) and the two study periods (dry and extremely dry)

phytoplankton of PB reservoirs had a similar pattern of functional traits dominance (both morphological and physiological) than SB reservoirs during the dry period (Fig. 4).

The two-way ANOVA indicated significant differences only for large round/ovoid, nitrogen fixing, and potential for mixotrophy. Large round/ovoid and potential for mixotrophy were different between the sub-basins (Figs. 5 a, c), and nitrogen fixing was different among the study periods (Fig. 5b). No interaction was found between periods and regions for the functional traits (Fig. 5).

The biomass of mixotrophic algae increased significantly both with inorganic and organic turbidity between the two regions (Fig. 6).

The results by detrended correspondence analysis (DCA) of the functional traits data indicated that gradient lengths of the first two axes (2.65 and 1,91 standard deviation units, respectively) were relatively short, and therefore linear ordination methods were appropriate, as redundancy analysis (RDA). The first axis of the RDA accounted for 23.0% and the second axis accounted for 13.9% of the functional traits and environmental variables. The Monte Carlo test indicated that the eigenvalue of the first and second axes was significant ($P < 0.001$). The first axis was negatively correlated with DO (0.63), chlorophyll-*a* (0.78), turbidity (0.52), and euphotic zone (0.65). The second axis was positively correlated with volume (0.70) and negatively correlated with TP (0.80) and temperature (0.63).

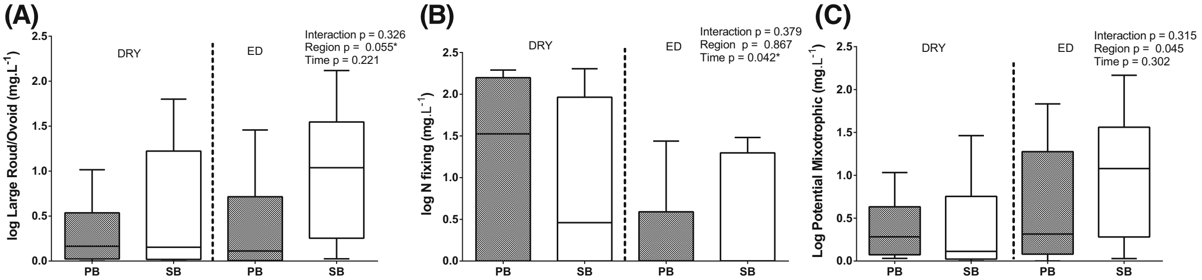

Fig. 5 Box plot of the significant functional traits: large round/ovoid shape (**a**), nitrogen fixing (**b**), and potential mixotrophs (**c**) between the two regions (PB and SB) and the two studied period: dry and extremely dry (ED). The box plot shows the median, minimum, maximum, first, and third quartiles. The results of the two-way ANOVA are shown for each variable

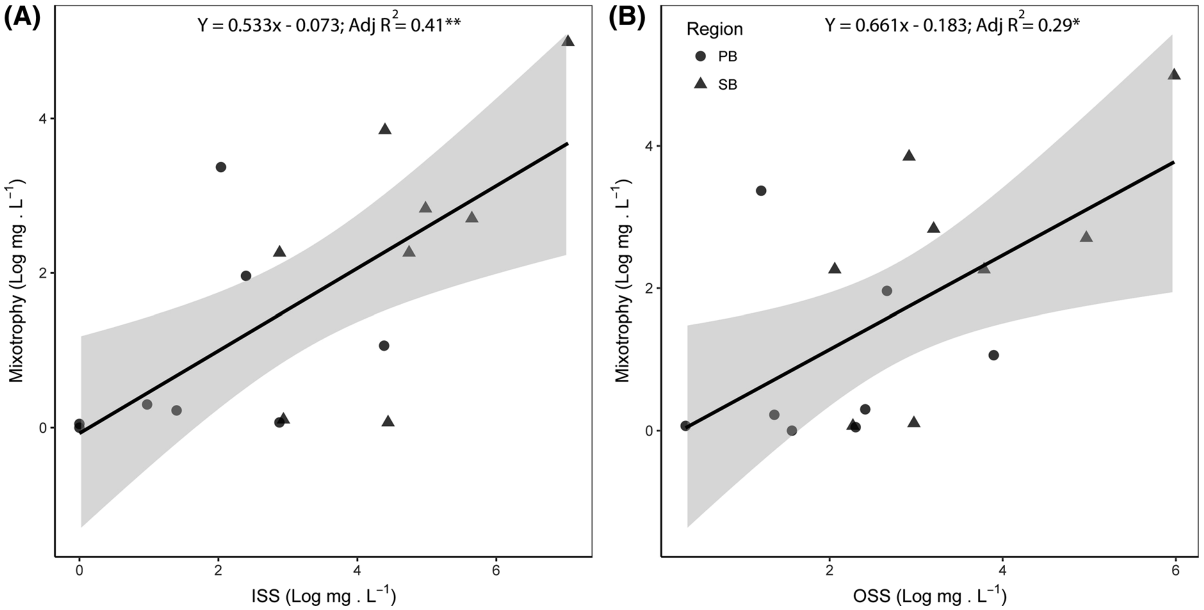

Fig. 6 Linear regression between the biomass of the potential mixotrophic algae and the source of turbidity: **a** inorganic suspended solids (ISS) and **b** organic suspended solids (OSS). Data represent the two regions PB (black circles) and SB (black triangles) together during the extremely dry period

The first axis of the RDA separated the two periods (dry and extremely dry), indicating a tendency to increase drought severity. The dry period was related to high volume, Zeu, and DO. The functional traits related to this period were coloniality and high light acquisition, and the extremely dry period was related to conductivity and temperature, given that algae have the potential for mixotrophy, complex shapes, and large round/ovoid, the functional traits most represented in this period (Fig. 7).

Discussion

This study evaluated the effects of decreasing rainfall on phytoplankton community structure in a tropical semi-arid region, based on a functional trait-based approach. The lack of rain in this region during the study period caused a drastic water level reduction, with some reservoirs reaching a critical level. As predicted in our hypothesis, we found that dry conditions increased nutrient concentrations that favored cyanobacteria, but in extremely dry conditions turbulent mixing caused resuspension, increasing the

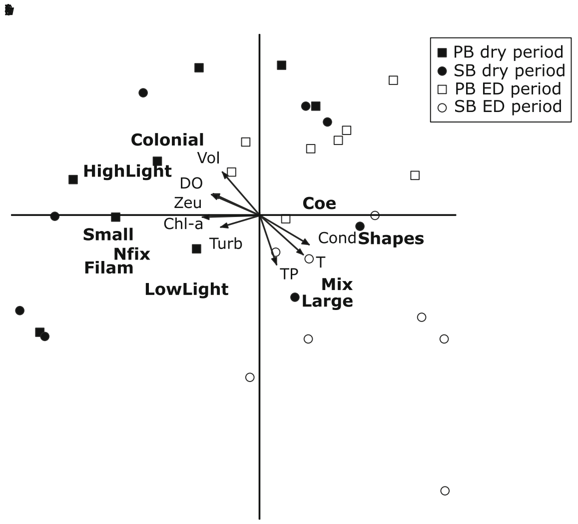

Fig. 7 RDA ordination of the phytoplankton functional traits and the environmental variables in the studied period. Dark squares and circles represent the dry period. White squares and circles represent the extremely dry period (ED). Squares represent the Piancó sub-basin (PB), and circles denote the Seridó sub-basin (SB). *Vol* volume, *Zeu* euphotic zone, *Turb* turbidity, *TP* total phosphorous, *Cond* conductivity, *DO* dissolved oxygen, *Chla* chlorophyll-*a*, *small* small round/ovoid, *large* large round/ovoid, *Coe* coenobial, *filam* filamentous, *shapes* complex shapes, *colonical* colonies, *Nfix* nitrogen fixing, *mix.* potential for mixotrophy, *HighLight* high light requirement, and *LowLight* low light requirement

relative biomass of potentially mixotrophic and low light-adapted phytoplankton species.

The differences between the precipitation regimes among sub-basins and the studied period (dry and extremely dry) significantly altered the physical and chemical water properties. We observed that the sub-basin with the lower annual precipitation (Seridó sub-basin, SB) had a degraded water quality. The prolonged drought led to a water level reduction due to water evaporation, increased nutrient concentration, organic and inorganic turbidity and conductivity, and decreased water transparency and water volume storage. The results for the inlet water:evaporation ratio, which was used as a proxy for water balance, confirmed our hypothesis that the Seridó region was drier than the Piancó region, revealing a major evapotranspiration rate for SB. The water volume in the SB reservoirs had a higher isotope concentration and consequently a higher ion concentration, thereby implying a lower water:evaporation ratio. Therefore, the isotope results confirm the differences in humidity between the two regions, with PB being less dry than SB.

Studies worldwide have indicated that eutrophication increases phytoplankton biomass and enhances the dominance of cyanobacteria (Paerl, 2009, Soares et al., 2012; Yang et al., 2016). This study showed a high phytoplankton biomass during the study period. However, the phytoplankton biomass decreased in the extremely dry period in some reservoirs of the drier basin (SB). This phytoplankton biomass reduction could be explained by light depletion and higher turbidity in these reservoirs along with the reduction of water column and the sediment and detritus resuspension. The RDA results presented the difference between the two distinct periods (i.e., dry and extremely dry period), indicating the increasing severity of drought and the environmental variables explaining the phytoplankton functional traits.

The relative biomass of the phytoplankton functional traits demonstrated an interesting pattern. Both the morphological and physiological traits in the SB during the dry period became similar to those observed in the PB during the extremely dry period. In other words, the phytoplankton traits in PB are shifting to become similar to those in the SB because of environmental changes through time. Conversely, with the critical water depth in the SB during the extremely dry period, the traits related to cyanobacterial (i.e., nitrogen fixing, filamentous, and colonies) decreased substantially, and the contribution of algae with low light demand with potential for mixotrophy (which in this study were practically all large round and ovoid cell shape) increased. The relationship between the biomass of mixotrophic algae and the sources of turbidity was confirmed with a positive significant linear regression. Thus, the low water volume of the reservoirs reached a critical depth. The sediment resuspension increased inorganic turbidity and led to a reduced water transparency (Fig. 8), thus limiting the phytoplankton and explaining the major contribution of algae to the potential for mixotrophy. We can infer that there is a critical threshold of water depth below which cyanobacterial dominance collapses and potentially mixotrophic algae dominate (Fig. 8).

Mixotrophy is a nutritional strategy that combines autotrophy and heterotrophy in a single organism, which acts as both a producer and a consumer (Sanders, 1991). This nutritional strategy is an

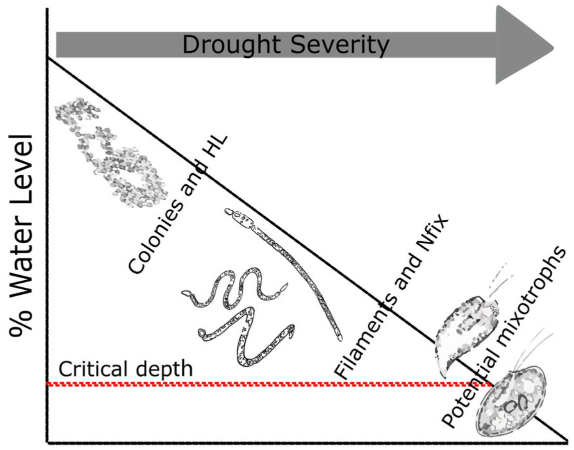

Fig. 8 Schematic diagram of the effect of water volume reduction altering the phytoplankton functional traits groups. *HL* high light acquisition, *Nfix* nitrogen fixation. Dashed lines imply the critical threshold for the column depth

important phytoplankton functional trait and provides an adaptive advantage in environments with limiting conditions and mainly low nutrient concentration and low light availability (Rothhaupt, 1996). The significant relationship of reduced water volume with the increasing biomass of mixotrophic algae demonstrates that the water level reduction caused by drought leads to the reduction of water transparency; this condition is favorable to mixotrophic algae because of the light limitation to photosynthesis and the competition with bacteria for inorganic phosphorous (Jones, 2000). The results of a laboratory grazing experiment showed high bacterial ingestion rates in the dark and low nutrient concentrations for three mixotrophic algal species (McKie-Krisberg et al., 2015). Other long-term dark experiments on phagotrophic flagellates suggested that some flagellates could change the nutritional strategy in the absence of light (Laybourn-Parry, 2002; Jones et al., 2009).

Natural climatic conditions of tropical arid and semi-arid regions are severe because of low precipitation, high temperature, high evapotranspiration ratio, and high aridity index (Barbosa et al., 2012). The South American climate model predicted rainfall reduction, a positive increase in the number of consecutive dry days, and intense and frequent droughts in such areas (Marengo et al., 2009). Since 2012, the Brazilian semi-arid region has been experiencing the worst drought in the last 50 years according to the Brazilian National Water Agency. Studies in the Brazilian semi-arid region showed that during severe drought periods, chlorophyll-*a* and phytoplankton biomass decreased (Jeppesen et al., 2015; Medeiros et al., 2015; Costa et al., 2016) and that flagellate mixotrophic algae increased probably because of light depletion due to the high resuspension of sediments and detritus at a shallow depth (Medeiros et al., 2015; Costa et al., 2016).

Climate change is considered the paramount emerging threat to global biodiversity, as it alters the composition, diversity, and functioning of many freshwater ecosystems (Woodward et al., 2010; Jeppesen et al., 2015). Although climate change has been reported worldwide, its effects are not distributed homogeneously and some regions are more susceptible to climate variability than others (IPCC, 2014; Jeppesen et al., 2014). Despite the number of studies on climate change effects on freshwater ecosystems (De Senerpont Domis et al., 2013a; Kritzberg et al., 2014; Yang et al., 2016), these predictions on tropical regions can be uncertain (Sarmento et al., 2013). This situation is particularly true for semi-arid regions, which have peculiar phytoplankton patterns (Medeiros et al., 2015; Costa et al., 2016).

In summary, our study shows the effect of rainfall reduction in two semi-arid regions on water quality and phytoplankton dynamics using the trait-based functional approach. On the basis of the current limnological knowledge (mainly from temperate latitudes), we expected to find that the water level reduction would favor filamentous and nitrogen fixing functional traits of phytoplankton. However, we observed that extreme droughts could reduce cyanobacterial biomass and favor mixotrophic organisms in tropical semi-arid regions. This finding suggests that this can be a possible scenario for phytoplankton communities in these kinds of systems if extreme droughts become more frequent in the future.

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