PHYTOPLANKTON BIOMASS INCREASES IN A SILT-IMPACTED AREA IN AN AMAZONIAN FLOOD-PLAIN LAKE OVER 15 YEARS

Vera Lúcia de Moraes Huszar[1]*, Caio Graco-Roza[2], João Carlos Nabout[3], Patrícia Nunes[4], Enoque G. Ribeiro[5], Sergio de Melo[6], Simone J. Cardoso[7], Uanderson J. Pereira[1], Marcos Paulo Figueiredo de Barros[5], Reinaldo L. Bozelli[8], Fabio Roland[4], Lucia Helena Sampaio da Silva[1] & Francisco A Esteves[8]

[1] Universidade Federal do Rio de Janeiro, Museu Nacional, Laboratório de Ficologia, Quinta da Boa Vista, São Cristóvão, CEP 20940-040, Rio de Janeiro, RJ, Brasil.

[2] University of Helsinki, Faculty of Science, Department of Geosciences and Geography, FI-00014, Helsinki, Finland

[3] Universidade Estadual de Goiás, Campus Central, Unidade Universitária de Ciências Exatas e Tecnológicas, BR 153, 310, CEP 75132-903, Anápolis, GO, Brasil.

[4] Universidade Federal de Juiz de Fora, Departmento de Biologia, Rua José Lourenço Kelmer, s/n, São Pedro, CEP 36036-900, Juiz de Fora, MG, Brasil.

[5] Universidade Federal do Rio de Janeiro, Instituto de Biodiversidade e Sustentabilidade, Laboratório Integrado de Ecologia Aquática, Av. São José Barreto, 764, São José do Barreto, CEP 27965-045, Macaé, RJ, Brasil.

[6] Universidade Federal do Oeste do Pará, Instituto de Ciências e Tecnologia das Águas, Rua Vera Paz, s/n, Bairro Salé, CEP 68040-255, Santarém, PA, Brasil.

[7] Federal University of Juiz de Fora, Departamento de Zoologia, Rua José Lourenço Kelmer, s/n, São Pedro, CEP 36036-900, Juiz de Fora, MG, Brasil.

[8] Universidade Federal do Rio de Janeiro, Departamento de Ecologia, Laboratório de Limnologia, Av. Carlos Chagas Filho, 373, Cidade Universitária, CEP 21941-540, Rio de Janeiro, RJ, Brasil.

E-mails: vhuszar@gbl.com.br (*corresponding author); caiogracor@gmail.com; jcnabout@gmail.com; patricia.nunes@ecologia.ufjf.br; yuegribeiro@nupem.ufrj.br; melo.joaopedro@gmail.com; simone.jcardoso@gmail.com; ujpereira@gmail.com; mpaulo.bio@gmail.com; bozelli@biologia.ufrj.br; fabio.roland@ufjf.edu.br; luciahssilva@gmail.com; festeves@globo.com

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Abstract: Tailings from bauxite mining in Porto Trombetas (Pará state, Central Amazonia, Brazil) was discharged (1979–1989) into Batata Lake affecting about 30% of its area. The lake belongs to a clear-water flood-plain system along the Trombetas River, a tributary of the Amazon River. Siltation is the main perceived factor impacting aquatic and flooded communities. Besides natural regeneration, a program to restore a section of *igapó* forest in the impacted area (IA) has been conducted since 1991. Decreased light is the main factor reducing total phytoplankton biomass (PhyBM) in IA. We hypothesized that PhyBM in IA increases over time because of the improvement of the underwater light conditions due to the natural regeneration and restoration. We sampled quarterly PhyBM and limnological variables (depth, transparency, temperature, pH, conductivity, dissolved oxygen, turbidity, suspended solids, total Kjeldahl nitrogen, and total phosphorus), over 15 years (2005–2019) at eight sampling sites in the two areas (N = 349). We also obtained daily climatic and hydrologic data. PhyBM was higher in NIA than in IA. The temporal trend in the annual mean of PhyBM increased significantly over time only in the IA,

approximating the NIA values, confirming our general hypothesis. The increase of PhyBM in the IA was negatively related to the residual light attenuation caused by non-phytoplankton turbidity and to total phosphorus, and positively to air temperature and site depth ($p < 0.05$; Marginal $r^2 = 0.18$; Conditional $r^2 = 0.29$). Instead, in NIA, PhyBM was explained only by the increase in air temperature ($p < 0.05$; Marginal $r^2 = 0.15$; Conditional $r^2 = 0.34$). We concluded that the PhyBM in the IA positively responds to the synergy between increasing light availability, air temperature, and site depth, and decreasing total phosphorus concentrations, regardless of hydrologic phase.

Keywords: Clear-water lake; inorganic turbidity; restoration; linear mixed-effect regressions

INTRODUCTION

Exploitation of natural resources for power generation, food production, mining, and the need for constant economic growth is increasing worldwide. In 2020, Brazil was the fourth-largest global producer of bauxite (USGS 2021), with some mines in the Amazon basin. Batata Lake, a mesotrophic clear-water flood-plain system belonging to the Trombetas River drainage basin, received bauxite tailings from 1979 to 1989 (Lapa & Cardoso 1988). Despite the non-toxic composition of those tailings (Lapa 2000), about 30% of the lake area was silted. The silt increased the inorganic turbidity of the system, forming a layer above the sediment, and damaging some of the *igapó*, a marginal periodically flooded vegetation (Bozelli *et al.* 2000). Then, the ecosystem structure and function, from viruses to the forest, were impaired (Anésio *et al.* 1997, Huszar 2000, Roland *et al.* 2002, Leal *et al* 2005, Lin & Caramaschi 2005, Barros *et al.* 2010, Dias *et al.* 2012, Scarano *et al.* 2018, Josué *et al.* 2021).

In 1988, a consistent long-term lake monitoring program started, with a restoration program created in 1991 (Bozelli *et al.* 2000, Scarano *et al.* 2018). Currently, both programs show signs of recovery of the impacted area. For instance, i) there was an increase in organic matter on the sediments (Bozelli *et al.* 2000, Josué *et al.* 2021); ii) accumulated detritus from aquatic macrophytes on the sediment in the littoral zone formed an organic layer, impeding the resuspension of the tailings and increased nutrient availability in the impacted area (Enrich-Prast & Esteves 2005); and iii) the number of zoobenthos groups increased in the impacted area, related to nutrient availability and turbidity reduction (Fonseca & Esteves 1999, Bozelli *et al.* 2000).

Time series are essential tools to study long-term dynamics (Bukaveckas 2021). They detect trends and signals that may be overlooked in studies with a shorter time span (Dowd *et al.* 2003) or processes with slow temporal dynamics. Most studies on phytoplankton using time series have focused on oligotrophication or eutrophication (Straile 2000, Bürgi & Stadelmann 2002), hydrologic fluctuations (Reynolds *et al.* 2012), and recently, global climate changes (Havens *et al.* 2019). Considering the Batata Lake, only a few studies performed long-term analyses, mainly for fish (Soares *et al.* 2017) and zooplankton communities (Carneiro *et al.* 2002, Garrido *et al.* 2003, Bozelli *et al.* 2009, Sodré *et al.* 2017).

Microorganisms (*e.g.*, phytoplankton) are excellent sentinels of environmental changes and threats (Everett *et al.* 2017). Phytoplankton is composed of critical organisms for investigating natural and anthropic changes (Reynolds 2006, Borics *et al.* 2021). Still, there is no long-term analysis of phytoplankton in Batata Lake, despite the knowledge of its seasonal composition and biomass (Huszar & Reynolds 1997, Huszar 2000, Melo & Huszar 2000). In Batata Lake, the flood pulse is the main phytoplankton driving force (Huszar & Reynolds 1997, Melo & Huszar 2002, Cardoso *et al.* 2017), alongside bottom-up resource control. Limiting phosphorus concentrations to phytoplankton growth (soluble reactive phosphorus <10 mg/L, Sas *et al.* 1989) occurred in both impacted (IA) and non-impacted (NIA) areas throughout the year, and low light in the IA is critical (Huszar & Reynolds 1997, Huszar 2000). Noteworthy, there is no information about top-down control by zooplankton and fish in the lake.

Here, we hypothesized that phytoplankton biomass (PhyBM) in IA increases through the

years due to improvement in the underwater light availability resulting from natural regeneration and the restoration program. We explored the differences between trends of PhyBM in the IA and NIA and related those to abiotic conditions. This study aims to elucidate how the phytoplankton biomass of a flood-plain system responds to the presence of bauxite tailings and indicates its recovery.

MATERIAL AND METHODS

Study site

Batata Lake (1° 30´ S, 56° 19´ W) is a clear-water lake situated on the right bank of the Trombetas River, Pará, Brazil (Figure 1). The regional climate is humid-tropical (annual mean temperature > 26 °C; mean of the total annual precipitation of 2200–2500 mm) (Am in Köppen classification, Alvares *et al.* 2014). The water level fluctuates in a conspicuous annual cycle with depth and lake area varying between 12 m and 31 km^2 at high-water (March to July), and 2 m and 18 km^2 at low-water levels (October to December). These dates approximately identify four phases: rising, high-water, falling, and low-water. The impact of bauxite tailings covers some 30% of the total lake area during high-water (Roland & Esteves 1993). These tailings arose from ore processing by Mineração Rio do Norte and were discharged into the northern part of Batata Lake between 1979 and 1989.

Sampling, laboratory analyses, and data collection

We sampled eight sites quarterly between 2005 to 2019 by filling bottles at the subsurface (0.5 m). Sites represent i) an IA where the bauxite tailings deposition occurred (S10, S10a, S10b, S10c, S10d; N = 212), and ii) an NIA with no deposition (S4, S7, S8; N=137), following the monitoring program (Figure 1).
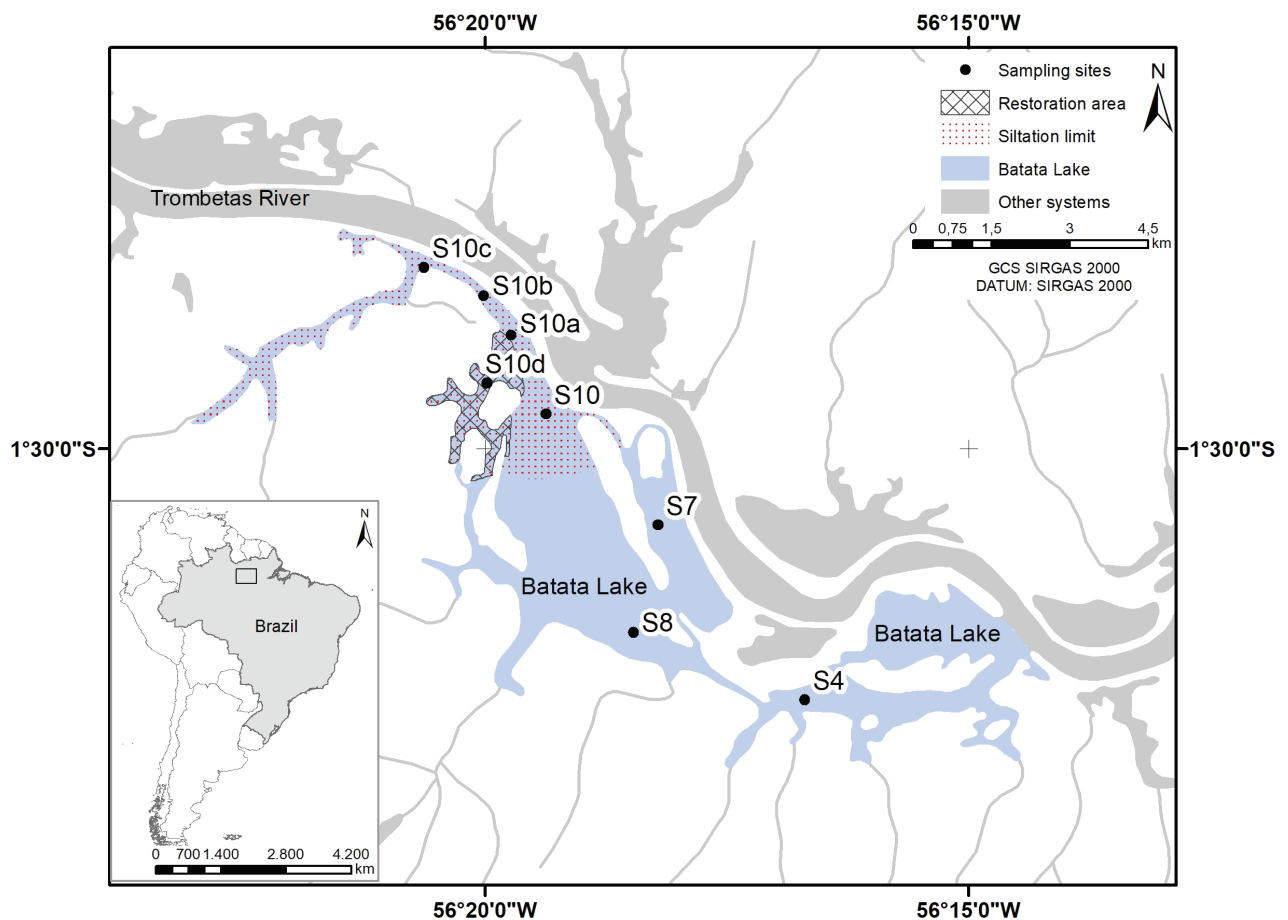

Figure 1. Map and location of Batata Lake, showing sampling sites in the non-impacted (S4, S7, S8) and impacted areas (S10, S10a, S10b, S10c, S10d). The squared area shows the limit where the igapó forest has an ongoing restoration program; the red line is the limit (from North to South) of the siltation impacted area.

We measured the depth (z_{site}, m), water transparency (Transp, m) using a Secchi disk; water temperature (WatT, °C), pH, electrical conductivity (Cond, µS cm^{-1}), and dissolved oxygen (DO, mg L^{-1}), using a YSI 550A meter, USA. We evaluated turbidity (Turb, NTU; a LaMotte 2020 turbidimeter, USA); suspended solids (SuspS, mg L^{-1} gravimetry), total Kjeldahl nitrogen (TN, mg L^{-1}; Mackereth *et al.* 1978), and total phosphorus (TP, µg L^{-1}; Golterman *et al.* 1978). Phytoplankton populations (organisms mL^{-1}) were estimated by the settling technique (Utermöhl 1958) under an inverted microscope (Zeiss Oberkochen Axiovert 10, Germany). Phytoplankton units (cells, colonies, and filaments) were enumerated in random fields to at least 100 specimens of the most frequent species (Lund *et al.* 1958). In the laboratory, chlorophyll-a (µg L^{-1}) was analyzed (Nusch & Palme 1975).

We obtained meteorological data (mean daily air temperature, AirT, °C, total monthly precipitation, Prec, mm) from the Instituto Nacional de Meteorologia at Óbidos, station 82178, Pará state (https://bdmep.inmet.gov.br/#; accessed on 12/04/2021), located 90 km from the lake at a straight line in flat relief. No air temperature data were available for 2019. Daily hydrometric levels (HL, m a.s.l.) of Trombetas River were provided by Mineração Rio do Norte.

Data analyses

All analyses and figures were done in the software R v.4.1.0 (R Core Team 2021) using the packages *lmerTest* v.3.1.3 (Kuznetsova *et al.* 2017), *lme4* v.1.1.2 (Bates *et al.* 2015), the *tidyverse* suite v.1.3.1 (Wickham *et al.* 2019), and *modifiedmk* v.1.6.0 (Patakamuri SK and O'Brien N. 2021). All models were checked for homoscedasticity, multicollinearity, autocorrelation, and normality of residuals; the statistical significance of $\alpha = 0.05$.

Euphotic zone (z_{eu}, m) was estimated as 2.7 times the Secchi disk (SD) extinction depth (Cole & Weihe 2016). Residual light attenuation (K_{res}, m^{-1}) from non-phytoplankton turbidity (colored organic matter and inorganic turbidity) was estimated from the difference between total light attenuation (K, m^{-1}) based on Secchi depth and the attenuation from phytoplankton (K_{phy}, m^{-1}) based on chlorophyll-a (see Huszar *et al.* 2006). Phytoplankton biomass (PhyBM, mm^3 L^{-1}) was estimated as biovolume (Hillebrand *et al.* 1999). In general, 30 individuals of each species were measured. Population biovolume was obtained through the population abundance (organisms mL^{-1}) of each species times the mean volume of organisms (µm^3). We used pairwise Pearson correlation to check collinearity among the variables and kept only those with $r < 0.70$, resulting in a subset of six variables (AirT, z_{site}, Turb, K_{res}, TN, and TP) and only these were considered further.

To test differences across temporal scales preserving the spatial structure, we used the sampling phase (rising, high-water, falling, low-water) and sampling area (IA *vs.* NIA) as grouping variables. Therefore, we focus on the interannual (years) variability in each sampling area. We first ran individual models for PhyBM, Turb, z_{site}, K_{res}, TP, and TN as a function of sampling year and its interaction with the sampling area (IA *vs.* NIA) using linear mixed-effect regressions (LMER; Bolker *et al.* 2009). We included a random factor term (sites) to allow the intercept to vary at the site level, and to quantify additional among-site variance not explained by fixed variables (Bolker *et al.* 2009).

We could not conduct LMER to HL and AirT, because these variables did not vary among sites. Thus, we tested the temporal trends using ordinary least-square regressions, including HL and AirT annual mean as a function of the sampling year.

We log$_{10}$-transformed Turb, TP, and TN before the analysis to reduce the effects of outliers. Because some PhyBM values were zero, we added 0.001 to the actual values prior log$_{10}$ transformation. Satterthwaite approximations of degrees of freedom were used to obtain estimated p-values (Satterthwaite 1946). The variance explained by each model is reported as marginal r^2, the proportion of the variance explained by fixed factors alone, and conditional r^2, the proportion of the variance explained by both fixed and random factors (Nakagawa & Schielzeth 2013).

We used non-parametric Mann-Kendall tests (Mann 1945, Kendall 1975) to test the significance of the temporal trends in annual mean values of PhyBM, Turb, z_{site}, K_{res}, TP, and TN in the IA and NIA. Because Mann-Kendall tests do not estimate the magnitude of the trends, these were calculated using Sen's slope non-parametric method (Sen 1966).

To test the effects of climatologic (AirT, Prec), hydrologic (HL, z_{site}), physical (Transp, Turb, z_{eu}, SuspS, K_{res}), and chemical variables (pH, Cond, DO, TN, and TP) on PhyBM, we ran LMER separately for the IA and NIA. After removing all missing observations from the dataset, we kept 233 observations included in PhyBM and all selected fixed factors. The sampling phase was added to the model as a random factor. All continuous variables were centered and standardized (x-mean/sd) to facilitate model convergence. We first performed the LMER with all the fixed and random factors, and then, selected the best model subset through a backward selection. We tested the significance of the random factor by comparing the models with and without the random effect, using Akaike's information criteria (AIC) (Bolker *et al.* 2009).

RESULTS

Hydrology and air temperature

There was no significant temporal trend in the annual mean of HL over the time series (Figure 2a). The lowest HL values occurred in 2005 and 2010, and the highest in 2009 and 2012 to 2015. The year 2016 showed the lowest pulse amplitude (5.95 m). Contrastingly, the annual mean of AirT

increased significantly over time (Figure 2b; Table S1). The lowest value of daily mean air temperature occurred in 2008 (22.8°C) and the highest in 2018 (31.2°C).

General trends in the phytoplankton biomass and abiotic conditions

Phytoplankton biomass

The total annual PhyBM ranged, on average, from 0.5 (2007) to 4.8 mm³ L⁻¹ (2018) in the IA, and from 1.8 (2006) to 10.8 mm³ L⁻¹ (2013) in the NIA (Table S2). The PhyBM was significantly higher in the NIA than in IA, with significant differences among years (Table S1 and Figure 3f). Also, PhyBM showed a significant positive temporal trend only in the IA, approaching the NIA values (Table 1).

Abiotic conditions in the Batata Lake

The mean annual TP concentrations ranged, from 4.5 (2018) to 33.5 μg L⁻¹ (2010) in the IA and from 6.3 (2016) to 47.9 μg L⁻¹ (2009) in the NIA (Table S2). TP concentrations differed across years but not between areas (Table S1, Figure 3e). Within IA, TP had a significant temporal decrease (Table 1). The mean annual Turb values ranged from 5.9 (2019) to 31.4 NTU (2016) in the IA and from 4.1 (2013) to 31.1 (2015) in the NIA (Table S2). Turbidity
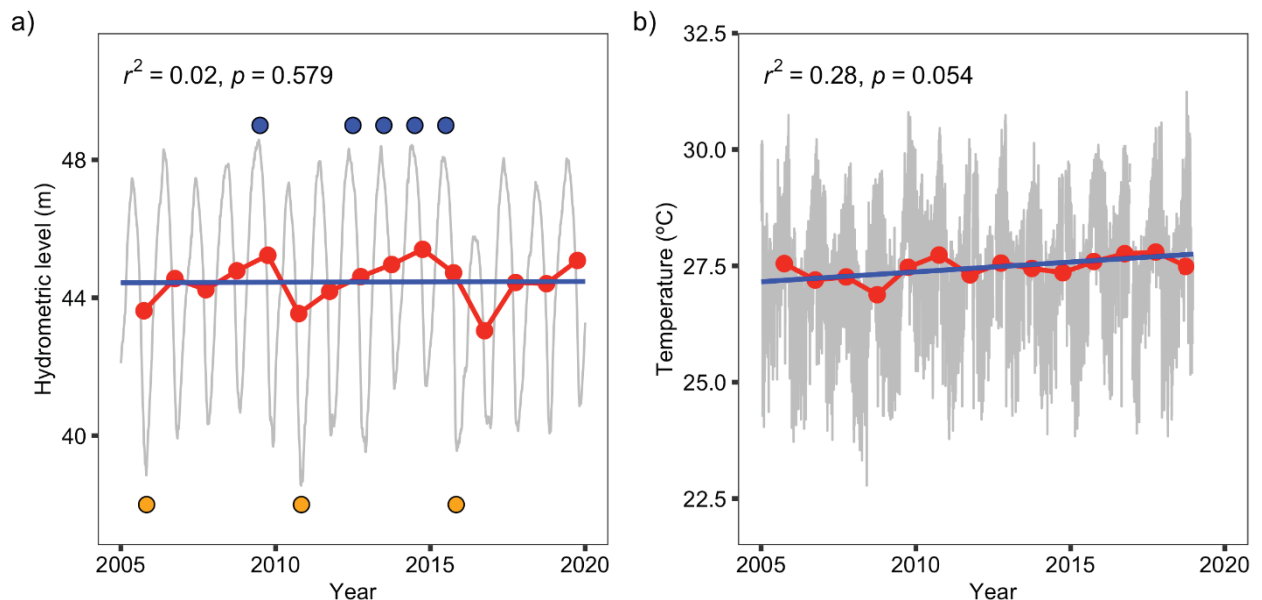

Figure 2. Daily hydrometric level of Trombetas River at Porto Trombetas (a) and daily air temperature at Óbidos, Pará State (b). Over 15 years (2005 to 2019), (a) no significant trend in hydrometric level over 14 years (2005–2018), and (b) a significant increase in temperature were found (blue lines). Red lines and dots indicate annual mean values. Blue and orange dots indicate extreme flood years and anomalously low river levels in Amazonia, respectively (Marengo & Espinoza 2016, Cunha *et al.* 2019).
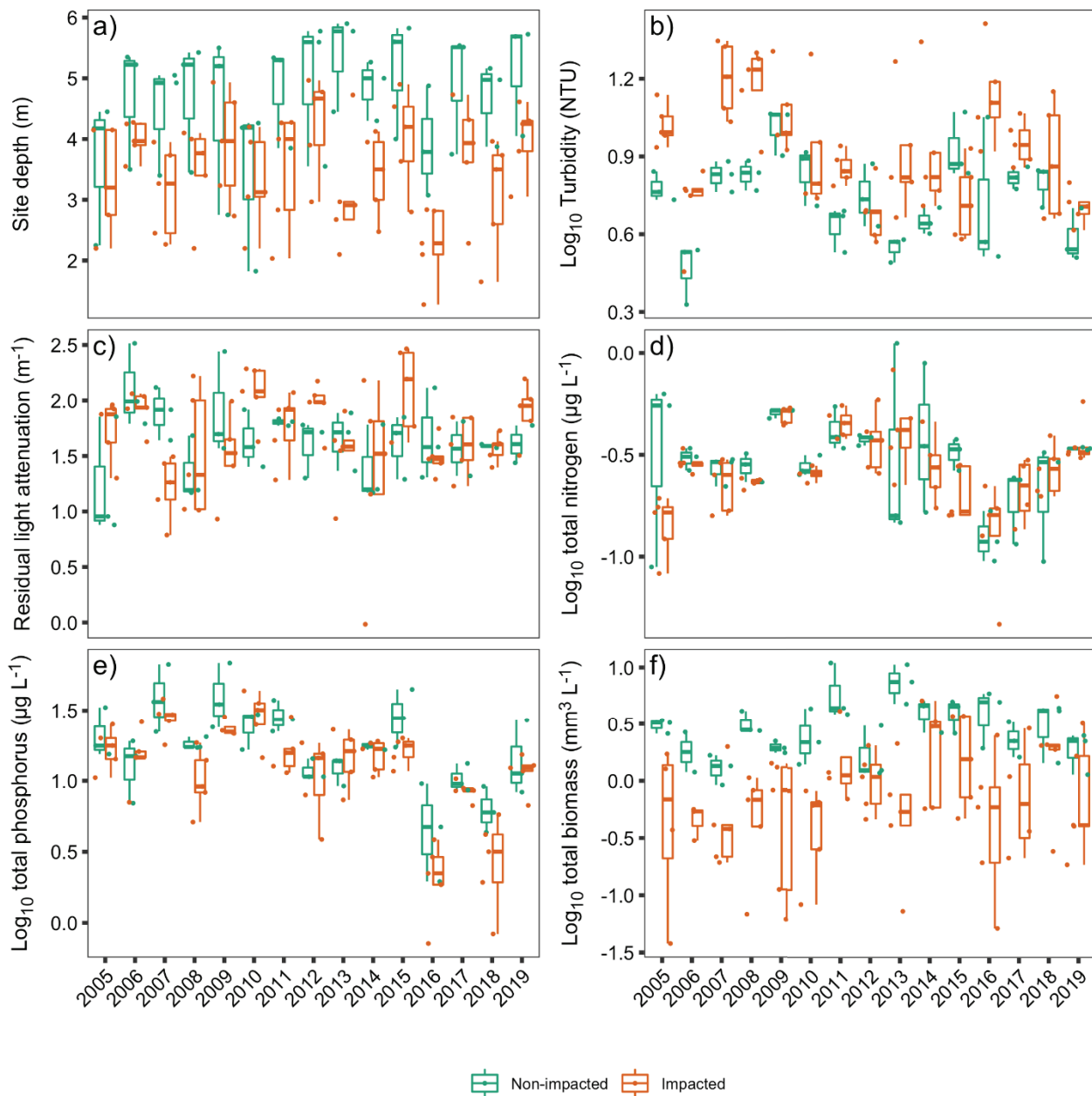
Figure 3. Box plots of the annual mean values at each site of abiotic variables and total phytoplankton biomass in the silt-impacted and non-impacted areas in Batata Lake over 15 years (2005–2019). Variation in each year was caused by spatial (sampling sites in each area) variability. The line within boxes is the median, while the box limits encompass 25 and 75%, whiskers 5 and 95%, and larger dots are outliers. The residual light-attenuation coefficient is due to non-phytoplankton turbidity. Smaller dots are the annual mean values at each site.

differed among years and between areas (Table S1, Figure 3b), but no temporal trend was observed (Table 1). There were no significant temporal or spatial differences for the remaining fixed factors (z_{site}, K_{res}, and TN) (Table S1, Figures 3a, 3c, 3d, respectively) nor significant temporal trends (Table 1). The mean annual z_{site}, ranged from 2.4 (2016) to 4.3 m (2012) in the IA and from 3.7 (2010) to 5.6 m (2013) in the NIA (Table S2). Because Batata Lake is continuously connected to the Trombetas River, z_{site} showed a similar pattern to

HL. The mean annual K_{res} ranged from 1.2 (2007, 2014) to 2.1 m^{-1} (2010) in the IA and from 1.3 (2005, 2008, 2014) to 2.0 m^{-1} (2006) in the NIA (Table S2). The mean annual TN concentrations ranged from 0.15 (2005) to 0.80 mg L^{-1} (2013) in the IA and 0.17 (2016) to 0.76 mg L^{-1} (2013) in the NIA (Table S2).

Relationships between total phytoplankton biomass (PhyBM) and environment

The best PhyBM model (LMER) for the NIA included only AirT (β = 0.22, p < 0.05) (Table 2).

Table 1. The Mann-Kendall test results for the temporal trends of Site depth, Turbidity, Residual light attenuation, Total nitrogen, Total phosphorus, and Total phytoplankton biomass over time in the impacted and non-impacted area. Table shows the Mann-Kendall correlation value (Z-value) and the magnitude of the trend (SS; Sen's slope). Significant p-values are in bold.

Variables	Z-value	SS	p-value
Impacted area			
Site depth	0.2477	0.0007	0.8043
Turbidity	−1.4846	−0.0440	0.1376
Residual light attenuation	0.4949	0.0135	0.6207
Total nitrogen	0.5938	0.0149	0.5526
Total phosphorus	−1.9795	−0.0589	**0.0478**
Total phytoplankton biomass	2.1774	0.0261	**0.0294**
Non-impacted area			
Site depth	1.3856	0.0169	0.1659
Turbidity	−0.4949	−0.0084	0.6207
Residual light attenuation	−0.8908	−0.0141	0.3731
Total nitrogen	−0.6928	−0.0126	0.4884
Total phosphorus	−1.6826	−0.0739	0.0925
Total phytoplankton biomass	1.1877	0.0157	0.2350

The model showed that years with higher AirT led to higher PhyBM in NIA. For the IA, the best model included AirT ($\beta = 0.37$, $p < 0.05$), z_{site} ($\beta = 0.29$, $p < 0.05$), TP ($\beta = -0.21$, $p < 0.05$), and K_{res} ($\beta = -0.21$, $p < 0.05$) (Table 2). The fixed factors of the best model explained a relatively low proportion of the PhyBM variance when controlled for the sampling phase (NIA $r^2 = 0.14$; IA $r^2 = 0.18$). The explanation was higher when considering the random and fixed effects together (NIA $r^2 = 0.34$; IA $r^2 = 0.30$) (Table 2).

DISCUSSION

Here, we searched for the long-term trends of the total PhyBM in the IA compared to the NIA of an Amazonian flood-plain lake, which received tailings from a bauxite mining for ten years. Although our data revealed differences in PhyBM among years and between areas, an increasing trend over time was detected in the IA, approximating the NIA values. Besides in the IA, PhyBM was inversely related to the residual light attenuation caused by non-phytoplankton turbidity and to TP concentrations, and directly to air temperature and site depth. However, PhyBM variance in the NIA was positively driven only by the air temperature.

Turbidity is the first factor for the lower PhyBM in the IA, given the siltation impact (Huszar 2000). This scenario was also found for planktonic primary productivity (Roland *et al.* 2002) and several planktonic (Anesio *et al.* 1997, Barros *et al.* 2010), benthic (Callisto & Esteves 1995), and fish communities (Caramaschi *et al.* 2000). PhyBM was sparser in this area, but there were no marked changes in composition, at least for major taxonomic algal groups (Huszar 2000). Potential mechanisms underlying these sparser algal populations are the light attenuation caused by inorganic turbidity and the increase in algal sinking due to their adhesion to clay particles (Guenther & Bozelli 2004a but see Guenther & Bozelli 2004b). Light attenuation is also caused by phytoplankters themselves, colored dissolved organic matter, detritus, and suspended inorganic material. Light attenuation in NIA may be more influenced by phytoplankton during low-water, in which biomass is highest, and in the IA, by inorganic turbidity due to silt and detritus. No temporal trend in turbidity was significant in any area, potentially because turbidity caused by PhyBM and inorganic compounds masked the final effect on this factor. Another proxy of light availability, the residual light attenuation, showed no significant difference or temporal trend among years or between areas. However, this light variable, and not turbidity, was selected in the model (lower light attenuation) to explain part of the PhyBM variance in the IA, confirming our general hypothesis.

Besides light availability, the temperature

Table 2. Summary of the linear mixed-effect regressions for total phytoplankton biomass ($\log_{10}$ PhyBM + 0.001) explained by the predictors, controlled by random factors (i.e., sampling phases) in Batata Lake over 15 years (2005–2019). The table shows the model estimates (β), confidence intervals (CI, 95%), and p-values for the full models and the best model selected via backward selection using Akaike's information criteria (AIC). The variance (σ^2) and residual variance (τ_{00}) of the random effects are given along with the number of groups (sampling phases, N_{HP}) and the total number of observations (Observations). The variance explained by the fixed factors alone (Marginal r^2) and both the fixed and random factors (Conditional r^2) is given. Significant p-values (< 0.05) are shown in bold.

	Impacted area					
	Full model			Best model		
Predictors	*Estimates β*	*CI*	*p*	*Estimates β*	*CI*	*p*
(Intercept)	–0.03	–0.40 to 0.34	0.884	–0.04	–0.37 to 0.29	0.814
Residual light attenuation	–0.25	–0.49 to –0.01	**0.042**	–0.21	–0.39 to –0.03	**0.021**
Total nitrogen	–0.07	–0.19 to 0.05	0.275			
Site depth	0.27	0.03 to 0.52	**0.026**	0.29	0.07 to 0.51	**0.009**
Air temperature	0.40	0.15 to 0.65	**0.002**	0.37	0.14 to 0.61	**0.002**
Total phosphorus	–0.20	–0.32 to –0.07	**0.003**	–0.21	–0.33 to –0.08	**0.001**
Turbidity	–0.05	–0.29 to 0.19	0.694			
Random factors						
AIC	343.32			341.67		
σ^2	0.53			0.53		
τ_{00}	0.11 $_{HP}$			0.08 $_{HP}$		
ICC	0.17			0.14		
N_{HP}	4 $_{HP}$					
Observations	138					
Marginal r^2 / Conditional r^2	0.19 / 0.33			0.18 / 0.29		
	Non-impacted area					
	Full model			Best model		
Predictors	*Estimates β*	*CI*	*p*	*Estimates β*	*CI*	*p*
(Intercept)	0.45	0.08 to 0.81	**0.017**	0.44	0.19 to 0.69	**0.001**
Residual light attenuation	–0.13	–0.28 to 0.02	0.083			
Total nitrogen	0.10	0.01 to 0.19	**0.03**			
Site depth	–0.09	–0.28 to 0.10	0.361			
Air temperature	0.20	0.03 to 0.36	**0.018**	0.22	0.07 to 0.37	**0.003**
Total phosphorus	–0.08	–0.18 to 0.02	0.129			
Turbidity	–0.11	–0.28 to 0.05	0.18			
Random factors						
AIC	163.12			155.73		
σ^2	0.19			0.20		
τ_{00}	0.12 $_{HP}$			0.06 $_{HP}$		
ICC	0.39			0.22		
N_{HP}	4 $_{HP}$					
Observations	95					
Marginal r^2 / Conditional r^2	0.23 / 0.53			0.15/0.34		

is also related to phytoplankton growth. Over a global climate-change period of decades or longer, we can expect reactions of phytoplankton such as floristic changes or impact on ecosystem productivity (Padisák 1998). Despite the growing number of studies on the temperature effects on PhyBM due to global warming, the outcomes are still fragmented. The synergy of biotic and abiotic, including different degrees of uncertainty affects the outcome (Jeppesen *et al.* 2014, Giani *et al.* 2020). The increasing air temperature in the Amazon was ca. 0.6 to 0.7 °C from 1950 to 2017, with 2016 as the warmest year in the 21st century (Marengo *et al.* 2018). The increase in the air temperature occurred was positively related to the PhyBM in the IA and NIA. Temperature was the fixed factor with the highest explanation of the PhyBM in the IA and the unique variable explaining the PhyBM variance in the NIA.

Hydrology (flushing rate) and hydrography (mixing frequency) (Reynolds 2006) were crucial factors for determining PhyBM in Batata Lake (Huszar & Reynolds 1997). The flood pulse leads to similar conditions in the IA and NIA every year, at least in the pelagic layers during high-water, when floods increase connectivity, promoting habitat homogenization; when they recede, the connectivity decreases, and the system gradually recovers its distinctive low-water properties (Bozelli *et al.* 2015). Batata Lake first decreases to a shallow, polymictic system and then, becomes deeper and transparent and less well-mixed (Huszar & Reynolds 1997). So, phytoplankton changes from sparse biomass at high-water to higher biomass when the lake is shallow. This trend is similar in the IA, but PhyBM is lower due to light limitation, primarily from siltation (Huszar 2000).

Despite the intra-annual PhyBM dynamic, the yearly mean of HL did not change over the 15-year time series. During the study, extreme droughts occurred in the Amazon, causing anomalously low-water levels in 2005, 2010, and 2015/2016 (the most severe and widespread in 100 years), and extreme floods in 2009 and 2012–2015 (Marengo & Espinoza 2016, Cunha *et al.* 2019). Despite this, neither HL nor site depth showed any temporal difference or trend over time. However, site depth related positively to PhyBM in the IA. Our LMER model, controlled by hydrologic phases, indicated that in the IA, the deeper the sites, the higher the PhyBM, potentially because of indirect factors such as decreasing inorganic turbidity. Site depth indicates a spatial gradient of inorganic turbidity caused by tailings within the IA, leading to a higher PhyBM at the deeper IA sites due to greater light availability, regardless of the hydrologic phase.

Besides hydrology, light availability, and temperature, control by nutrients can be essential for PhyBM in Batata Lake. During our 15-year study, PhyBM (3.5 mm^3 L^{-1}), nitrogen, and phosphorus mean levels were like other mesotrophic systems. We found differences among years in TP but not between IA and NIA. A significant decreasing trend of TP was documented in the IA, and only in this area was TP explained (negatively) PhyBM. Usually, PhyBM increases with TP concentrations because P is the primary limiting nutrient to phytoplankton growth in freshwaters and the documented negative relationship was somewhat surprising. We recognize that it is precarious to infer causality from correlational field data. Interpretation of a relationship between total nutrient concentrations and PhyBM (chlorophyll-a or biovolume) is problematic because nutrients are typically locked up in cells; the relationships may be consequential, at least in part, rather than causative (Kosten *et al.* 2012). We expected an opposite trend for TP in the IA because consistent signs of recovery are continuing due to the natural contribution of the flood-plain area and the restoration of the *igapó* forest neighboring the lake IA (Bozelli *et al.* 2000, Josué *et al.* 2021.

The apparent inconsistency in the negative TP-PhyBM relationship must be analyzed, considering the extreme drought in 2015–2016, unprecedented in the last 100 years in the Amazon. The drought led to anomalously low-water levels and the highest temperature in the 21st century, due to El Niño years (Marengo *et al.* 2018). During our time series, one of the lowest water levels of the Trombetas River occurred in 2016, followed by the slightest flood (5.9 m). Consequently, a larger area in the shallower northern part of the lake dried for longer, leading to more compact sediment. Despite the higher percentage of organic matter (E. Ribeiro, unpublished data)

and potentially higher P on the sediment, P did not return to the water column. The expected seasonal sediment resuspension and the organic-matter loading from the flood-plain might have had more difficulty reaching the water column, leading to the observed low TP concentrations. Therefore, we can infer a lack of causality for the negative relationship between TP and PhyBM. Also, these uncertainties and the high spatial and temporal variability in a dynamic ecosystem may explain our modest r^2 values.

Besides the challenge of inferring causality from correlational field data, the potential bias from unmeasured variables, and the inherent chaotic behavior of phytoplankton (Benincà *et al.* 2008), we recognize a long-term trend of increase in PhyBM in the IA, converging to the levels of NIA.

The signs of recovery in the nearby impacted lake area due to natural and induced (restoration) processes might further influence the new scenario, improving underwater light availability. We concluded that the PhyBM in the IA positively responds to the synergy between increasing light availability, air temperature, and site depth, and decreasing TP concentrations, regardless of hydrologic phase. To better understand the recovery process, it is essential to continue monitoring the ecosystem´s functioning, including phytoplankton composition and as many ecological communities as possible, as well as some abiotic variables and their interactions. By this means, we will improve our understanding of how a flood-plain ecosystem responds to siltation by bauxite tailings in a sensitive area such as the Amazon.

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SUPPLEMENTARY MATERIAL

Table S1. Summary of linear mixed-effect regressions (LMER) testing differences in the Total phytoplankton biomass (mm^3 L^{-1}) and abiotic variables (fixed factors) (Residual light attenuation m^{-1}; Turbidity, NTU; Total nitrogen, mg L^{-1}; Total phosphorus, μg L^{-1}; Air temperature, ºC; site depth, m) between impacted and non-impacted areas and among years (2005–2019), controlled for sites (random factor) and their interactions in Batata Lake. The table shows the degrees of freedom from the numerator (numDF) and denominator (denDF) after the Satterthwaite correction and the F and p-value associated with it. Marginal r^2 describes the proportion of variance explained by the fixed factors alone, and Conditional r^2 represents the proportion of variance explained by fixed and random factors. Significant p-values are in bold.

Table S2. Annual mean, standard deviation (SD), and number of samples (n) per year of the variables selected in the models. AirT = Air temperature, z_{site} = Site depth, Turb = Turbidity, TN = Total nitrogen, TP = Total phosphorus, PhyBM = Total phytoplankton biomass, IA = impacted area, NIA = non-impacted area.