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Article

Unraveling Flooding Dynamics and Nutrients' Controls upon Phytoplankton Functional Dynamics in Amazonian Floodplain Lakes

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Abstract: The processes in tropical floodplain lakes enable maintaining phytoplankton nutrient requirements over a hydrological year. The nutrients such as nitrogen, phosphorus and carbon compounds play an essential role in phytoplankton growth. However, the way that nutrients and phytoplankton interact and how this relationship varies seasonally in tropical freshwater ecosystems is not clear. In this study, we evaluate the relationship between phytoplankton–nutrients over the hydrological cycle in Amazonian floodplain lakes and verify if this relationship influences the biomass of cyanobacteria. We also check what factors linked to nutrients act in structuring phytoplankton community. Using the phytoplankton functional approach, we verified how their ability to respond to hydrological and environmental variations reflects the ecological conditions and investigated how these interactions work. The results show that the Amazonian floodplain lakes could maintain long-term nutrient enrichment status. The nutrients input conduces to cyanobacteria dominance, that allied to other factors, play an essential role in supporting the stability of the phytoplankton–nutrients relationship over the hydrological cycle.

Keywords: nutrient enrichment; floodplain dynamics; phytoplankton ecology; hydrological process

1. Introduction

Nutrients are factors that may limiting the primary productivity of the phytoplankton community [1–3], and affect the efficiency in food chain ecological transfers [4]. Due to its low concentration in relatively pristine freshwater environments [5], phosphorus (P) in its bioavailable form for autotrophic organisms (orthophosphate) has long been considered as the main limiting factor for primary production [6]. Moreover, although Nitrogen (N) is also relatively rare, primary production requirement could be partly satisfied through atmospheric fixation, a capacity shared by some cyanobacteria genera [7]. However, at the ecosystem level, N₂ fixation serves only a fraction

of primary and secondary production demands [8,9]. Furthermore, current research showed that nitrogen and phosphorus enrichment produces a positive synergistic response in environments [10]. Disentangling what nutrient (P or N) is the most significant for primary production is strongly dependent on the environmental conditions and biological characteristics (especially related to phytoplankton community) prevailing in the considered aquatic ecosystem [6,7,11,12].

Moreover, the relationship between nutrient concentrations and phytoplankton is problematic, since nutrients can be blocked in phytoplankton cells in different ways. In addition to the ability of some genera of cyanobacteria that can fix atmospheric nitrogen [2,6,12], other genera may also store phosphorus [13], and the settled phytoplankton can stimulate mineralization at the sediment surface and consequently nutrient release to the water column [14,15]. The carbon available in the environment also plays an essential factor in the aquatic ecosystem and influences the phytoplankton community, at the same time, that can have their cycle influenced by this community [16–18]. Thus, even though the loading and concentrations of nutrients have a strong influence on the phytoplankton community, their relationship may be, in part, consequential rather than causative.

Regardless of cause and effect, what is known is that nutrient enrichment in the aquatic environments leads to the eutrophication process, which may cause cyanobacteria bloom that represents risks due to the potential release of toxins, as evidenced by several studies [19–23]. The phytoplankton community have diverse responses to varying nutrient enrichments [18,20,24] and should not be treated as a single group when considering the effects of nutrient loading on community structure [25]. The use of the functional groups approach may improve the understanding and the prediction of phytoplankton community responses to environmental changes [26,27]. It is expected that species of the same functional group change their biomass in response to environmental conditions, making it possible to predict the dynamics of natural phytoplankton populations [28]. The functional classification of Reynolds et al. [29] updated by Padisák et al. [30] comprises 40 functional groups whose share ecological affinities, tolerances and sensitivities to different environmental conditions. This classification has been tested successfully in a variety of aquatic systems and is one of the most validated phytoplankton functional classifications [27,31–33]. Indeed, these approaches allow the assessment of biological responses to environmental conditions where the species of different taxonomic groups can share the same ecological characteristics [29,30,34,35]. It is worth mentioning that the nutrients–phytoplankton relationship is expected to vary with time. It is even more true for aquatic systems such as the Amazon floodplains submitted to highly variable hydrological conditions throughout the hydrological year.

The annual hydrological variation known as flood pulse [36,37], drives the Amazonian floodplains production and diversity throughout different hydrological phases with different characteristics [38,39]. This monomodal variation promotes water oxygenation, brings nutrients into these areas, leading to peaks in primary productivity [40,41]. The autogenic organic material is partly locally degraded [42]. In addition, the hydrological variation tends to be more effective than spatial variation in structuring environmental and biological conditions in tropical floodplain systems [43–46]. Here, we aimed to study the relationship between the phytoplankton community structure and variations in nutrients on Amazonian floodplains, a topic which has been addressed only a little in the literature. Our working hypothesis is that the annual hydrological variation is more effective in producing changes on phytoplankton community than the spatial variation of environmental conditions and these changes are related to variation in different kinds of nutrients over the hydrological cycle. Hence, we evaluated (i) if changes in hydrological conditions are more important than nutrients in structuring the phytoplankton community; (ii) the importance of different kinds of nutrients in the structure of the phytoplankton community (functional groups); (iii) how it changes on the relationship driving the phytoplankton over the hydrological cycle; and (iv) if these relationships have an influence on the cyanobacteria biomass.

2. Materials and Methods

The study site is the Curuai floodplain, a large system composed of several temporally interconnected lakes located along the Amazon River (Figure 1). Several channels link the lake's

system with the mainstem, but only the easternmost channel remains permanently connected [39]. Waters from the Amazon River, local drainage basin, seepage, and local precipitation seasonally flood the system leading to an important seasonal water level variation (in average around 6 m). The large amplitude of water level combined with flat relief, induces a substantial difference of flood extent between low- and high-water periods [39]. The river water, rich in inorganic suspended material and nutrients [47–49], contrasts with the water quality of the other water sources that are poor in nutrients and rich in dissolved organic matter [41,50]. We collected samples during two consecutive years spreading over four hydrological periods, 2013 rising (RS) and flushing (FL) (March and September respectively), and 2014 high-waters (HW) and low-waters (LW) (July and November respectively), with 23 stations in each period.

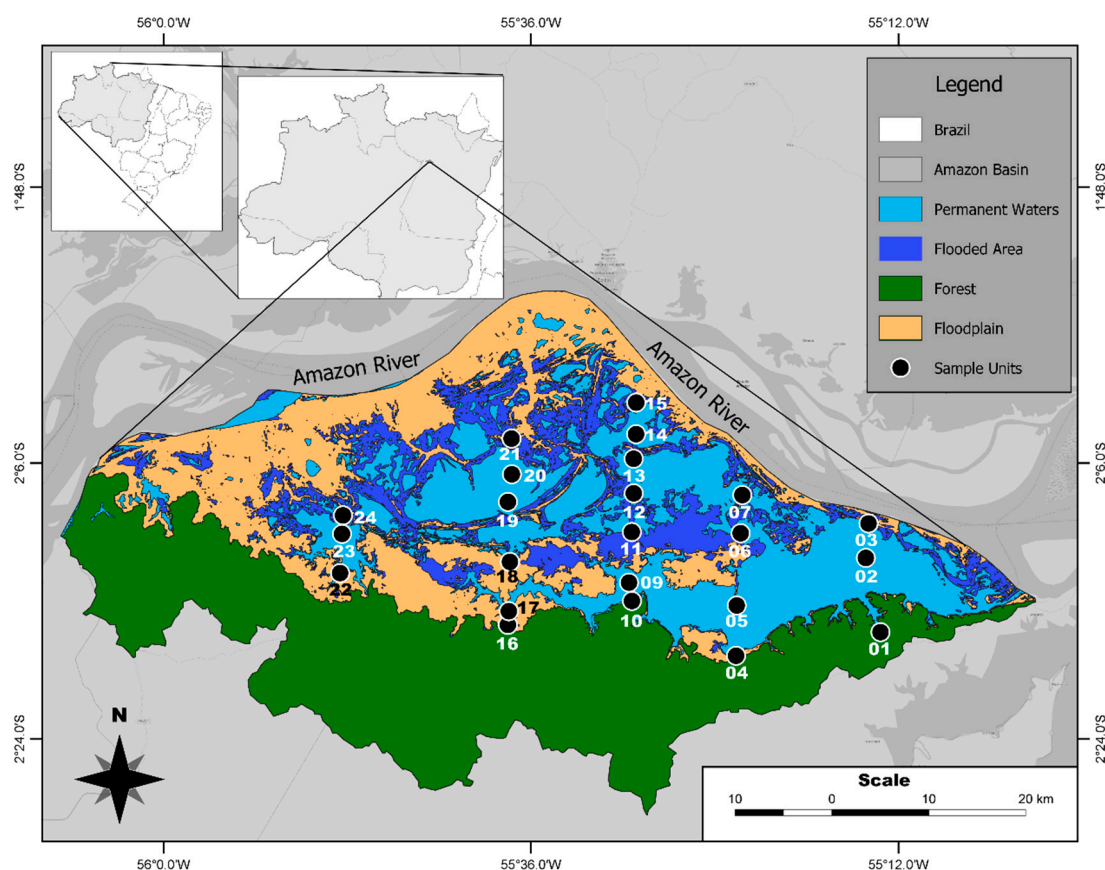


Figure 1. Map of study area, Curuai floodplain basin, with lakes sites of sampling units, flooded area and permanent waters over hydrological periods.

2.1. Environmental and Phytoplankton Data

Sub-surface water samples for nutrients and carbon analyses were collected at the same locations where phytoplankton was collected (Figure 1). Additionally, at these locations, depth (Dep) was recorded and dissolved oxygen (DO), oxygen saturation (O_2 Sat), and electrical conductivity (Cond) were measured with a multi-parameter probe (YSI 6820-V2). Total phosphorus (TP), orthophosphate (PO_4), hydrolyzable reactive phosphorus (HdrP) and organic phosphorus (OP) were quantified following the methods of [51]. Total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3) and nitrite (NO_2) were analyzed with the non-dispersive infra-red (NDIR). Total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), and volatile suspended solids (VSS) were measured following procedures in the Standard Methods for the Examination of Water and Wastewater [52].

The quantitative samples of phytoplankton were collected and were stored in 100 mL amber vials and fixed with acetic Lugol solution. Phytoplankton was counted following the Utermöhl method [53], at 400× magnification. The counting was done randomly until obtaining 100 individuals (cells, colonies, or filaments) of the most frequent species, keeping the error less than 20%, with a confidence coefficient of 95% [54]. The adopted system for classifying phytoplankton was that of Guiry and Guiry [55]. The algal biovolume was calculated by multiplying the abundance of each species by the mean cell volume [56], based on the measurement of at least 30 individuals and was expressed in $\text{mm}^3 \text{L}^{-1}$. This biovolume was used to select the phytoplankton functional groups (FGs). FGs were classified according to Reynolds [29], with the modifications made by Padisák [30]. The FGs' specific biomass was estimated from the product of the population and mean unit volume and only species that contributed with at least 5% of the total biovolume per sample unit were considered [57].

2.2. Data Analysis

The space-time interaction test (STI) [58] was used to verify how significant the variation in time and in space of the structure of the phytoplankton community was. It is worth mentioning that in our study, time variation is primary linked with hydrology cycling, whereas spatial variation would also be related to processes that have taken place in the different locations of the floodplain. The STI test consisted of a two-way ANOVA to test the space-time interaction, and the main effects of space or time using one among a set of possible models [58]. Firstly, space and time were coded using Helmert contrasts for the main factor effects. Then, they were coded using distance-based Moran Eigenvector Maps variables (dbMEM) for the interaction term. If the interaction was not significant, the test of the main factors was also done following the method for the previous step. If the interaction was significant, then we tested spatial and temporal structures using dbMEM variables to know whether separate spatial or temporal structures exist. For more details consult [58]. These analyses were implemented using the R packages “adespatial”.

To evaluate the importance of nutrients in the structure of the phytoplankton community, we divided the environmental variables into two subgroups, one with the variables related to the nutrients (nitrogen, phosphorus, carbon, and oxygen) and another group with the other variables to which we refer to as hydrological variables. These two groups were used to perform a partial redundancy analysis [59]. This analysis allowed us to estimate the importance and influence of different environmental variables partitions (i.e., nutrients and hydrological) in the structure of the phytoplankton community. To test the significance of each partition we performed an ANOVA test. These analyses were implemented using the R packages “vegan” [60].

We performed an analysis of the organization of three-way tables with Co-Inertia analysis' (STATICO) to evaluate the relationships between the phytoplankton biomass and nutrients. With this method, we calculated the stable part of the relationships between nutrients and phytoplankton throughout the hydrological periods. STATICO combines two analyses, the STATIS that is finding the stable part of the structure in a series of tables and the co-inertia that consists in finding the common structure in two data tables [61]. The STATICO maximizes the covariance between the row coordinates of two tables. The pair of tables here consist of one for the phytoplankton biomass and one for the nutrient conditions. This analysis had three-steps: (i) Each table was analyzed with a primary analysis; so, (ii) each pair was linked by co-inertia analysis that produces a cross table; then (iii) the partial triadic analysis (PTA) was used to analyze the series of cross tables [62]. We evaluated four pairs of tables: Rising (RS), flushing (FL), high-water (HW) and low-water (LW). With the interstructure, we evaluated the variation of the phytoplankton–nutrients relationship. Hence, it is possible to quantify the strength of the phytoplankton biomass–nutrients relationship over the hydrological periods. The compromise determines the part of the structure between phytoplankton biomass and the nutrients that remain stable throughout the hydrological periods. These analyses were implemented using the R packages “ade4” [61].

We used a forward selection procedure [63] to keep only the environmental variables that significantly influence the phytoplankton community structure. This procedure consists of a global test using all possible explanatory variables. Then, if, and only if, the global test was significant, one can proceed with the forward selection. The procedure has two stopping criteria, and when a variable that brings one or the other criterion over the fixed threshold is identified, that variable is rejected, and the procedure is stopped. For more details consults [63]. With the selected variables, we performed a Multiple Regression Tree [64] to evaluate if the relationship between phytoplankton and the selected environmental variables were an important factor in structuring the community. The Multiple Regression Tree (MRT) consists of a constrained partitioning of the data parallel cross-validation of the results that produce a model that forms a decision tree [65]. This method forms clusters of sites by repeating splitting of the data along axes of the explanatory variables. Each split was chosen to minimize the dissimilarity of data within the clusters [64,66] that were presented graphically by a tree. The overall fit of the tree was specified as adjusted R^2 ($\text{adj}R^2$), and the predictive accuracy was assessed by cross-validated relative error (CVRE) [66]. The MRT was implemented using the R packages “mvpart” [67] and “MVPARTwrap” [68]. We also performed an Indicator Species Analysis (Ind-Val) to find a statistically significant phytoplankton functional group for each data split and groups resulting from MRT [69]. The method combines FG mean abundance (“specificity”) and frequency of occurrence (“fidelity”). FGs that are both abundant and occur in most of the hydrological periods, belonging to one MRT group have a high Ind-Val. Ind-Val ranges between 0 to 1, where 1 refers to a perfect indicator regarding both “specificity” and “fidelity.” We applied the Ind-Val to groups obtained with the MRT analysis using the R package “MVPARTwrap”.

3. Results

3.1. Hydrological and Nutrients Data

Depth, conductivity, and suspended solids presented contrasted mean values in function of the hydrological periods (Table 1). Depth was comparable between FL and RS, it was three time higher during HW than during LW. Conductivity was comparable between FL and LW periods but was 60% higher during FL than during HW. Suspended solids (TSS and FSS) were minimum during HW and maximum during LW.

The total nitrogen mean value (TN) was maximum during LW, about one third greater than during FL when it was minimum. On the other hand, if total inorganic nitrogen (DIN) was also maximum during LW, it was minimum during the RS. The main form of inorganic nitrogen was NO_3 except during LW when NH_4 was more than half DIN. NO_2 remained low below $10 \mu\text{g L}^{-1}$ except during LW when it reached up to $80 \mu\text{g L}^{-1}$, while NO_3 is very low. Total organic carbon (TOC) was maximum during RS and minimum during LW with a mean value ranging between 4 and 5.5 mg L^{-1} . The dissolved fraction (DOC) represented up to 93% of TOC during FL and 65% during RS. During the rising and flushing periods, PO_4 only represents a small part of total phosphorus, respectively 6% and 2%. During the high- and low-water periods, it represents 40% and 78% respectively. The water column remained oxygenated with saturation above 58% regardless of the hydrological period.

Table 1. Summary of environmental and nutrients data analyzed. Depth (Dep), dissolved oxygen (DO), oxygen saturation (O₂Sat), electrical conductivity (Cond), total phosphorus (TP), orthophosphate (PO₄), hydrolysable reactive phosphorus (HdrP), organic phosphorus (OP), total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH₄), nitrate (NO₃), nitrite (NO₂), total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), volatile suspended solids (VSS). Minimum value recorded (Min), maximum value recorded (Max), standard deviation to mean (SD).

	Dep m	DO mg L ⁻¹	O ₂ Sat %	Cond μS/cm	TP μg L ⁻¹	PO ₄ μg L ⁻¹	HdrP μg L ⁻¹	OP μg L ⁻¹	TN μg L ⁻¹	DIN μg L ⁻¹	NH ₄ μg L ⁻¹	NO ₃ μg L ⁻¹	NO ₂ μg L ⁻¹	TOC mg L ⁻¹	DOC mg L ⁻¹	POC mg L ⁻¹	SST mg L ⁻¹	SSF mg L ⁻¹	SSV mg L ⁻¹
RS																			
Min	1.70	4.5	61.9	38.0	22.1	0.1	2.2	0.1	225.4	86.0	0.4	5.0	5.0	1.9	1.6	0.0	32.0	0.0	0.0
Max	5.70	7.6	107.2	82.0	186.4	75.0	74.3	136.7	629.6	422.4	187.9	148.0	17.0	8.9	5.4	5.6	108.0	98.0	40.0
Mean	4.00	6.2	83.6	70.0	85.8	5.0	11.7	69.3	379.0	225.9	37.2	63.9	8.8	5.1	3.6	1.9	56.7	37.0	19.7
SD	1.43	0.9	13.1	12.0	38.9	16.3	14.8	32.8	93.9	76.9	39.7	41.9	2.6	2.3	1.0	1.8	21.3	30.6	14.6
CV	0.36	0.15	0.16	0.17	0.45	3.24	1.27	0.47	0.25	0.34	1.07	0.66	0.29	0.45	0.29	0.96	0.38	0.83	0.74
HW																			
Min	4.11	0.4	6.0	35.0	34.2	0.1	1.3	5.3	277.4	187.9	8.0	36.2	1.0	2.9	2.6	0.2	4.0	1.0	0.5
Max	7.53	9.6	131.2	50.0	105.4	306.6	173.1	136.7	519.4	415.8	306.6	136.8	68.6	5.9	4.5	3.4	24.0	16.8	13.4
Mean	6.30	4.4	58.5	44.1	62.4	24.9	41.4	53.4	362.5	275.3	66.6	80.6	8.3	4.5	3.6	1.2	14.6	8.3	6.3
SD	1.03	1.9	26.2	3.7	18.4	64.3	37.5	28.8	68.6	56.2	70.7	31.9	14.0	0.7	0.6	0.7	5.2	4.6	3.5
CV	0.16	0.44	0.45	0.08	0.30	2.33	0.90	0.54	0.19	0.20	1.06	0.40	1.69	0.16	0.16	0.57	0.36	0.55	0.57
FL																			
Min	2.50	0.5	6.8	39.0	7.1	0.1	0.1	0.1	187.1	175.2	7.0	10.0	10.0	2.9	2.8	0.0	6.5	3.0	1.5
Max	4.30	12.5	172.4	81.0	111.3	25.0	79.7	77.9	570.0	608.9	183.0	246.2	10.0	7.1	6.8	0.8	66.5	62.0	12.5
Mean	3.77	6.5	86.9	51.1	52.1	1.2	26.4	25.2	314.0	288.7	30.0	84.0	10.0	4.0	3.8	0.3	29.0	23.9	5.2
SD	0.71	3.1	42.4	11.4	26.7	5.2	23.0	21.3	105.9	101.0	41.9	68.8	0.0	1.0	0.9	0.2	15.5	15.1	3.0
CV	0.19	0.48	0.49	0.22	0.51	4.39	0.87	0.84	0.34	0.35	1.39	0.82	0.00	0.25	0.25	0.76	0.53	0.63	0.58
LW																			
Min	0.45	6.2	83.0	19.0	9.9	0.0	22.2	0.1	125.6	106.8	6.9	3.6	0.1	2.8	2.6	0.1	20.0	14.0	2.0
Max	2.40	11.0	150.9	69.0	119.2	306.6	268.3	20.0	756.0	732.3	450.5	12.5	381.5	7.0	6.0	1.3	284.0	263.0	21.0
Mean	1.24	7.8	106.1	50.9	49.9	39.1	98.7	1.0	475.0	362.5	195.1	5.9	80.1	4.1	3.5	0.5	67.0	58.0	9.0
SD	0.54	1.0	14.4	13.5	28.1	78.3	51.6	4.1	141.6	121.4	114.9	2.2	90.1	1.1	0.8	0.3	53.3	49.9	4.5
CV	0.44	0.13	0.14	0.27	0.56	2.01	0.52	4.30	0.30	0.33	0.59	0.38	1.13	0.26	0.23	0.57	0.80	0.86	0.50

3.2. Biological Data

The proportion of classes in the composition of the phytoplankton community varies throughout hydrological periods (Figure 2A). The Coscinodiscophyceae phytoplankton class had the highest biovolume during RS, the representative species was *Aulacoseira* spp. The Cyanophyceae phytoplankton class presented the highest biovolume during HW, FL and LW periods. The species with the highest biovolume during HW were *Phormidium* spp and *Aulacoseira granulata* var *granulata*. The species that were representative during the FL also presented the highest biovolume in this period were *Dolichospermum* spp and *Gleiterinema splendidum*. During LW, the species *Oscillatoria* spp and *Phormidium* spp presented the highest biovolume. Interestingly, the proportion of Cyanophyceae increased along the hydrological cycle from RS to LW when the phytoplankton is almost entirely composed (up to 98%) of representatives from this class. Species were distributed in 11 functional groups that contributed to at least 5% of the total biovolume in at least one of the hydrological periods (Figure 2B). During RS, the functional groups P, Y, and Lo comprised 61.4% of the total biovolume. The group P is composed of species adapted to shallow lakes that tolerate high trophic states such *Aulacoseira granulata*, *Closterium* sp, and *Fragilaria* sp. The group Y comprises species adapted to lentic ecosystems and in the study was represented by *Cryptomonas* spp. The group Lo contains species adapted to deep and shallow lakes that tolerate oligo to eutrophic states such *Peridinium* spp, and *Merismopedia* spp. During HW, functional groups were Tc, P, and Lo that represented 58.2% of the total biovolume. The group Tc encompasses species adapted to eutrophic standing waters, or slow-flowing rivers and was here composed by *Oscillatoria* spp and *Phormidium* spp. During FL, the group H1 represented 61.1% of the total biovolume. The group H1 comprises species adapted to shallow lakes with eutrophic state and low nitrogen content and was here composed by *Dolichospermum* spp that may have the ability to fix nitrogen. During LW, the group Tc represented 77.0% of total biovolume, and *Oscillatoria* spp comprised about 90% of this total. This group encompasses species adapted to eutrophic standing waters, or slow flowing rivers and was here composed by epiphytic cyanobacteria as *Oscillatoria* spp and *Phormidium* spp.

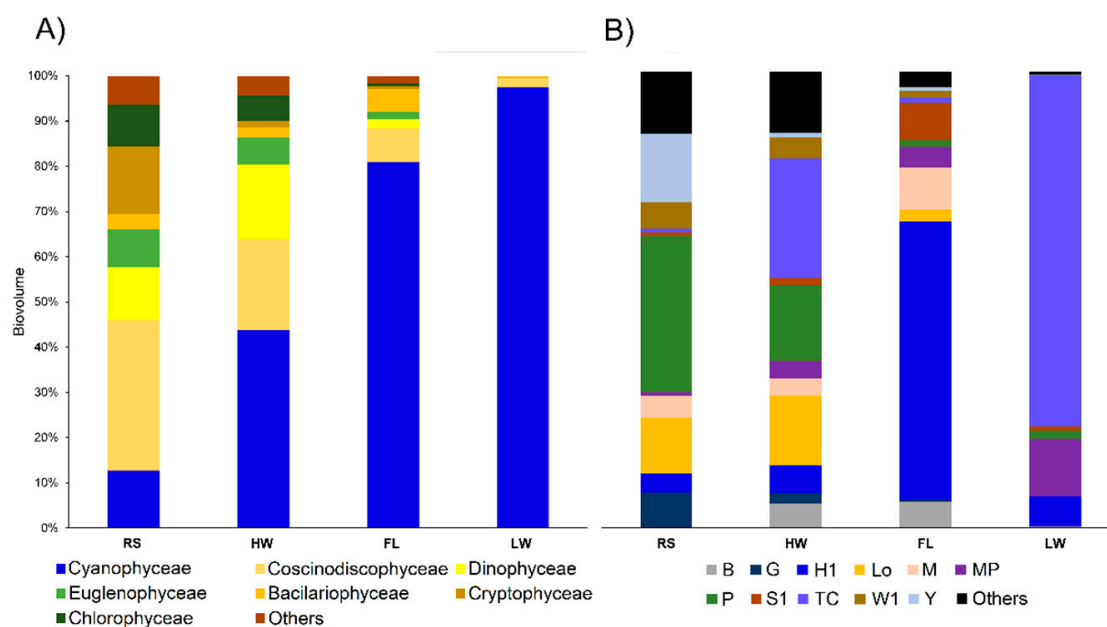


Figure 2. Relative phytoplankton class biomass (A) and functional groups biomass (B). Rising period (RS), high-water period (HW), flushing period (FL), low-water period (LW), B–G–H1–Lo–M–MP–P–S1–Tc–W1–Y are functional groups that had at least 5% of total biovolume in at least one hydrological period. Others are the sum of functional groups that did not respect the 5% threshold.

3.3. Statistical Results

The STI test indicated that the space-time interaction is not significant. That is there was no significant influence of space-time on the structuring of the phytoplankton community at the functional group level. The second step returned that only time had a significant importance in structuring the phytoplankton community, hence indicating that spatial distribution of sample units had no significant influence (Table 2). The time influence indicates that the hydrological cycle was the main factor in the dynamics of the phytoplankton community. The partial redundancy analysis (pRDA) for partition environmental data shows that both, nutrients and hydrological variables, had a significant influence in structuring the phytoplankton community, but the strength of the nutrients partition was higher than that of hydrological variables (Table 2). The pRDA also returns a great residual, indicating that there were other important factors, not measured, which influenced the phytoplankton community structure.

Table 2. Results of the space-time interaction test (STI) and pRDA tests. Space-time interaction (Space + Time), common temporal structures (Time), common spatial structure (Space), variation due to nutrients (Nutr), variations due to nutrients and hydrology together (Nutr + Hydr), variations due to hydrology (Hydr), not-explainable variation (Res), adjusted R² value (AdjR²), significance ($p < 0.05$).

	Space-Time Test				Partition Test		
	R ²	F	p		Adj.R ²	F	p
Space-time	0.060	1.18	0.221	Nutr	0.128	1.89	0.001
Time	0.530	35.09	0.001	Hydr	0.068	2.00	0.001
Space	0.128	1.15	0.114	Nutr + Hydr	0.126	-	-
				Residuals	0.679	-	-

The STATICO analysis showed stability in the phytoplankton–nutrient relationship along periods as illustrated by the longer arrows in the interstructure graph (Figure 3A). In these graphs, the greater length of arrows (or in case of points, the distance from the center), the higher the stability in this relationship. However, the weight of each hydrological period on the phytoplankton–nutrients relationship was different (Figure 3B). The first and second axes represented, respectively, 19% and 10% of the total variability. The first axis (horizontal axis) in the compromise graph (Figure 3C) accounted for 42% of the explained variance and the second axis (vertical axis) accounted for 20% of the explained variance and was less significant. Flushing and low-water periods were more related to the first axis which has twice the explanatory power of the second axis. Hence, the phytoplankton–nutrients relationship might be considered stronger during these two periods.

As shown by the environmental variables compromise plot (Figure 3C), the first axis (horizontal), was more related to hydrolyzable phosphorus and suspended solids. The second axis (vertical) was more related with PO₄ and NO₂ (Figure 3C). Other variables such as conductivity and oxygen, are related to both axes and also have a great compromise (long arrow). The environmental variables with shorter arrows have weak stability with the hydrological cycle and are more related to a specific period, as detailed below. For the functional groups compromise plot (Figure 3D), the most important groups are those more distant to the center of the graph. The FG's MP and H1 although have great stability with the hydrological cycle, also play an important role on specific period (Figure 4).

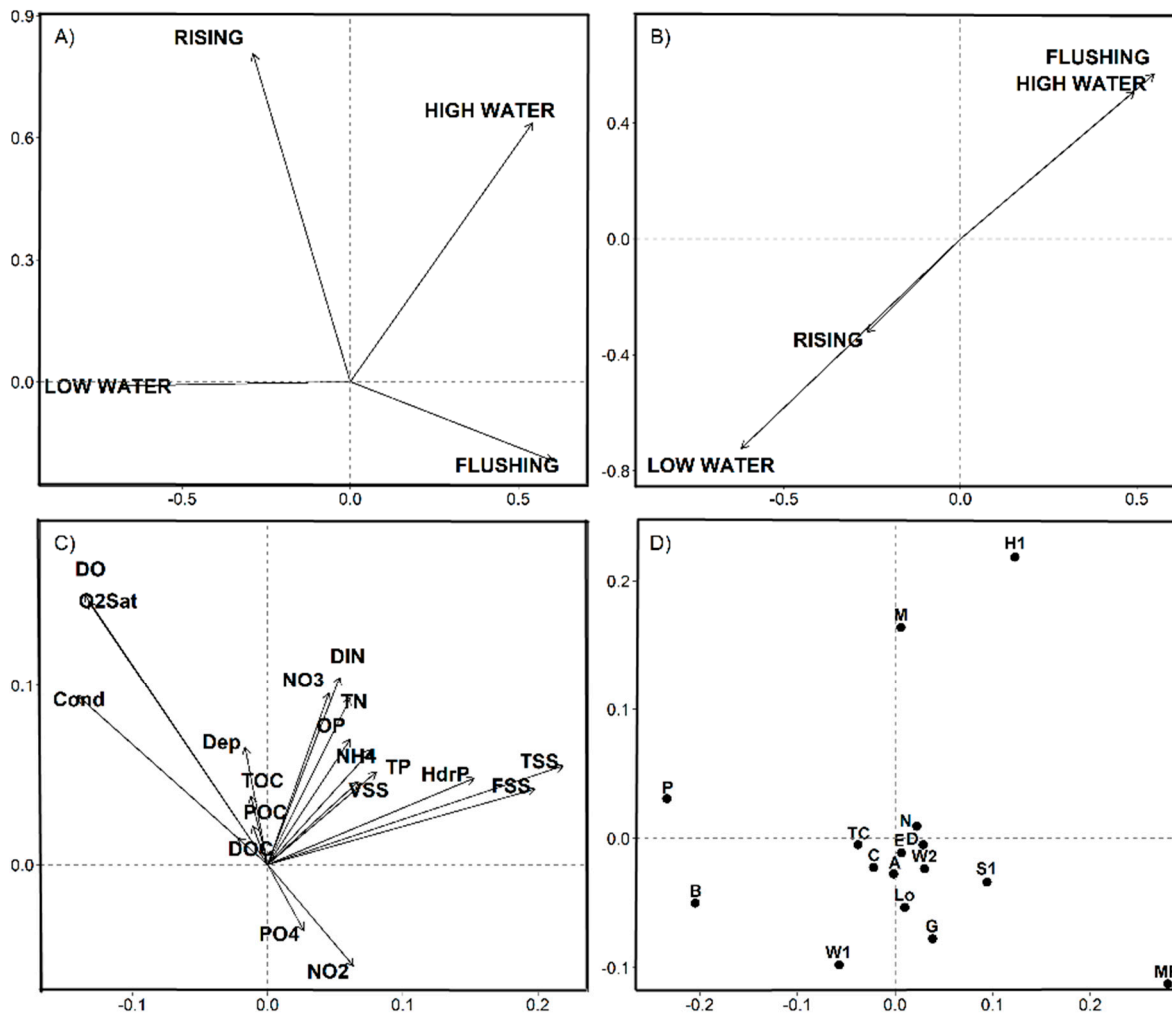


Figure 3. STATICO graph. The length of arrows (A–C), or distance from the center (D) indicates the strength of a relationship. Interstructure graph (A), weight of each hydrological period (B), environmental and nutrients compromise (C), species compromise (D).

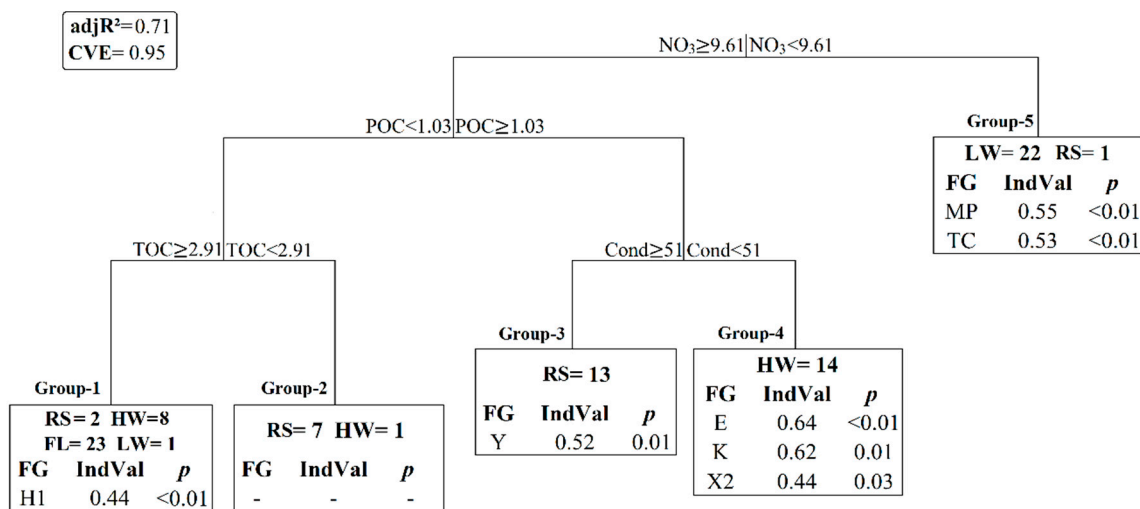


Figure 4. Multiple Regression Tree (MRT) map. Rising period (RS), high-water period (HW), flushing period (FL), low-water period (LW), species indicator value (Ind-Val), significance (p), adjusted R² (R²), cross-validation error (CVE). Groups 1 to 5 MRT clusters results.

MRT applied to the data resulted in five groups, the model explained 71% of the phytoplankton data variability ($\text{adj}R^2 = 0.71$). The predictive power of the model expressed as the cross-validation relative error (CVRE) was 0.95. MRT clearly separated LW samples (22 samples) apart from those collected during the other periods based on NO_3 concentration (Figure 4); LW samples belonged to group 5 with low NO_3 concentration. Further group divisions were based successively upon particulate organic carbon, total organic carbon and conductivity. Interestingly, similarly as LW period, all samples from the FL period are gathered into a single group (group 1) characterized by high NO_3 , POC and TOC concentrations, whereas samples collected during HW or RS are spread over three groups. A majority of samples collected in HW were gathered into group 4 (high NO_3 , high POC and low Cond), and those collected during RS mostly divided into two groups, a majority in group 3 (high NO_3 , high POC, high Cond). Indicator value (Ind-Val), coupled with MRT analysis, enabled extracting sets of FG's indicators of the MRT groups (Figure 4). Based on the Ind-Val, four groups are characterized by seven significant FGs ($p < 0.05$). Group 2 does not have any FG indicators with a significative value.

4. Discussion

4.1. Space-Time Components and Environmental Partitions

As we expected, the hydrological variation (time), is a more significant factor of structuration of the functional phytoplankton community than the environmental spatial variability (space). Besides the STI test, the STATICO also showed that most of the phytoplankton community variation is strongly linked with variables related with hydrological conditions (TSS, Cond). MRT further confirmed the groups according to the hydrological periods. The analyses show that only the hydrological variation is strong enough to produce functional changes in the phytoplankton community and this reflects the importance of flood pulse dynamics in the Amazon basin. In fact, the hydrological variation or flood pulse, is acknowledged as a strength that can promote changes in these environments and biological communities in several studies [36,70,71]. In addition, our results showed that these changes are more related to nutrients changes (and especially nitrogen changes as indicated by MRT) than changes in another factors (among those we have measured). Indeed, the partition test showed that although the hydrological variables measured were significant in structuring the community, the nutrients variables were two times more decisive in this process, thus confirming our starting hypothesis. In addition, the partition involving both variables (Hydr + Nutr) has the same proportion than that of the nutrients partition. The hydrological annual variability promotes a lot of changes over the year, and one of them is a variability of the different kinds of nutrients. In general, we measured only total nitrogen and total phosphorus when performing research in this field, for many reasons, but the different fractions of nitrogen and phosphorus compounds have different influences on the phytoplankton community.

4.2. Nutrients-Phytoplankton Relationships over Hydrological Cycle

Our results showed that over the hydrological year, (i) the interaction between phytoplankton community and phosphorus compounds is more stable than that of nitrogen compounds (Figure 3C,D), and (ii) that the rising period has the weakest weight in the phytoplankton–nutrients interaction (Figure 3B). While the phytoplankton biovolume becomes higher, the weight of the relationship in subsequent hydrological periods increases, suggesting that there are both top-down and bottom-up controls, for the phosphorus and nitrogen cycles in tropical floodplain system. Top-down refers to the input which occurs in the rising period from waters coming from the Amazon river, while bottom-up refers to phosphorus (or nitrogen) cycle processes occurring inside the floodplain.

Regarding phosphorus, our results suggest that bottom-up control is stronger than top-down, or in other words, that phosphorus compounds already present or in situ recycled in the system have a greater influence upon phytoplankton than allogenic phosphorus compounds. It is well known that Amazonian rivers that drain the Andes (classified as white-water rivers according to Sioli, 1984

typology) [47] carry high concentration in suspended solids and dissolved and sediment-bound nutrients [37]. The river incursion across the floodplain during rising brings nutrients and sediment into the floodplain ecosystems and promotes a high peak in primary productivity [39,72]. However, our results also showed that the phytoplankton–phosphorus relationship is stable along the hydrological year. Many processes can participate to maintain a rather constant concentration of phosphorus in the water column: Seasonal herbaceous plants that pump nutrients from the sediment to support their growth and release nutrients in the water column during their decay [73,74]; sediment early diagenesis processes and resuspension may also participate [74].

Although weaker than with phosphorus compounds, our results showed that there is a stable interaction between nitrogen compounds (TN and DIN) and phytoplankton. Wetlands such as floodplains can be considered aggrading ecosystems where the nitrogen can come from adjacent drained areas or the mainstream, and in some cases, from biological nitrogen fixation and atmospheric deposition [75–77]. The phytoplankton primary productivity peak occurring in the rising period is followed by a significant increase of nitrogen-fixing cyanobacteria biovolume. Nitrogen fixation is an essential process for eutrophic wetlands, once it may contribute from 5% to 80% of the total nitrogen inputs in these systems [8]. NO_3 is the most common reactive nitrogen species [74], and the high concentration in flushing period allied to higher biovolume of FG H1 suggest that nitrogen-fixing process plays an essential role in maintaining the stability along the hydrological cycle.

Besides nitrogen-fixation processes, the increases in nitrogen compounds between rising and subsequent periods, similar to phosphorus, can be influenced by processes mentioned above, especially the seasonal herbaceous plants growth/decay cycle that may release NH_4 and NO_3 in the water column. Thus, the sediment nutrients pool mobilization is another crucial factor that permits the nitrogen concentration to remain stable during the hydrological cycle. Hence, like phosphorus, the phytoplankton–nitrogen interaction also suggests that there is both a top-down and bottom-up interaction for its cycle in tropical floodplain system.

The idea that the phytoplankton has the potential to influence pools of nitrogen and phosphorus that would be available is not new [77], but works with this approach are scarce in tropical environments. For temperate lakes, the work of Cottingham et al. [77], has demonstrated that cyanobacteria have the potential to drive nitrogen and phosphorus cycles in lakes. They remarked that the ability of many cyanobacterial taxa to fix nitrogen and to access pools of phosphorus in sediments and bottom waters is the key behind this influence. Their work suggests that cyanobacterial blooms warrant attention as potential drivers of the transition from a low-nutrient clear-water regime to a high-nutrient turbid-water regime. Our results show that there is a considerable increase in cyanobacteria biovolume, but it is difficult to know how much is a consequence of allochthonous nitrogen inputs and how much is a consequence of autochthonous nitrogen inputs. However, it is certain that this increase is an important factor for maintaining the stability of nutrients over the hydrological cycle. Thus, the cyanobacteria dynamics are an essential factor in both nutrients cycling and phytoplankton dynamics. Increases in nutrients leading to a dominance of cyanobacteria have been reported by Dokulil and Teubner [78], and in Curuai, Affonso et al. [79] they found that the flushing period was the most eutrophic period. Thus, the extent to which the floodplain becomes shallow, and water flow less intense, the cyanobacteria community can be established [80].

4.3. Cyanobacteria Dynamics

The results showed that while the phytoplankton biomass increased, and the environment became more eutrophic, the phytoplankton functional group diversity was decreasing until the phytoplankton was almost entirely composed by the cyanobacteria group. Even if phytoplankton species differ in their nutritional requirements [81], and although nitrogen and phosphorus are essential factors for the phytoplankton growth, they are not the unique. Other factors play a vital role for the phytoplankton in specific periods. Unlike during the flushing and low-water periods, samples collected during the rising and high-water periods spread over a larger number of MRT groups with functional groups

with significant Ind-Val. The Amazon river incursion extent across the floodplain, the flow magnitude and the mixture of this inflow with the water residing on the floodplain cause a significant directional gradient [82]. Additionally, the rising period is probably the period that is the most influenced by the floodplain geomorphology. The FG Y has a significant value of Ind-Val for 13 sites in rising period and it is an indication that this period is marked by a great dynamism. Indeed, the group Y refers to a wide range of habitats, thus reflecting the ability of species to live in almost all lentic ecosystems [30]. During the high-water period, a majority of the samples were gathered into a group that exhibited three functional groups with significant Ind-Val. These results are an indication of heterogeneity and of a state of a transition period.

The reduction of water speed and input of nutrients from the previous periods turns the environment favorable to cyanobacteria community development. High NO_3 concentration with lower concentrations of POC and higher concentrations of TOC characterize all sites in the flushing period. NO_3 and NH_4 are the preferred uptake forms of nitrogen by phytoplankton, but NH_4 might have an inhibitory or repressive effect in NO_3 uptake and assimilation [10]. During the flushing period NH_4 is very low, while NO_3 is high: A condition that favors the NO_3 uptake by the phytoplankton during this period. During this period also, POC was very low and TOC was almost entirely in DOC form. As mentioned in Moreira-Turc et al. [42], contrasting with the rising period when DOC is mainly imported from the Amazon River, high DOC lability is expected during the flushing period because it is mainly originating from phytoplankton production. Higher labile DOC concentration also helps to provide nutrients for the development and establishment of the cyanobacteria community [16–18]. Lowest concentrations of NH_4 also favor the increase of nitrogen-fixing cyanobacteria and our results show that functional group H1, composed of species with nitrogen-fixing ability, has a significant Ind-Val for samples collected during the flushing period. NO_3 depletion characterized almost all the samples collected during the low-water period, while NO_2 increased. Due to lowest water level and increasing interaction between water column and sediment, denitrification bacteria in the sediment (that might have anoxia or hypoxia condition), can be responsible for the characteristics of the low-water period. Even though the low-water period was composed almost entirely by one functional group, the Ind-Val comprised two groups with significant indicator-values, composed of species adapted to eutrophic waters and shallow turbid lakes with the presence of inorganic compounds. These results demonstrate that despite the dominance of cyanobacteria, the conditions begin to be favorable for the establishment of other phytoplankton groups that will encounter favorable conditions during the next hydrological cycle.

5. Conclusions

Our analyses confirm the predominant role of hydrology upon the phytoplankton community. The seasonal hydrological variation is strong enough to produce functional changes in phytoplankton community, especially because the changes in nitrogen and phosphorus contents and chemical speciation along the water year. Besides, biogeochemical processes in tropical floodplain lakes, such as the Curuai floodplain lake, enable maintaining phytoplankton nutrient requirements even long after the nutrient inputs from the river water has declined. The nutrient inputs in rising periods increases the phytoplankton biomass which becomes dominated by cyanobacteria during the low-water period. The cyanobacteria, allied to other organisms (not evaluated in this study such as macrophytes and bacteria), play an important role in maintaining the stability of nutrients along hydrological periods. Interestingly, it was possible to identify a limited number of phytoplankton functional groups indicating the particular environmental conditions during the flushing and low-water periods. During the rising and high-water periods, the environmental and biological conditions seem to be more spatially structured in part because of higher water contribution from the local watershed at these periods. These features highlight the large variability in phytoplankton activities in tropical floodplain ecosystems that may cause issues for the global Amazonian trophic chain. Although our study contributes disentangling hydrology and nutrients control upon the phytoplankton community and

better understands how the nutrients–phytoplankton relationship changes along the water year, still more research is required upon the phytoplankton–nutrient relationship in tropical aquatic ecosystems. Most of the knowledge upon this relationship is based on experimental investigations and research in temperate environments, and thus limiting our understanding of what controls such processes in tropical freshwater ecosystems.

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