Chapter 4
Broadscale Variation of Phytoplankton Richness in Brazilian Inland Waters

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Abstract Species richness is a primary biodiversity measure in ecosystem functioning studies. The main factors shaping broadscale patterns of phytoplankton species richness (PhyRich) are temperature, system area, productivity, and less assessed light, flushing, and grazing. Our understanding of how the environment affects PhyRich is limited on broad spatial scales because of the lack of data using the same sampling and analysis methods. We selected three essential factors and hypothesized that PhyRich increases with water temperature, light availability (as turbidity), and intermediate productivity (as total phosphorus) levels. We assessed PhyRich from samples taken by a specially equipped hydroplane at 1045 sites across subcontinental (entire dataset) and regional (hydrographic regions) scales in Brazil (4°N–33°S and 34°–73°W) by quantifying the species number per site (settling technique). We selected models using the Akaike Information Criterion to understand which combination of variables better described PhyRich patterns. On our subcontinental scale, PhyRich was positively related to water temperature and negatively to light availability and productivity, although PhyRich was similar in oligo- and mesotrophic conditions, approaching the expected unimodal relationship. The trend for a slight reduction at the end of all gradients (univariate models) may have implications for the ecological functioning of freshwater systems.

Keywords Light · Productivity · Regional and subcontinental scales · Water temperature

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4.1 Introduction

Species richness has been used as a primary measure of biodiversity and to assess its relationship to ecosystem functioning (Díaz and Cabido 2001; Magurran 2005; Vogt et al. 2010; Magurran and McGill 2011). Except for the neutral theory (Hubbel 2001), the ability to predict patterns of species richness is based on the assumption that different species respond differently to environmental gradients (Tilman 2004; Cadotte et al. 2011). As for macroorganisms, microbial communities also affect ecosystem processes, including respiration and decomposition, autotrophic and heterotrophic production, and nutrient cycling.

Phytoplankton is a highly diverse community composed of 10,000 to 25,000 marine and freshwater species (Sournia et al. 1991; Falkowski et al. 2004; Vargas et al. 2015). The rapid response of phytoplankton to environmental changes may reflect water quality (Padisák et al. 2006; Chen et al. 2021; Zhang et al. 2018). Although quantifying species richness changes (or lack thereof) has been considered only one measure of a much more complex phenomenon of biodiversity change through time and space (Chase et al. 2019), phytoplankton species richness can help to understand ecosystem processes.

The main ecological drivers of phytoplankton species richness are temperature, system area, productivity, and light and, to a lesser extent, hydraulic flow and grazing pressure. Water temperature directly affects individual and population metabolic processes through its direct relationship with the growth of phytoplankton communities (Roland et al. 2010; Weyhenmeyer et al. 2013; Kruk et al. 2017) and its indirect effect on the thermal structure of the water column (Winder and Hunter 2008). Several phytoplankton studies have shown positive relationships between species richness and temperature (Ptacnick et al. 2010; Thomas et al. 2012; Weyhenmeyer et al. 2013; Kruk et al. 2017). This is in line with the metabolic theory of ecology, where a more intense flow of energy in the food chain increases the productivity of systems and consequently the availability of resources, enabling the coexistence of a larger number of species (Hawkins et al. 2003; Segura et al. 2017).

In addition to water temperature, a positive relationship between phytoplankton species richness and ecosystem surface area has been observed in both natural and experimental aquatic ecosystems. In an experimental study, Smith et al. (2005) confirmed that patterns in microbial diversity are highly consistent with those that have been repeatedly reported for macroorganisms. However, in a study of 30 subarctic rock pools, phytoplankton richness was not positively related to the pool volume, i.e., it did not support the species-area relationship (Soininen and Meyer 2014).

A unimodal relationship (higher values at intermediate levels) between phytoplankton species richness and productivity has been reported along the entire nutrient enrichment gradient (Dodson et al. 2000; Smith 2007). This relationship depends on the productivity interval analyzed: it is direct in systems with increasing productivity, inverse when the productivity decreases, and absent at intermediate productivity levels (Smith 2007). However, the mechanisms that lead to this pattern are still widely debated. At low productivity levels, competition for resources and essential variables (e.g., temperature) directly affects individual phytoplankters and population metabolic processes and can be determinant for phytoplankton richness and composition.

Light availability is another critical factor, but the relationship patterns remain unclear. The duration of the open-water season (as a proxy of light) was positively related to the PhyRich along a latitudinal gradient in Sweden, favoring growth and increasing the number of available niches (Weyhenmeyer et al. 2013). In highly productive systems, high biomass can lead to lower PhyRich due to greater competition for light (Zhang et al. 2018). In experimental studies, species richness decreased in treatments with high and low light availability, but the decrease was larger in conditions of high light availability due to photoinhibition (Litchman 1998).

Although hydrology is not as crucial for most large lakes, in small lakes, the runoff during large storm events can potentially increase the rate of loss from communities to the drainage basin. Hydraulic flow tends to be important in reservoirs, especially run-of-river reservoirs (inflow = outflow) and, more markedly, in lotic ecosystems where unidirectional flow is one of the main factors controlling pelagic communities (Reynolds et al. 1994; Schmidt 1994). In floodplain systems, the hydrological pulse is the main regulatory factor for phytoplankton (Zalocar de Demitrovic 2002; Devercelli 2006; Salmaso and Zignin 2010; Talling and Prowse 2010), with phytoplankton showing negative (Huszar et al. 1998; Nabout et al. 2007; Borges and Train 2009) or positive relationships (Train and Rodrigues 1998) to the hydraulic flow. Grazing pressure is an essential factor for controlling phytoplankton, and selective predation may cause low diversity and lead to a negative relationship (Muylaert et al. 2010; Vallina et al. 2014; Kruk et al. 2017).

These responses of phytoplankton species richness to different environmental gradients result in a nonlinear relationship between biodiversity and ecosystem functioning and may differ between local and regional scales, as illustrated by data obtained from several river basins (Chase and Ryberg 2004). The importance of understanding these responses is due mainly to the impact of global changes on biodiversity and ecosystem functioning (Weyhenmeyer et al. 2013). Despite the importance of species richness, our understanding of how the environment affects PhyRich at large spatial scales is limited. This metric can only be used with confidence when phytoplankton sampling and quantification are correctly performed, to provide an accurate survey of the taxa in a system (Várbiró et al. 2017; Borics et al. 2021).

Here, we offer a comprehensive analysis based on 1045 sites (Moss and Moss 2005; Abe et al. 2006) to assess how PhyRich varies concerning common major factors (temperature, light, and productivity). We followed the space-for-time-substitution approach by retrieving samples through a specially equipped hydroplane in motion, over an unprecedentedly large spatial scale in Brazil (*Brasil das Águas* Project). We hypothesized that PhyRich increases with water temperature and light availability (decreases with turbidity as a proxy) and increases at intermediate productivity (total phosphorus as a proxy) levels. We explicitly addressed species richness as estimated from single phytoplankton samples, most directly related to ecosystem processes carried out by phytoplankton.

4.2 Material and Methods

4.2.1 Study Area

The sampling points were based on broad latitudinal and longitudinal scales (4°N–33°S and 34–73°W) in 12 hydrographic regions (HRs; Fig. 4.1) defined by the National Water Resources Council (CNRH) and ANA (National Water Agency). We included as wide a variety of water bodies as possible, such as rivers, coastal lagoons, floodplain lakes, other natural lakes, reservoirs, rivers, and estuaries. Brazil is about 8.5 million km^2 in area, with between 12% and 16% of all freshwater production on the planet. The climate ranges from humid temperate to humid equatorial (Köppen-Geiger classification, updated by Alvares et al. 2013). It varies from areas with sparse (<1 inhabitant per km^2) to high human population densities (>400

Fig. 4.1 Map of Brazil, showing the sampling sites in the 12 hydrographic regions. Information obtained in the "ANA Metadata Catalog" (https://metadados.snirh.gov.br/geonetwork/srv/por/catalog.search;jsessionid=01A66BC206AAB137A73D5C4F7D761A89#/metadata/0574947a-2c5b-48d2-96a4-b07c4702bbab, accessed in September 21)

Table 4.1 Main features of the 12 Brazilian hydrographic regions, with abbreviations used in the text. Data for population and treated sewage refer to the study period and were extracted from Moss and Moss (2005)

Hydrographic regions/ abbreviation	Area (km^2)	Biome	Human population (million inhabitants and %)	Treated sewage (%)
Amazon (Ama)	3,805,850	Amazon rainforest	7.6 (4.5)	2.3
Coastal east (CoastE)	374,677	Atlantic Forest, Cerrado	13.6 (8)	30
Coastal northeast (CoastNE)	287,348	Atlantic Forest, caatinga	21.6 (12.7)	18.2
Coastal northwest (CoastNW)	254,100	Amazon rainforest, Cerrado	4.7 (2.8)	0.1
Coastal southeast (CoastSE)	229,972	Atlantic forest	25.6 (15.1)	26.4
Coastal south (CoastS)	185,856	Atlantic Forest, pampa	11.6 (6.8)	8.2
Paraguay (Parag)	363,445	Cerrado, Pantanal	1.9 (1.1)	17.2
Paraná (Paran)	879,860	Atlantic Forest, Cerrado	54.6 (32.2)	24.9
Parnaíba (Parnb)	344,112	Cerrado, caatinga	3.6 (2.1)	4.8
São Francisco (SFranc)	638,324	Atlantic Forest, Cerrado, caatinga	12.8 (7.6)	3.2
Tocantins/Araguaia (TocArag)	967,059	Amazon Rainforest, Cerrado	7.9 (4.7)	2.4
Uruguay (Urug)	174,612	Atlantic Forest, pampa	3.8 (2.3)	6.0

inhabitants per km^2; Moss and Moss 2005; Abe et al. 2006; Table 4.1). HRs include areas with different land uses, from large natural forest areas, savanna (Cerrado), and caatinga, to anthropic landscapes such as urban regions, mining, and agriculture (Table 4.1).

4.2.2 *Sampling*

We followed the space-for-time-substitution approach (Jeppessen et al. 2014; Meehrhof et al. 2012) by retrieving samples through a specially equipped hydroplane in motion, over an unprecedentedly broad spatial scale in Brazil (*Brasil das Águas* project. www.brasildasaguas.com.br). Water temperature, turbidity, and total phosphorus (TP) were analyzed at 1164 and PhyRich at 1045 sampling sites. Sampling was conducted from November 2003 to December 2004, encompassing 177 lakes and reservoirs and 366 watercourses, including the broadest possible variety of protected, agricultural, and urban areas. Samples were taken through a tube 20 cm below the water surface, connected to an autosampler on board a hydroplane

(Lake LA-250 Renegade, Lake Aircraft, USA) in motion. The system was flushed with lake and river water four times before samples were taken.

We describe richness patterns and three of the most reported drivers of PhyRich: (i) temperature, as water temperature (WTemp); (ii) total phosphorus (TP), as a proxy of productivity; and (iii) turbidity (Turb) as a proxy of light availability. Because many sites were sampled in lotic systems and the sampling approach did not allow us to assess zooplankton, we did not evaluate the crucial relationships between PhyRich vs. area and grazing, respectively. We focused on the subcontinental (whole country) and regional (hydrographic regions) scales. WTemp and Turb were measured directly on board the hydroplane with a YSI 660 multiparameter water quality probe (Yellow Springs, USA). Phytoplankton samples were fixed with Lugol's solution. Samples for TP were frozen immediately after sampling, using liquid nitrogen. Upon arrival in the laboratory, they were stored at −20 °C and analyzed within 20 days after sampling.

Maps were constructed using ArcMap 10.8 software. Information obtained in the "ANA Metadata Catalog" (https://metadados.snirh.gov.br/geonetwork/srv/por/catalog.search;jsessionid=01A66BC206AAB137A73D5C4F7D761A89#/metadata/0574947a-2c5b-48d2-96a4-b07c4702bbab, accessed in September/21) was used as a reference to delimit the hydrographic regions. The points indicated on the maps (1045 for PhyRich and 1164 for WTemp, Turb, TP) correspond to the sampling sites. For PhyRich, Turb, and TP, we used the manual classification to define the different categories of values, and for WTemp, we used the Jenks Natural Breaks algorithm (Smith et al. 2018).

4.2.3 Analytical Methods

TP concentrations in water samples were analyzed by digestion with potassium persulfate and subsequent colorimetric reaction by ascorbic acid (Valderrama 1981), using a Varian Cary 50 spectrophotometer. PhyRich was assessed by quantifying the species number from single samples per site, using the settling method (Utermöhl 1958) under an inverted microscope (Zeiss Axiovert 10, Oberkochen, Germany). Only two counters analyzed the phytoplankton samples.

4.2.4 Data Analyses

All data obtained (1164 samples) were included for environmental variables and, for regression and GLM analysis, only samples containing phytoplankton data (1045 samples). Trophic states were assessed according to Nürnberg (1996) based on TP concentrations: oligotrophic <10 μg/L; mesotrophic 10–30 μg/L; eutrophic 30–100 μg/L; and hypereutrophic >100 μg/L.

To perform the cumulative species curve at the subcontinental scale (all sample points), we used the estimator Chao 2 (Chao 1987), which includes rare species, as the species number found in one sample (unique) and as the species number found in two samples (duplicates). To compare PhyRich at the regional scale (for each HR), we used the rarefaction method. This allowed us to compare the number of species between communities when the abundance of individuals was not the same (Gotelli and Chao 2013). Rarefaction calculates the expected number of species in each HR, based on a value where all samples reach a standard size, or comparisons based on the community with fewer individuals as a comparative basis. The analyses were carried out in R 4.1.1 (R Core Team 2021). The cumulative species curve was constructed using the vegan package (Oksanen et al. 2020). Sample-based rarefaction curves were performed using the iNEXT package (Hsieh et al. 2016).

We tested the statistical differences of the variables among HRs using the nonparametric Kruskal-Wallis test (Kruskal and Wallis 1952), followed by Dunn's post hoc pairwise comparisons. Statistical analyses were performed in SigmaPlot 12.5 software at the significance level of $p < 0.05$. Turb and TP were $\log_{10}$-transformed before the analysis. To avoid zeros in Turb values, we added 0.2 (lowest observed value) before the $\log_{10}$ transformation.

To describe the pattern of phytoplankton richness along the gradients of WTemp, Turb, and TP, we regressed with a generalized linear model (GLM). We plotted 95% confidence intervals on the fitted function, with the function *geom_smooth* and the generalized additive model (GAM) in the R package *ggplot2*. The significance of the relationship was calculated with GAM function in the R package *mgcv*. We used TP as a proxy for productivity (Ptacnick et al. 2010) and Turb for light availability.

To understand the PhyRich patterns at subcontinental and regional scales, we performed multiple combinations of environmental variables. First, we $\log_{10}$ transformed the data to reduce the dispersion of Turb (plus its minimum value) and TP. Then, from each environmental gradient tested, we removed the variation of the other variables using a generalized linear model (GLM) with a Gaussian error distribution, with the function *glm* in the R package *stats*. We selected models using the Akaike Information Criterion (AIC), with the regression residuals from the first step. For each dataset, we first constructed a full model with all variables (i.e., WTemp, TP, and Turb). Then, the best models, which retained the most information with the fewest variables, were selected using a model selection table based on ΔAICc (difference between the AICc of a given model and the AICc of the best model – Akaike Information Criterion) (Burnham and Anderson 2004), with the function *aictab* in the R package *AICcmodavg*. We also used the Dsquared (D2) model selection, which is the explained deviance of the model expressed as a percentage and is considered a pseudo r^2 of the best-selected model and a measure of model fit (Guisan and Zimmermann 2000).

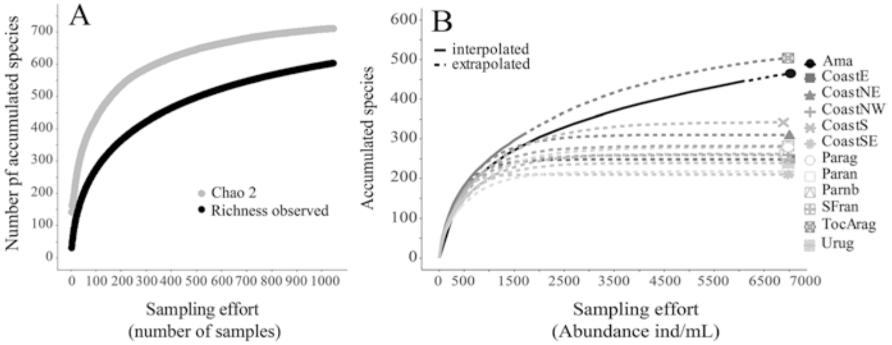

Fig. 4.2 (**a**) Measured and estimated (Chao 2) cumulative species curves for the subcontinental scale ($n = 1045$) in Brazil; (**b**) sample-based rarefaction curves for phytoplankton samples in the 12 hydrographic regions in Brazil. The curves show the observed (interpolated; solid lines) and extrapolated (dashed lines) cumulative phytoplankton species numbers. *Ama* Amazon, *CoastE* coastal east, *CoastNE* coastal northeast, *CoastNW* coastal northwest, *CoastSE* coastal southeast, *CoastS* coastal south, *Parag* Paraguay, *Paran* Paraná, *Parnb* Parnaíba, *SFranc* São Francisco, *TocArag* Tocantins/Araguaia, *Urug* Uruguay

4.3 Results

The combined phytoplankton dataset from the 12 hydrographic regions (HRs) contained 605 species (morphospecies). They belonged to 10 algal taxonomic classes: 102 cyanobacteria, 18 cryptomonads, 22 dinoflagellates, 85 diatoms, 43 chrysophyceans, 10 xanthophyceans, 30 euglenoids, 3 raphidophyceans, 204 chlorophyceans, and 68 zygnematophyceans. Of the total morphospecies, only 20 were observed in at least 1 sample in the 12 HRs. At the continental scale, we observed many rare species; 134 occurred only at 1 site (singletons) and 86 twice (doubletons). Accumulation (Fig. 4.2a) and rarefaction (Fig. 4.2b) curves, both based on Chao 2 estimator, showed no tendency to stabilize at an asymptote. It also estimated the possibility of finding 100 more species with a greater sampling effort. The rarefaction curves did not show differences between the cumulative number of phytoplankton species in the TocArag and Ama HRs. Nonetheless, these two basins showed almost twice as many cumulative numbers of species as the other HRs (Fig. 4.2b).

4.3.1 Phytoplankton Richness

Phytoplankton richness (PhyRich) at the subcontinental scale ranged between 0 and 62 spp./sample, with a median of 10 spp./sample. CoastE and CoastSE showed the significantly lowest PhyRich (median = 3 spp./sample), and TocArag and Urug showed the highest (median = 16 spp./sample; $p < 0.001$; Figs. 4.3a and 4.4a).

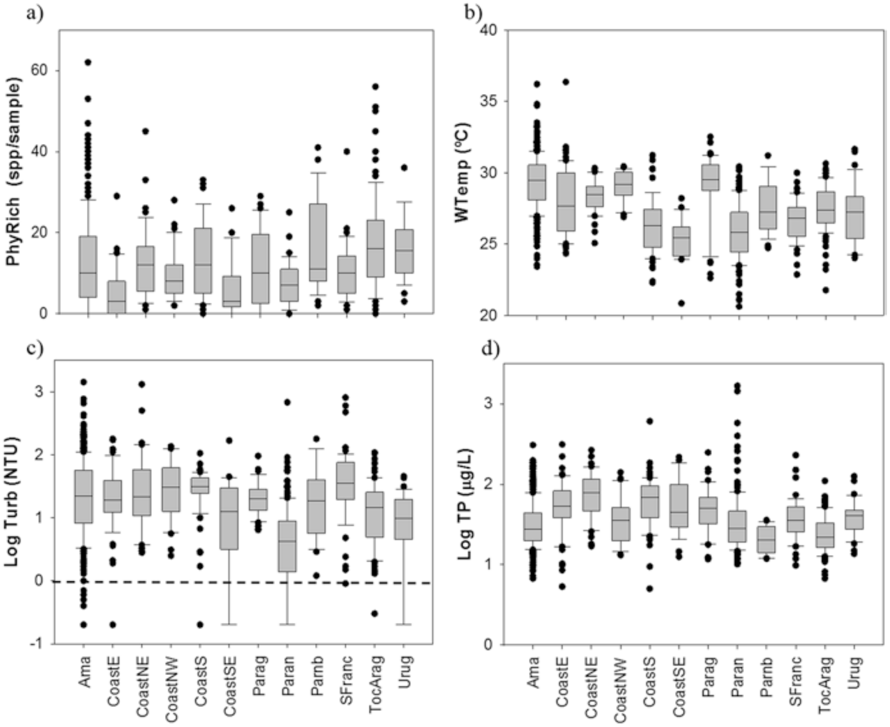

Fig. 4.3 (**a**) Phytoplankton richness, PhyRich; (**b**) water temperature, WTemp; (**c**) turbidity, Turb; and (**d**) total phosphorus, TP, expressed by box-whisker plots, where the horizontal lines inside the box plots indicate the median and the boundaries of the box plots indicate the 25th and 75th percentiles. Whiskers above and below indicate the 90th and 10th percentiles; dots are outliers in the 12 Brazilian hydrographic regions. *Ama* Amazon, *CoastE* coastal east, *CoastNE* coastal northeast, *CoastNW* coastal northwest, *CoastSE* coastal southeast, *CoastS* coastal south, *Parag* Paraguay, *Paran* Paraná, *Parnb* Parnaíba, *SFranc* São Francisco, *TocArag* Tocantins/Araguaia, *Urug* Uruguay

4.3.2 Environmental Variables

Variables described in this section are some of the most often reported to drive PhyRich over a broad spatial scale. WTemp ranged from 20.6 °C (Paran) to 36.4 °C (CoastE). Median values were significantly higher in Parag, Ama, and CoastNW and lower in CoastSE, CoastS, and Paran (Figs. 4.3b and 4.4b).

The range of Turb was between 0.2 (Ama, CoastE, CoastS, Paran, and Urug) and 1429 NTU (Ama). Two hundred and forty-four sites had Turb <5 NTU, 655 from 5 to 50, and 212 > 50 NTU over the subcontinental scale. For the regional scale, median values were highest in SFranc, CoastS, and CoastNW and lowest in Paran and Urug (Figs. 4.3c and 4.4c). Our data also showed that clear waters influenced sampling sites in the Amazon HR (Fig. 4.4c).

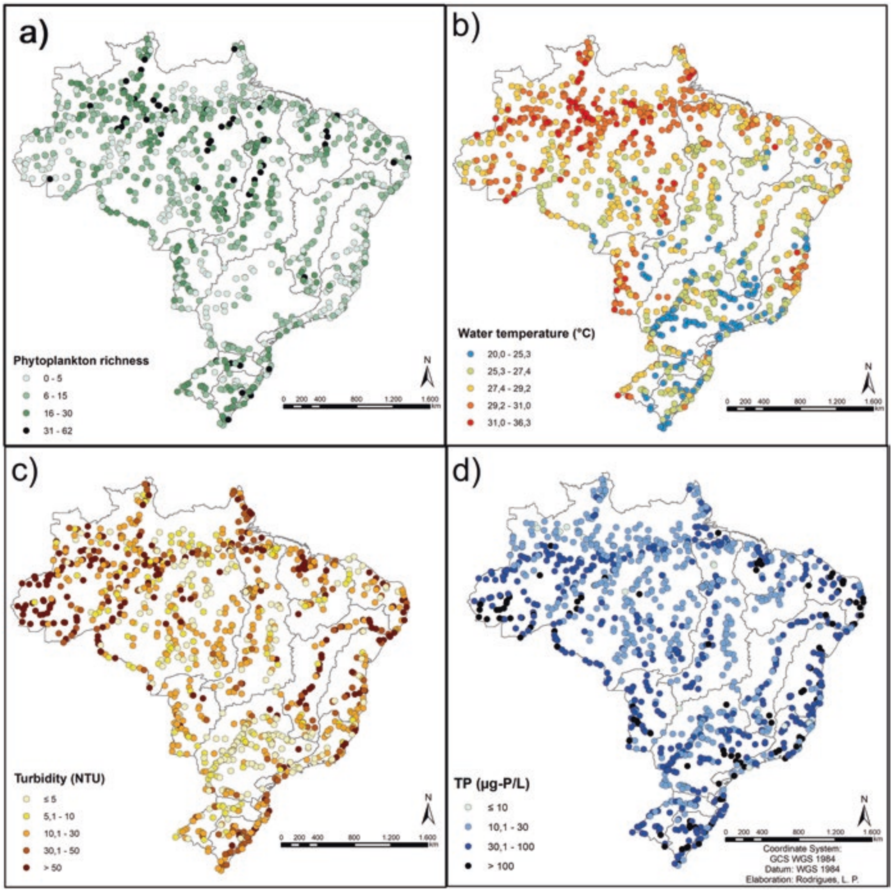

Fig. 4.4 (**a**) Spatial structure of phytoplankton richness, PhyRich; (**b**) water temperature, WTemp; (**c**) turbidity, Turb; (**d**) total phosphorus, TP. Values increase from the lighter to the darker color (*n* = 1045 in **a** and *n* = 1164 in **b, c, d**)

Based on TP concentrations, 21 sites were oligotrophic, 528 mesotrophic, 490 eutrophic, and 109 hypereutrophic. TP concentrations ranged from 5 µg/L in Ama, CoastS, CoastE, SFranc, and TocArag to 1671 µg/L (Paran). Median values were at mesotrophic levels (20.4–28.1 µg/L) in Ama, Parnb, and TocArag. The other nine HRs showed median values at eutrophic levels (35.4–79.2 µg/L; Fig. 4.3d). Furthermore, some sampling sites in the coastal RHs, Paran, and Parag were hypereutrophic (Fig. 4.4d).

4.3.3 Relationships Between Species Richness and Environmental Variables

The univariate relationships between PhyRich and environmental drivers showed different patterns. PhyRich was similar from 20 to ~28 °C, increased to 34 °C, and then decreased slightly to the end of gradient (Fig. 4.5a). PhyRich increased slightly until turbidity ~40 NTU L and then reduced to the end of the gradient (Fig. 4.5b). PhyRich remained similar until TP concentrations ~30 μg/L and then decreased to ~350 μg/L (Fig. 4.5c). At the beginning and end of the WTemp and TP gradients, we observed greater variability at the 95% confidence range.

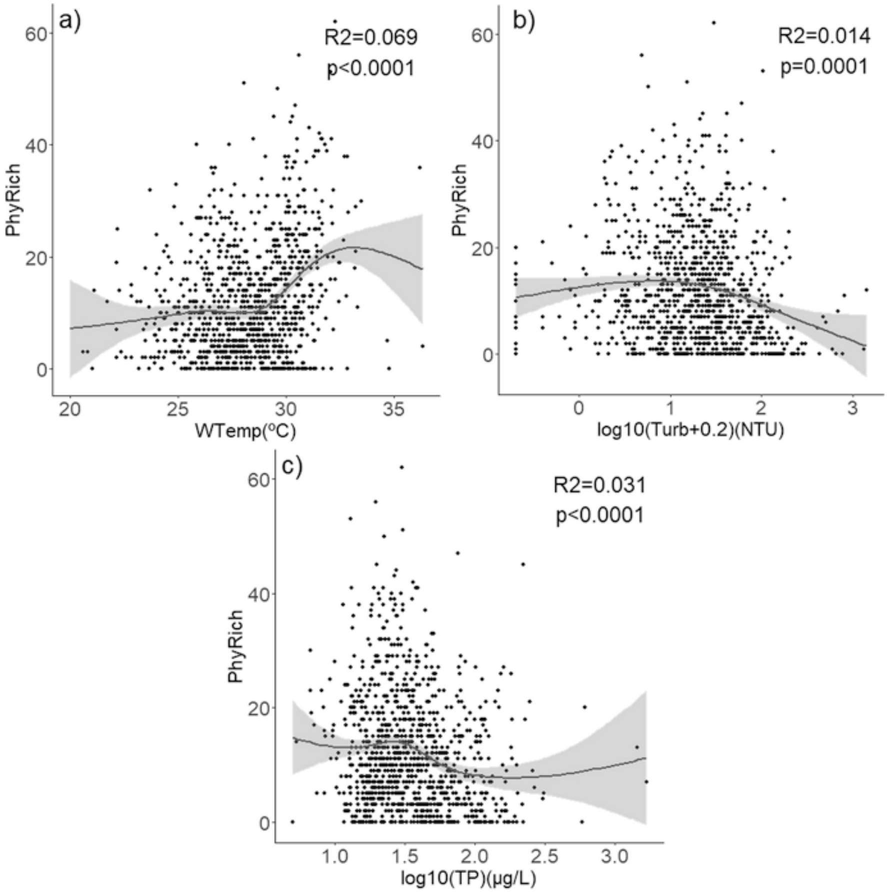

Fig. 4.5 The relationship between phytoplankton richness (PhyRich, taxa/sample) and (**a**) water temperature (Wtemp, °C, $n = 1025$), (**b**) turbidity (Turb, NTU, $n = 1017$), and (**c**) total phosphorus (TP, μg/L, $n = 1045$) obtained by GLMs (Generalized linear model regressions). The gray area is the approximate 95% confidence interval of the fitted function

The full GLM for the subcontinental scale selected WTemp, Turb, and TP (Table 4.2). PhyRich was significant and positively associated with WTemp and negatively with TP and Turb. For the regional scale, the three factors were significant only in the Ama HR, following a similar signal of the entire dataset. WTemp and Turb, both positively, explained the variability in PhyRich in the Parnb HR. In CoastNW, TocArag, and Parag, PhyRich was explained by WTemp as the only significant variable, and Urug and CoastE only by TP.

CoastNW showed the highest PhyRich variance explained by the environmental conditions (D2 = 35.303%), followed in descending order by Parnb (D2 = 31.357%), Ama (D2 = 25.160%), and Urug (D2 = 24.011%). For 5 of the 12 HRs, no model significantly explained PhyRich variability: CoastNE, CoastSE, CoastS, SFranc, and Paran (Table 4.2).

Table 4.2 The selected models for subcontinental and regional scales, where a significant combination of the environmental variables (autocorrelation removed) best explained the variation in phytoplankton richness

Regions	Model	AICcWt	D2	*n*
	Subcontinental scale			
	12.183*** + 1.255 Wtemp*** – 2.606 log(Turb+0.2)*** – 7.586 log(TP) ***	0.999	10.192	1017
	Regional scale			
CoastNW	9.513*** + 2.399 Wtemp** – 6.734 log(Turb+0.2) + 5.890 log(TP)	0.481	35.303	39
Parnb	16.423*** + 3.671 Wtemp* + 10.790 log(Turb+0.2)* + 34.530 log(TP)	0.282	31.357	26
Ama	12.781*** + 2.659 Wtemp*** – 5.806 log(Turb+0.2)*** – 15.518 log(TP)***	1.000	25.160	456
Urug	16.056*** + 0.453 Wtemp +0.662 log(Turb+0.2) – 20.439 log(TP)**	0.560	24.011	36
TocArag	17.302*** + 2.737 Wtemp*** + 3.527 log(Turb+0.2) – 3.768 log(TP)	0.344	14.961	96
Parag	12.318*** + 1.617 Wtemp* – 3.385 log(Turb+0.2) + 0.506 log(TP)	0.541	14.823	44
CoastE	5.217*** + 0.607 Wtemp – 0.199 log(Turb+0.2) – 6.917 log(TP)*	0.395	10.867	69

AICcWt AIC weight for the most parsimonious among the candidate model set, *D2* explained model deviance (%). All ΔAICc were zero. *WTemp* water temperature, *Turb* turbidity, *TP* total phosphorus. PhyRich in the five remaining hydrographic regions was not significantly explained by any variable

Ama Amazon Rainforest, *CoastE* coastal east, *CoastNE* coastal northeast, *CoastNW* coastal northwest, *CoastS* coastal south, *CoastSE* coastal southeast, *Parag* Paraguay, *Paran* Paraná, *Parnb* Parnaíba, *SFranc* São Francisco, *TocArag* Tocantins/Araguaia, *Urug* Uruguay. Signif. codes: ***p = <0.001; **p = <0.01; *p = <0.05

4.4 Discussion

Species richness (PhyRich), the number of morphospecies per site, is a primary measure of biodiversity in ecosystem functioning studies. The main factors shaping the broadscale patterns of PhyRich are temperature, system area, productivity, and, less often assessed, light, flushing, and grazing (Litchman 1998; Train and Rodrigues 1998; Smith et al. 2005; Nabout et al. 2007; Smith 2007; Muylaert et al. 2010; Weyhenmeyer et al. 2013; Vallina et al. 2014). Here, we evaluated PhyRich along with three of these gradients: temperature, productivity (total phosphorus as a proxy), and light availability (turbidity as a proxy). Our dataset is unprecedented in its broad spatial scale and inclusion of difficult-to-reach sites in Brazil. We hypothesized that PhyRich increases with water temperature and light availability (i.e., decreases with turbidity) and increases at intermediate productivity levels. Our hypotheses were partially confirmed since our broad spatial scale study showed that PhyRich was positively related to Wtemp and negatively to turbidity (lower light availability) and TP. Regarding the productivity gradient, PhyRich remained similar under oligo- and mesotrophic conditions, approximating the expected unimodal relationship. On a regional scale, we observed similar tendencies: for temperature, PhyRich initially increased to 34 °C and then slightly decreased; for turbidity, it smoothly increased until ~40 NTU and then decreased to the end of the spectrum; and for total phosphorus, it remained similar from 5 to 30 μg/L and then decreased until ~350 μg/L.

Phytoplankton is a highly diverse group composed of 10,000 to 25,000 extant species in marine and freshwater ecosystems (Sournia et al. 1991; Falkowski et al. 2004; Vargas et al. 2015). The 605 morphospecies found here comprise about 17% of the total number of freshwater phytoplankton species (~4000 spp.; Reynolds (2006). On our subcontinental scale, the most important major taxonomic groups were chlorophyceans and cyanobacteria, followed by zygnematophyceans, comprising ~60% of the total morphospecies. Of this total, only 20 (3%) were found in at least one sample in the 12 HRs. On a large scale, common species drive the species richness patterns (Jetz and Rahbek 2002; Lennon et al. 2004; Vázquez and Gaston 2004) because the richness of common species is more closely related to environmental variations than the richness of rare species (Jetz and Rahbek 2002; Kreft et al. 2006; Rahbek et al. 2007). Despite the extensive sampling program, we found no trend for the cumulative species curve to stabilize at an asymptote. With a greater sampling effort, we estimate that 100 more species could be found. The role of rare species in communities has been widely discussed through maintaining ecosystem processes and perhaps as a hidden driver of microbiome function (e.g., Jain et al. 2014; Mouillot et al. 2013; Jusset et al. 2017; Säterberg et al. 2019). However, the role of these species remains controversial because it may vary with local abundance, habitat specificity, and geographical spread (Rabinowitz 1981). The role of rare species can also be interpreted as complementarity or redundancy of the specific function. Some authors have suggested that rare species have low functional redundancy and are likely to support the most vulnerable ecosystem functions, with no other species carrying similar trait combinations. Rarity can result from different mechanisms, such as stochastic processes, inherent trade-offs in life-history strategies, and biotic and abiotic interactions (Jusset et al. 2017). On our subcontinental scale, of the 605 species, 22% were singletons and 14% doubletons.

The lowest PhyRich on our subcontinental scale – algae not detected by the method employed – occurred in ~10% of the samples, mainly in Ama (Amazonas main system, Madeira and Purus rivers) and CoastE HRs (Doce River). The highest PhyRich (62 species/sample) was found in a floodplain lake in the Ama HR (Xingu River watershed). Floodplain lakes are usually rich in phytoplankton species due to their strong interaction with the floodplain, modulated by the regular pulse of the hydrometric level, such as in the TocArag (Nabout et al. 2007) and Ama HRs (Huszar and Reynolds 1997; Cardoso et al. 2017).

The univariate relationships between PhyRich and the selected environmental drivers showed different patterns. On our subcontinental scale, the water temperature range was relatively narrow (20.6 to 36.4 °C). Despite this somewhat limited range, we found an increase of PhyRich with increasing temperature. PhyRich remained steady at the beginning of the gradient and then increased as the temperature rose to 34 °C. This finding contradicts the view that the low amplitude of temperature and irradiance through the entire annual cycle in tropical systems allows a permanently high biological activity, i.e., the alleged “endless summer” (Kilham and Kilham 1990). Even in warmer climates, the temperature matters and influences phytoplankton responses in tropical systems (Lewis 1987, 1996; Sarmento 2012; Silva et al. 2014; Rangel et al. 2016).

The positive influence of temperature as a determinant factor for diversity is well recognized in macroorganisms (Allen et al. 2002; Currie et al. 2004; Mittelbach et al. 2007). Particularly for phytoplankton, the temperature is among the major factors acting directly on growth rates and nutrient stoichiometry and indirectly on the lake mixing regime, shaping the spatial and temporal distribution of populations in freshwater systems (Schabhüttl et al. 2013; Kruk et al. 2017). Several phytoplankton studies have shown positive relationships between species richness and temperature (Ptacnick et al. 2010; Weyhenmeyer et al. 2013; Thomas et al. 2012; Kruk et al. 2017). This finding agrees with the metabolic theory of ecology, where a larger flow of energy in the food chain increases the productivity of systems and consequently the availability of resources, enabling more species to coexist (Hawkins et al. 2003; Segura et al. 2017). Temperature acts as an essential selective agent in species adaptation, influencing the occurrence of certain functional traits and maximizing their performance and maintenance in the system (Thomas et al. 2012; Schabhüttl et al. 2013).

Our models also indicated that temperature was essential to explain PhyRich at the regional scale, particularly for HRs above latitude 20°S (Ama, CoastNW, Parnb, TocArag, and part of Parag). Water temperature was positively related to PhyRich, but the largest increase was observed between 28 and 34 °C, with a tendency to decline in higher temperatures. However, the slight decrease at the end of the spectrum was driven by only three lotic sites with high temperatures and low PhyRich, located in the CoastE (Jequitinhonha River) and Ama (Negro River) HRs.

Besides temperature, light availability is another critical factor, favoring growth and increasing the number of available niches (Weyhenmeyer et al. 2013). The relationship between light and PhyRich remains controversial, but there is some convergence toward a decrease of PhyRich with decreasing light (Weyhenmeyer et al. 2013; Zhang et al. 2018), although Litchman (1998) found a reduction of PhyRich at both low and high light levels.

Turbidity, as a proxy for light availability, was an essential factor for explaining PhyRich, mainly on our subcontinental scale. PhyRich smoothly increased until turbidity was ~40 NTU and then decreased toward the end of the spectrum (~1000 NTU). The highest PhyRich at the intermediate levels may be linked to the productivity gradient based on the photoinhibition process. High light availability in clear water and low nutrient conditions are on one side of the gradient. On the other, turbid water promotes self-shading conditions in enriched waters (Zhang et al. 2018). On both sides, PhyRich was lower, as experimentally shown by Litchman (1998), who found a decrease of PhyRich in treatments with high and low light availability. At low light intensities, species that disappeared had low initial densities and low growth rates, explaining their exclusion. With high light availability, species had high growth rates, and some species may have been competitively excluded (Litchman 1998).

Our models indicated a decrease in PhyRich with increasing turbidity at the subcontinental scale and the Ama HR at the regional scale. The negative relationship in the Ama HR may be related to the broad spectrum of turbidity. One of the factors contributing to the increase in turbidity in this HR is the flux of suspended matter transported by the Amazon River to the ocean and the Andean contributions, transported mainly by the Solimões and Madeira rivers (Abe et al. 2006; Silva et al. 2013). On the other hand, waters draining the old Precambrian terrains have low suspended-matter content (Junk et al. 2011). Random field data may explain the positive relationship between PhyRich and turbidity in the Parnb HR since high PhyRich values were observed in samples from less- or more-enriched sites and with a wide variety of turbidity values. For example, in the eutrophic Parnaíba River, the smallest and largest PhyRich values (0 and 18 spp., respectively) were observed, with Turb between 13 and 603 NTU. Higher PhyRich values were observed in conditions of intermediate light availability and may be related to different niches provided by variations in light availability in the water column. Since light incidence decreases with increasing depth, different species have various light absorption capacities. Besides, light availability was not significantly related to PhyRich in any other HR.

In addition to temperature and light availability, productivity is essential for explaining PhyRich variability. Over our sizeable total phosphorus gradient (5–1671 μg/L), used as a proxy of productivity, 45% of the sites were mesotrophic and were primarily located in HRs where more pristine areas occur (Ama, Parnb, and TocArag); and 42% were eutrophic and located mainly in the other nine HRs. The remaining sites were hypereutrophic (~10%), located in the most populated and agricultural areas (coastal RHs, Paran, and Parag), and oligotrophic (~3%), sparsely distributed in all HRs except CoastNE and Urug.

Over large gradients, unimodal patterns of PhyRich have been observed (Dodson et al. 2000; Smith et al. 2005; Stomp et al. 2011), but some positive (Korhonen et al. 2011; Weyhenmeyer et al. 2013), negative, or nonsignificant relationships (Smith 2007) can occur over smaller gradients. This apparent contradiction has been attributed to the scale of a productivity gradient and synergy with other environmental factors (Smith et al. 2005; Cermeño et al. 2013; Rodríguez-Ramos et al. 2015; Zhang et al. 2018). Over our wide productivity gradient at the subcontinental scale, PhyRich was negatively related to productivity, remaining similar in oligo- and mesotrophic conditions (TP concentrations <30 μg/L) and decreasing toward eutrophic and hypereutrophic waters (~350 μg/L), approximating the expected unimodal relationship. The competition for resources explains the lower species richness at the extremes of the productivity gradient, with low productivity on the one hand and limitation by light in highly productive systems on the other (Zhang et al. 2018).

At the regional scale, PhyRich tended to decrease with increasing trophic states in Ama, Parnb, and TocArag, the HRs with the highest proportions of relatively pristine areas and with lower human population densities (see Table 4.1). In Ama, sites with high Turb and TP concentrations are primarily of natural origin, resulting from the weathering of rocks in the Andes where their sources are located (Abe et al. 2006; McClain and Naiman 2008; Almeida et al. 2015). These rivers exert a significant influence on the concentration of fine P-rich suspended sediments in the Amazon basin. The good water conditions in TocArag and Parnb, with low population densities (Moss and Moss 2005), may explain the high PhyRich.

On the other hand, the Paran and coastal regions, except CoastS, showed a trend toward lower PhyRich and high Turb and TP concentrations. These densely populated regions have poor sanitation and extensive agricultural and industrial areas (Moss and Moss 2005; Abe et al. 2006). The CostS and Parag HRs showed relatively high PhyRich. Notably, CoastS was also marked by high concentrations of TP due to the extensive agricultural areas with heavy use of fertilizers, as well as areas where the high TP concentration may be related to natural enrichment processes due to the influence of a large community of migratory birds that feed in these systems (Moss and Moss 2005). In the Parag HR, the high TP concentrations may be due to the low percentage of treated sewage and the influence of extensive cultivation areas, mainly soybean and cotton, as well as intensive livestock ranching (Abe et al. 2006). At some sites in Parag, high TP concentrations may also be of natural origin; in that region, the many bird roosts on the riverbanks can significantly contribute to phosphorus input (Moss and Moss 2005; Abe et al. 2006).

Over our wide TP gradient, the high data variability within the same hydrographic region may explain the D2 values of our results. Furthermore, the causality of field data, bias from potential unmeasured variables, and the inherent chaotic behavior of phytoplankton communities must be considered to explain the PhyRich results (Beninca et al. 2008; Kosten et al. 2012). Despite this, we still observed higher PhyRich at sites with intermediate concentrations. In low TP concentrations, competition for resources may explain the lower PhyRich. In contrast, at sites with high TP concentrations, light limitation due to either high phytoplankton biomass or high concentrations of other solids in suspension may have determined the lower

PhyRich. Massive phytoplankton blooms, especially cyanobacteria, can accumulate in surface waters, reducing light availability to other phytoplankton species and thus biodiversity (Chorus et al. 2000; Smith 2003; Huisman et al. 2018; Zhang et al. 2018). The negative relationship between PhyRich and Turb in Ama may be related to the high correlation of TP with the fine suspended sediments transported from the Andes to Amazonian rivers (Devol et al. 1995; Abe et al. 2006). For 5 of the 12 HRs, no model significantly explained PhyRich variability (CoastNE, CoastSE, CoastS, SFranc, and Paran).

In summary, by combining the variables that best described the PhyRich patterns on subcontinental and regional scales, WTemp most frequently explained PhyRich. On our subcontinental scale, PhyRich was positively related to water temperature and negatively to turbidity (lower light availability) and productivity, although PhyRich was similar in oligo- and mesotrophic conditions, approaching the expected unimodal relationship. Furthermore, we observed a tendency toward a slight reduction in the univariate models at the end of all gradients, with implications for the ecological functioning of freshwater systems.

Across a subcontinental scale, these findings contribute to a better understanding of how the environment affects phytoplankton species richness, with implications for their ecological functioning in freshwater ecosystems. In addition, our data include information from locations that have never been reached previously, many of them in a pristine state of conservation, serving as a reference for future studies that enable the identification of impacts in these areas.

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