



Drivers of planktonic chlorophyll *a* in pampean shallow lakes

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ARTICLE INFO

Keywords:

Phytoplankton biomass
Shallow lakes
Total phosphorus
Submerged macrophytes
Agriculture
Regional

ABSTRACT

Although agricultural intensification has been linked with the increment of lake eutrophication and shallow lake research has demonstrated the importance of submerged macrophytes for maintaining water clarity, less is known about the role of macrophytes and the effects of agriculture on shallow lakes of the global south. Shallow lakes in the Pampean region of Argentina are subjected to high anthropic pressure and are classified as eutrophic and hypereutrophic and, in spite of most of them are turbid and dominated by phytoplankton biomass, some remain in a clear-vegetated regime with profuse submerged macrophytes. We studied the potential drivers of phytoplankton biomass (estimated as Chlorophyll-*a* - Chl*a*) by applying a regional approach and a model selection process for a dataset of 58 shallow lakes that represent the variability of the Pampean region. For the 58 lakes, the presence of submerged macrophytes, total nitrogen, and nearby agriculture of each lake were the main drivers of Chl*a* with -1.55 , 0.19 and 0.02 coefficient values, respectively. Moreover, a high proportion of the variance in this dataset (37.7%) was explained by the regional location of each lake (hydrographic systems). For lakes with macrophytes ($N = 8$), Chl*a* exhibited a positive relationship with total phosphorus (coefficient value = 3.05), whereas for lakes without macrophytes ($N = 50$) Chl*a* showed a positive relationship with nearby agricultural development (coefficient value = 0.02) and 36.4% of variance explained by the hydrographic system. Our regional approach highlighted the importance of submerged macrophytes in shaping phytoplankton biomass in Pampean shallow lakes. Our results support the idea that the conservation of submerged macrophytes, as well as the control of agriculture in the riparian zones of lakes, will help to stabilize the shallow lakes in clear regime, even in regions highly impacted by agriculture and in lakes under eutrophic conditions.

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<https://doi.org/10.1016/j.ecolind.2022.109834>

Received 3 October 2022; Received in revised form 14 December 2022; Accepted 20 December 2022

Available online 24 December 2022

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1. Introduction

In the last decades, there have been large-scale changes in nutrient cycles mainly due to additional inputs from fertilizers, livestock and human wastes, and biomass burning (MEA, 2005). All of these changes have increased the nutrient loading to inland waters, intensifying the eutrophication process (e.g. Moss, 2008, Anderson et al., 2014). Concerns about eutrophication's impact on freshwater bodies have led to the empirical study of relationships between planktonic algal biomass, measured as chlorophyll *a* (Chla), and total phosphorus (TP) (e.g., Sakamoto, 1966, Dillon and Rigler, 1974, Carlson, 1977, Smith and Shapiro, 1981, Havens and Nürnberg, 2004, Yuan and Jones, 2020) as well as the design and implementation of different management strategies to alleviate eutrophication (Jeppesen et al., 2007).

Many of these studies predicted the effect of the increase of TP loading on Chla, and TP was often considered to be the limiting factor of Chla, exhibiting a wide range of coefficients values and different shapes of response curves (e.g. Vollenweider, 1968, Dillon and Rigler, 1974, Chapra and Tarapchak, 1976, Jones and Lee, 1986, Stauffer, 1991, Yuan and Jones, 2020, Quinlan et al., 2021). Some studies additionally focused on assessing the changes in TP:Chla ratio as a way to estimate the transfer efficiency between TP and phytoplankton biomass and to infer the response of phytoplankton to diminishing TP loads (Spears et al., 2013). Other authors have proposed additional factors that play roles in the eutrophication process and should be included as predictor variables in these models (Smith and Shapiro, 1981). For instance, total nitrogen (TN) and/or the TN:TP ratio have been reported as factors limiting the biomass of primary producers in some systems and were incorporated into the models as predictor variables (Smith, 1982, Prairie et al., 1989), as well as watercolor, mixing regimes (Havens and Nürnberg, 2004), depth, water residence time (Vollenweider, 1975, Pridmore et al., 1985, Phillips et al., 2008, Spears et al., 2013) and alkalinity (Phillips et al., 2008, Spears et al., 2013, Hammer et al., 2019). Water transparency measured as Secchi depth has also been reported as a factor influencing the TP:Chla relationship (Quinlan et al., 2021).

However, some of these driving factors of Chla and TP:Chla relationships differ when the studies are focused on shallow lakes, or when examining lakes across large spatial extents. For example in clear shallow lakes, the dominance of submerged macrophytes exerts a negative effect on Chla by different mechanisms (e.g. competition with phytoplankton, reduction of turbulence, refuge for zooplankton) (Scheffer et al., 1993), therefore leading to deviations from the expected positive linear TP:Chla relationship (Quinlan et al., 2021).

In recent years, a regional perspective has been developed that incorporates a multiscale and hierarchical approach to limnological studies (Soranno et al., 2015). As conceptualized by Soranno et al. (2009, 2010) in their landscape-context framework, the hierarchical organization of different components can be illustrated as follows: the geological characteristic of a region influences the type of soils and the morphometry of a lake (terrestrial features), and these components interact with the connectivity among lakes (aquatic features) and with the land uses in the catchment (human features), which overall determine the limnological characteristics of a lake. Studying the multiscale drivers and hierarchical organization of local and regional drivers (aquatic, terrestrial and human landscape features), helps us understand broad-scale variation in physical, chemical or biological characteristics of lakes (Soranno et al., 2009). In recent decades, new statistical tools offer ways to deal with spatial and/or temporal dependence among data (Beckerman 2014), as well as the analysis of different components acting and interacting at different scales (Soranno et al., 2014). Thus, the incorporation of a regional approach allows us to have a more complete picture of the system and to analyze the interaction of factors that directly or indirectly affect phytoplankton biomass (Taranu and Gregory-Eaves, 2008). Applying such a landscape perspective, studies have found that variables acting at a regional scale (e.g., climatic factors; Carvalho et al., 2011) or the percentage of different *land use and land*

cover (LULC) types in the watershed of the lakes (e.g. agriculture, wetland, urbanizations; Wagner et al., 2011, Filstrup et al., 2014; Cheruvilil et al., 2022) have been described as important variables affecting the relationship between TP and Chla.

Although statistical models are very useful tools for understanding the main factors that influence limnological characteristics, several different functional and ecological metrics are needed to understand and predict changes in lake characteristics (Spears et al., 2013). This fact can result in complex models circumscribed for a certain group of lakes in a specific region (Havens and Nürnberg, 2004, Phillips et al., 2008). Additionally, most limnological models are based on datasets from oligotrophic, deep, and dimictic lakes from the northern hemisphere and it is known that these models are not applicable to other types of lakes in different regions (Baigún and Marinone, 1995, Reynolds, 2006, Zhang et al., 2015, Špoljar et al., 2017), such as the eutrophic polymictic shallow lakes considered in this study. For example, Phillips et al. (2008) found that above 100 $\mu\text{g L}^{-1}$ of TP – a similar range to our study lakes – there exists an inflection point in the relation of Chla vs TP with a marked reduction in the slope of the linear regression while Prairie et al. (1989) reported an asymptotic behavior around 100 $\mu\text{g L}^{-1}$ of TP. Therefore, other factors are acting as drivers of Chla when phosphorus is not limited. Moreover, models applied to large numbers of temperate shallow lakes are still scarce (Borics et al., 2013, Ginger et al., 2017; but see Cheruvilil et al., 2022), despite being the most numerous lentic water bodies distributed worldwide (Downing et al., 2006). Therefore, it is essential to develop models to understand the drivers of Chla in these Pampean shallow lakes, which belongs to the south hemisphere and in spite they are very numerous and ecologically relevant, are underrepresented in global models.

The Pampean Plain, a very productive region located in the central part of Argentina (South America), is an extensive wetland landscape where shallow lakes are the dominant aquatic ecosystems. Most of them are eutrophic or hypereutrophic (Diovisalvi et al., 2015) and have experienced a progressive eutrophication due to increasing loads of nutrients from anthropogenic activities (e.g. cattle breeding, agriculture and urban discharges) (Quirós et al., 2002a, 2006, Izaguirre et al., 2022). In the last decades, an intense process of changes in the LULC of the region has occurred, mainly due to an increase in the area dedicated to agriculture (Ríos Satuf 2013). These changes are accelerated because of the expansion of industrial agriculture, with the implementation of genetically modified crops and the use of huge amounts of agrochemicals associated with them (Viglizzo et al., 2010, Castro Berman et al., 2018). Shifts in shallow lakes from clear-vegetated to phytoplankton-turbid regimes have been described over the last 20 years (Quirós et al., 2006, Kosten et al., 2012, Sánchez et al., 2015, Izaguirre et al., 2022). Currently, most lakes are in a phytoplankton-turbid regime; however, there are still regions where some lakes remain in a clear-vegetated state, with a profuse abundance of submerged macrophytes.

Although most Pampean shallow lakes are eutrophic and hypereutrophic, they show high variability in terms of their phytoplanktonic biomass. Therefore, the main drivers of Chla in these aquatic systems remain unknown. Our main objectives are to: 1) investigate the relationship between phytoplankton biomass (as estimated by Chla) and TP; 2) identify the main drivers of phytoplankton biomass in shallow lakes; and 3) explore how the presence of submerged macrophytes might alter the drivers of Chla in these shallow lakes with high nutrient concentrations. In order to achieve these objectives, we applied a regional perspective and a modeling approach with a data set of 58 shallow lakes located across 250,000 km^2 of the Pampean Plain and limnological and landscape factors operating at different spatial scales.

2. Methods

2.1. Study area

The 58 studied shallow lakes represent the heterogeneity of those

located in the Pampean Plain (33°–39°S, 57°–66°W), the central area of Argentina (Fig. 1). This region represents one of the largest wetland areas of South America (Quirós, 2005). This is a heterogeneous geological and geomorphological area, with formations that can be dated back to the Precambrian-Paleozoic or Cenozoic-late Holocene eras (Zárate and Rabassa, 2005), although the area's shallow lakes have a more recent origin (Diovisalvi et al., 2015). The modern landscape, characterized by dune fields, floodplains, fluvial valleys and lake systems, was originated during the last 10,000 years (Zárate and Rabassa, 2005) and contains nutrient-rich soils composed mainly of loess (Rodrigues Capítulo et al., 2010). According to the classification of Giraut et al. (2003), at least 15 hydrological systems can be distinguished within this region, all characterized by a very low regional slope and drainage densities (Sala et al., 1983, Kruse and Laurencena, 2005). Mean annual air temperatures in the region range from 20 °C in the northeast to 14 °C in the southwest (Viglizzo and Frank, 2006), with a characteristic temperate-humid climate (Burgos and Vidal, 1951). The mean annual rainfall average is 935 mm (Iriondo and Drago, 2004), ranging from 1000 mm in the northeast to 400 mm in the southwest (Viglizzo and Frank, 2006). The mean annual wind speed is around 10 km h⁻¹ and the prevailing wind directions are N and NW (Diovisalvi et al., 2015). In this region, there are around of 13,800 large and 146,000 small shallow lakes (Geraldini et al., 2011). Most of them are in turbid regime, with high phytoplankton biomass (Allende et al., 2009). Shallow lakes that remains in clear-vegetated regime are dominated by different species of submerged vegetation as *Ceratophyllum demersum* and *Myriophyllum* sp. (Pérez et al., 2010, Sánchez et al., 2017).

2.2. Dataset curation

The original data set was composed of local (limnological and morphometric) and regional (landscape) variables from 58 shallow lakes, some of which were sampled more than once (N = 102; Table S1). We subset this data set to include values from sampling conducted during the warm seasons from September 2015 to March 2019 for each shallow lake. Data were obtained from a combination of published papers (Castro Berman et al., 2018, Schiaffino et al., 2019, 2020, Sánchez et al., 2021, O'Farrell et al., 2021, Izaguirre et al., 2022, Baliña et al., 2022) and existing data that have yet to be published (Table S1). Since data came from multiple projects, we started by reviewing metadata and performing a homogenization of units. We calculated the mean value for each variable and for each lake, resulting in a data set corresponding to 58 lakes located within 7 different hydrographic systems (hereinafter "Subregions") within the Pampean Plain (Giraut et al., 2003) (Fig. 1). The data set, and their corresponding sources are presented in Supplementary material Table S1.

2.3. Limnological variables

The limnological variables included were: Chl_a, TP, TN, pH, Conductivity, Dissolved Oxygen (DO), Turbidity, Total Suspended Solids (TSS), Percentage of Inorganic Material (Perc_Inorg) and Water Temperature. For chemical determinations, methods described in APHA (2009) were followed; details of the methodology used for the measurements of the limnological variables were published in previous papers (Schiaffino et al., 2019; O'Farrell et al., 2021). Based on field observations and visual exploration (Google Earth®), we classified the shallow lakes according to the dominance or not of submerged

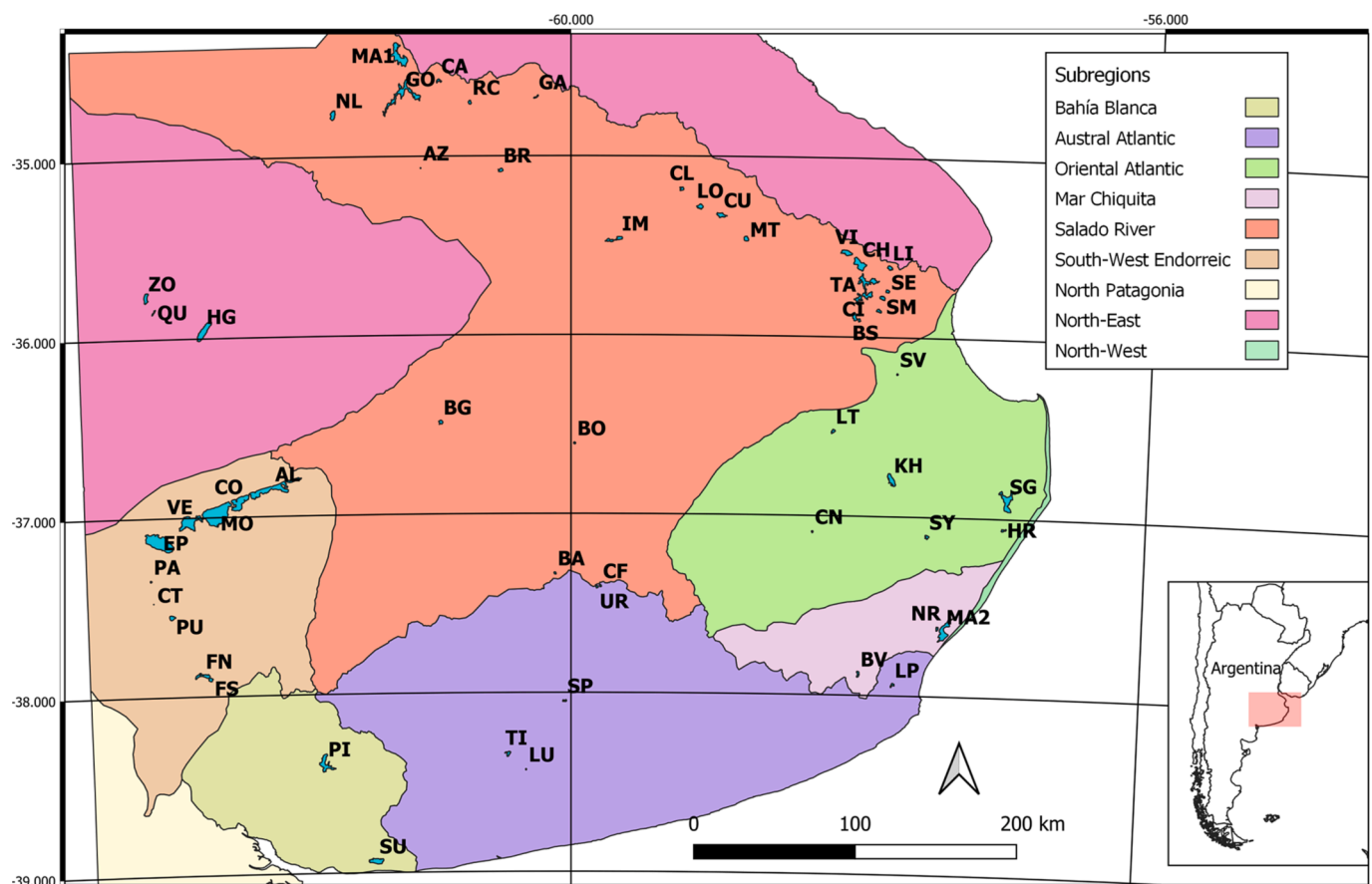


Fig. 1. Map of the Pampean plain with the 58 selected shallow lakes and their codes. See Supplementary Table 1 for names and geographic position. Each color represents a different subregion according to the classification of Giraut et al. (2003).

macrophytes. Presently, only a few shallow lakes in the study extent are in a clear vegetated regime (Izaguirre et al., 2022) and our dataset includes only 8 lakes in this condition. This information was included as a categorical variable indicating presence or absence of submerged macrophytes.

2.4. Morphometric variables

Morphometric variables were retrieved with QGIS using a raster layer of Google satellite corresponding to the region as a base (<https://www.google.cn/maps/>). We created a “shape” file containing polygons describing the shape of each lake. With the polygon shape file, we estimated the Lake Area and Lake Perimeter of each shallow lake.

Catchment area for each lake was extracted from the shape file “Cuencas Hidrográficas Etapa I SSRH” (<http://gis.ada.gba.gov.ar/gis/>) and we calculated Drainage Ratio as the catchment area/lake area. However, these catchments were very large and often included more than one study lake (i.e., network watersheds). Therefore, we also calculated the 1000 m buffer around each lake, which can be a proxy for the local lake watershed (Soranno et al., 2015).

Since several lakes in the region are interconnected, we included the categorical variable “Chain” to indicate that a lake was connected directly to other lakes (1) as opposed to not connected in chain (0). We also estimated surface water connectivity using visual inspection of satellite images and creating a categorical variable as follows: 0-isolated lake (not connected), 1-stream leaving lake (only with outlet), 2-stream

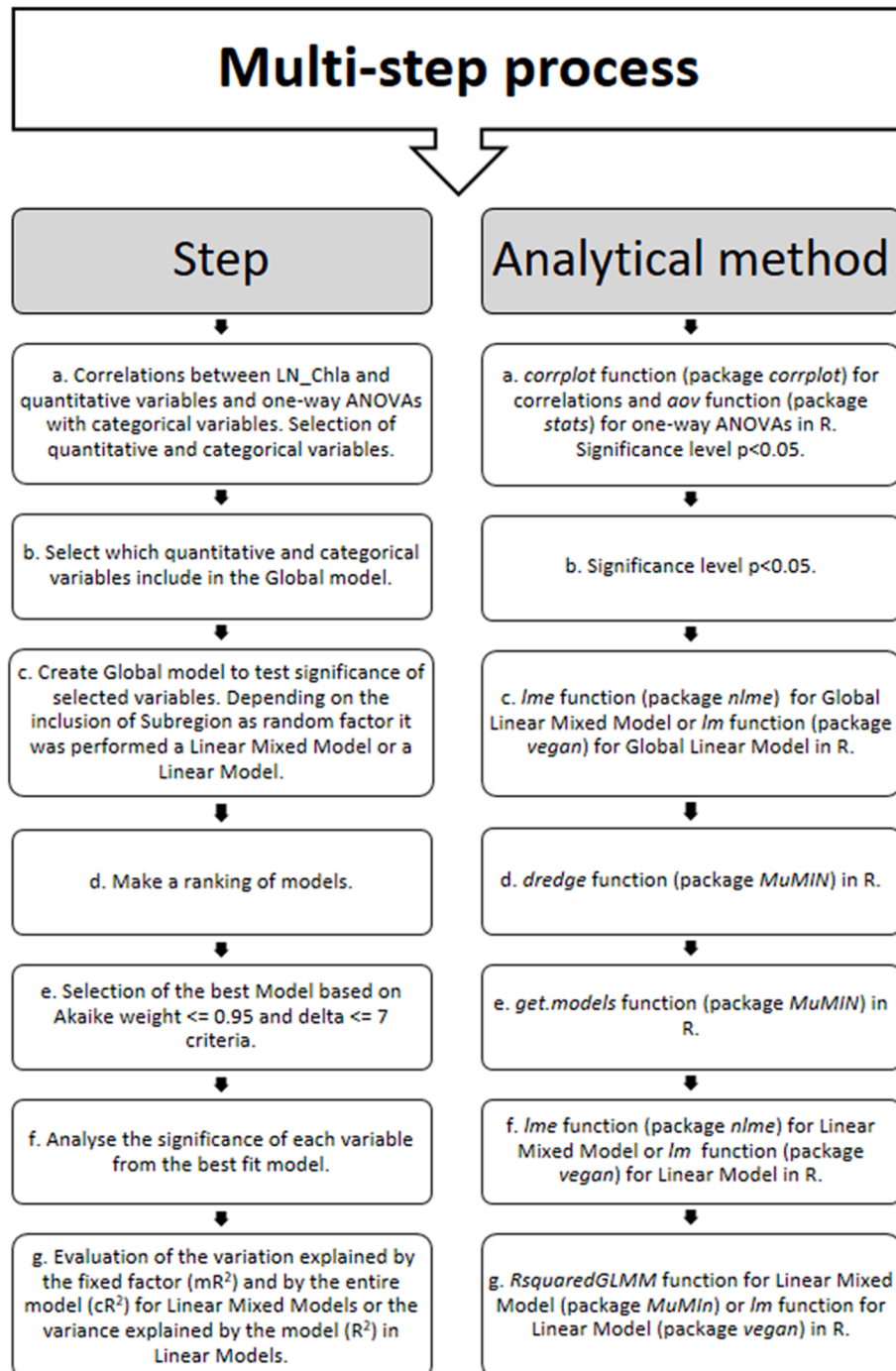


Fig. 2. Diagram of the steps and analytical method followed in the process of model selection. LN_Chla: LN_chlorophyll *a*.

into lake (only with inlet), 3-streams in both directions (with both and inlet and outlet).

2.5. Landscape variables

The landscape variables included were Subregion Membership (Subregion) and measures of LULC using an available LULC map for the region (de Abelleira et al., 2019). Using the 1 km buffer around each lake, we extracted the Percentage of Agriculture (Perc_Agr) from the raster file of the LULC map. These analyses were performed with the software QGIS (v3.12.2). We also created a categorical variable, by visual exploration of satellite images, to describe the presence (1)/absence (0) of any urbanization on the shore of each lake.

2.6. Data analysis

We used a multi-step process to meet our objectives (Fig. 2). Previously, we transformed response and predictor variables, if necessary to meet statistical requirements. Then, we performed Pearson correlations and One-way ANOVAs for continuous and discrete predictor variables, respectively, at local and regional scales to preselect variable candidates that could be influencing phytoplankton biomass for inclusion in the model selection process (Fig. 2, step a). We included in the global model those variables that resulted in significant correlations or were statistically significant ($p < 0.05$) with LN_Chla (Fig. 2, step b). Next, we created a Global Model, applying Linear Mixed Models or Linear Models (depending on the inclusion of Subregion as a random factor) with LN_Chla as our dependent variable (Fig. 2, step c). Then, we performed a model selection process by applying the function *dredge* to make a ranking of potential models from the Global model (package MuMIn) (Burnham and Anderson 2002) based on their AICc (Akaike Information Criteria ccc) which is a measure of the goodness of fit of each model (Fig. 2, step d). After that, we selected the best model(s) using the function *get.models* (package MuMIn) that established a subset of models using criteria of Akaike weight ≤ 0.95 and $\Delta AICc \leq 7$ (Gutiérrez-Cánovas and Escribano-Ávila, 2019) (Fig. 2, step e). The inclusion of Subregion membership as a random factor in the models was evaluated by the percentage of variance explained by this variable. If this value was higher than 20 % we included it in the final model. Then, we selected the best fit model by analyzing the significance of each variable using the function *lme* (package nlme) or *lm* (package stats) depending on whether we included Subregion as a random factor or not in the model, respectively (Fig. 2, step f). If we have two or more model candidates to be selected as the best one, we also evaluated the variation explained by the fixed factor (marginal R^2) and by the entire model (conditional R^2) in the case of linear mixed models with the function *R.squaredGLMM* (package MuMIn) or the variance explained in linear models (R^2), for those models that did not include Subregion (Fig. 2, step g).

To explore how the drivers of phytoplankton biomass differ depending on the presence or not of submerged macrophytes in the lakes, we split our data set into lakes with ($N = 8$) and without ($N = 50$) submerged macrophytes. We repeated the process of model selection (Fig. 2) and selected the best fit model for each subset of lakes. All these analyses were performed in R (version 4.1.0) and RStudio (version 1.4.1717).

3. Results

3.1. Limnological characterization

Most of the 58 studied lakes (Table S1) are eutrophic or hyper-eutrophic according to their Chla, TP and TN mean values (Table 1). Chla ranged from 1.6 to 242.7 $\mu\text{g/L}$, TP from 57.5 to 4538 $\mu\text{g/L}$ and TN from 960 to 8422 $\mu\text{g/L}$. All the studied lakes are alkaline ($\text{pH} = 8.1\text{--}9.4$), with conductivity ranging from 0.3 to 202.1 mS cm^{-1} and are generally

well-oxygenated (mean $\text{DO} = 9.8 \text{ mg L}^{-1}$, ranging from 4.2 to 17.2 mg L^{-1}). The percentage of the area dedicated to agricultural activities within a 1 km-width buffer area ranged from 0 to 79.6 %, mean = 16.7 ± 18.9 %, and 13.8 % had urbanization on their shore. Approximately a third of lakes (36.2 %) were connected directly with other lakes (chain) and 81.1 % had stream inlets and/or outlets. Only 13.8 % of the lakes had submerged macrophytes (Table S2).

3.2. Whole data set

Preliminary analysis showed that the linear regression between LN_Chla and TP was non-significant ($F = 1.989$, $\text{df} = 1$; 56, $p\text{-value} = 0.16$). Furthermore, the correlation coefficient between LN_Chla and TP for the whole data set was -0.18 and non statistically significant (Fig. 3). Correlations among LN_Chla and quantitative variables were significant for Perc_Agr, Turbidity and TN (Fig. 4a). Moreover, the categorical variables Macrophytes and Subregion were also statistically significant (One-way ANOVA: $F = 13.6$, $\text{df} = 1$; 56, $p\text{-value} < 0.005$; $F = 3.7$, $\text{df} = 6$; 51, $p\text{-value} < 0.005$; respectively). The Global model was built with LN_Chla as a dependent variable and Perc_Inorg, Perc_Agr, TN, Macrophytes and their interactions as independent variables. We included Perc_Inorg instead of Turbidity because the two are positively correlated (Fig. 4a) and Turbidity is not entirely independent of the dependent variable (LN_Chla) since it is comprised of the effect of dispersion and absorption of light due to chlorophyll particles. Subregion membership of each lake was included in the model as a random factor to take into account the inter-variability among Subregions (Zuur et al., 2009).

After the selection process for the global model, we obtained a ranking of models (Table S3). According to the Akaike weight ≤ 0.95 criteria for model selection, three models were selected (1–3 in Table 2 and Table S4). In model 1 only Macrophytes was selected as a predictive variable, in model 2 both TN and Macrophytes were selected and in model 3 both variables were selected as well as their interaction (Table 2). Coefficient values were negative for Macrophytes and positive for TN, the coefficient of the interaction between Macrophytes and TN was positive in model 3 (Table 2). The random factor Subregion explained 42.7 % of the variance in model 1, 44.7 % in model 2, and 45.0 % in model 3 (Table 2).

We closely examined the results of multiple criteria in order to decide on the best model for the whole dataset. First, although model 1 had a slightly lower AICc value than the other two models (Table S3), we opted for model 2 as the model that better explains the variability in the region. This decision was based on the fact that the AICc value was similar to that of model 1 (Table S3) and the marginal R^2 (mR^2 : the variation explained by the fixed factor) and the conditional R^2 (cR^2 : the variation explained by the entire model) were higher than in model 1 (Table 2). The only difference between model 2 and model 3 was the inclusion of the interaction between TN and Macrophytes; however, this interaction was not significant (Table 2). Second, we considered the $\Delta AICc \leq 7$ criteria for model selection, which showed that model 4 and model 5 (Table S3) were just as strong candidate models as 1–3. Both of these models included Macrophytes with negative coefficients and Perc_Agr with positive coefficients as predictive variables (Table 2). In model 5 TN was also selected as a factor with a positive coefficient. Subregion explained 37.7 % of the variance in model 4 and 38.5 % in model 5 (Table 2). The values of mR^2 and cR^2 were higher for model 4 and model 5 in comparison with models 1, 2 and 3 (Table 2). Third, we tested a model that included Macrophytes, TN and Perc_Agr; the three variables were statistically significant (Table 2). Taking into consideration all of the evidence (criteria in Table 2, mR^2 and cR^2) we chose model 5 as the best model for the whole data set (Table 3).

3.3. Subset of shallow lakes with submerged macrophytes

For the subset of lakes with submerged macrophytes ($N = 8$), the

Table 1

Main statistical descriptive variables (mean, median, Min: minimum, Max: maximum and SD: standard deviation) of the limnological, morphometric and landscape variables of the 58 selected shallow lakes. Chla: chlorophyll *a*, Cond.: conductivity, DO: dissolved oxygen, TP: total phosphorus, TN: total nitrogen, Turb.: turbidity, TSS: total suspended solids, Perc_inorg: percentage of inorganic material, Temp.: temperature, Perc_Agr: percentage of agriculture.

		Mean	Median	Min	Max	SD
LIMNOLOGICAL VARIABLES	Chla ($\mu\text{g/L}$)	59.41	42.05	1.58	242.74	63.72
	pH	8.75	8.75	8.09	9.40	0.27
	Cond. (mS cm^{-1})	6.92	2.26	0.32	202.10	26.35
	DO (mg L^{-1})	9.81	10.00	4.18	17.20	2.22
	TP ($\mu\text{g/L}$)	708	514	57.5	4538	844
	TN ($\mu\text{g/L}$)	4384	4295	960	8422	1394
	Turb. (NTU)	75.8	64.7	2.0	363.0	66.9
	TSS (mg L^{-1})	93.86	71.35	6.80	788.40	116.03
	Perc_inorg (%)	51.35	56.06	0	96.51	21.86
	Temp. ($^{\circ}\text{C}$)	20.31	20.00	7.00	34.30	5.03
LANDSCAPE VARIABLES	Perc_Agr (%)	16.68	10.76	0	79.64	18.92
MORPHOMETRIC VARIABLES	Area (km^2)	18.18	5.56	0.06	149.67	29.41
	Perimeter (km)	22.89	11.49	0.93	137.54	25.20
	Drainage ratio	10,215	3092	12	216,366	230,262

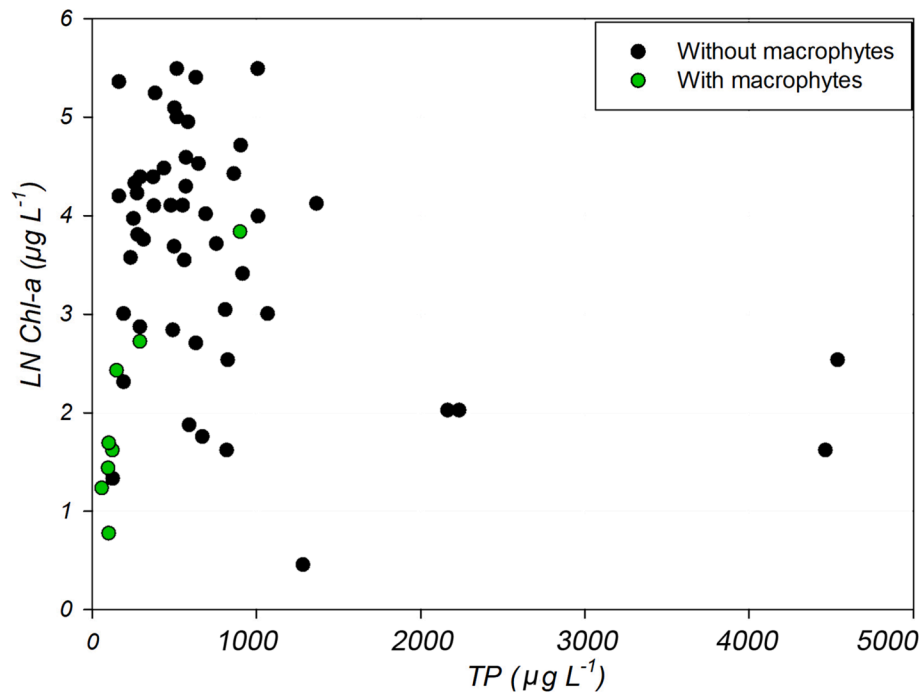


Fig. 3. LN_Chla ($\mu\text{g L}^{-1}$) vs TP ($\mu\text{g L}^{-1}$) for the whole data set: green dots are lakes with macrophytes ($N = 8$), black dots are lakes without macrophytes ($N = 50$). LN_Chla: LN_chlorophyll *a*, TP: total phosphorus.

correlation between LN_Chla and TP was 0.87 and statistically significant ($p\text{-value} < 0.05$) (Fig. 3 green dots). We also detected a negative and significant correlation between DO and LN_Chla (Fig. 4b). No categorical variables were statistically significant in the One-way ANOVAs for this subset. Best-fitted model included only TP as the independent variable (Table 3) with a positive and significant coefficient (Table 2, model 6). The alternative model that included DO and TP resulted in either one of these two variables being insignificant (Table 2, model 7). The introduction of Subregion as a random factor did not increase the percentage of explanation of the model (Table 2, model 8).

3.4. Subset of shallow lakes without submerged macrophytes

For the subset of lakes without submerged macrophytes ($N = 50$), a statistically significant ($p < 0.05$) negative correlation between LN_Chla

and TP ($r = -0.38$) was found (Fig. 3, black dots). We included in the full model the following quantitative variables: TP, Conductivity, Lake Area, Perc_Inorg (instead of Turbidity) and Perc_Agr, all of which had significant correlations with the dependent variable (Fig. 4c). Only Subregion was significant among categorical variables (One-way ANOVA: $F = 6.3$, $df = 6; 43$, $p\text{-value} < 0.005$) and it was included as a random factor. Since the function *dredge* does not support global models built with more than four variables, we ran the selection process five times in order to include all the possible combinations (Table S4). Based on the criteria of selecting a group of models whose Akaike weights were ≤ 0.95 and $\Delta_i \leq 7$, we obtained a subset of predictor variables from each global model (Table S4). The selected variables were: TP, Perc_Agr and Conductivity. However, when we ran the full model including the three predictor variables and Subregion as a random factor, only Perc_Agr was statistically significant (Table 2, model 9). Therefore, the best-fitted

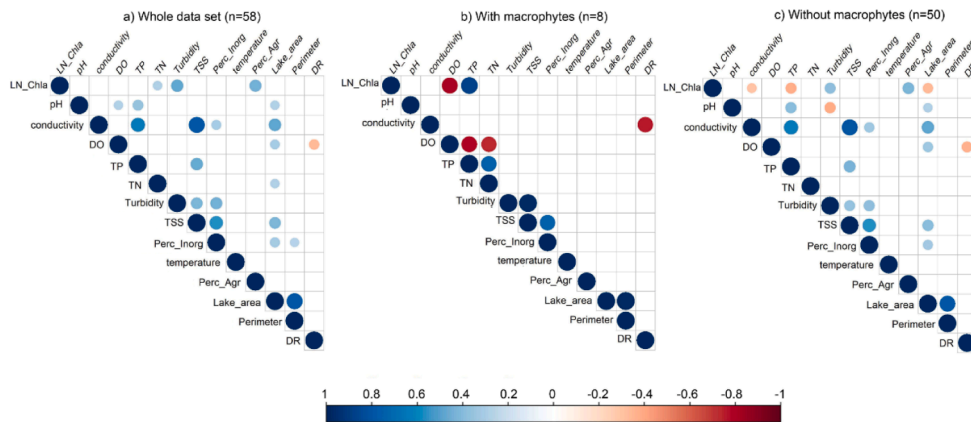


Fig 4. Correlations among the continuous variables for the studied shallow lakes. Only statistically significant coefficients are shown: blue circles represent positive values; red circles represent the negative ones, the intensity of colors represent the magnitude of the correlation coefficient (see the scale color bar at the bottom of the figures). (a) The whole data set, (b) Lakes with macrophytes, (c) Lakes without macrophytes. LN_Chla: LN_chlorophyll *a*, Cond.: conductivity, DO: dissolved oxygen, TP: total phosphorus, TN: total nitrogen, TSS: total suspended solids, Perc_inorg: percentage of inorganic material, Perc_Agr: percentage of agriculture, DR: drainage ratio.

model for this subset of lakes was $\text{LN_Chla} \sim \text{Perc_Agr}$ (Table 3), with 36.4 % of the variance explained by Subregion as random factor (Table 2, model 10). Taking into account all the results of this subset of lakes we consider that the negative relationship between LN_Chla and TP is a spurious correlation and is not reflecting the drivers of phytoplankton biomass, since when we performed the model selection process LN_Chla was positively related to Perc_Agr (Table 3) and TP was not selected as a significant variable, a result that is in line with the previous results of the whole data set (Table 3) and reflects the effect of agriculture in the water quality of these shallow lakes.

4. Discussion

We investigated potential drivers of Chla in a set of 58 shallow lakes that encompass a great deal of the heterogeneity and that characterize the Pampean region of Argentina. For this purpose, we adopted a regional perspective that included local and landscape variables as potential drivers. Furthermore, we asked if these drivers differed between lakes with and without submerged macrophytes.

These Pampean shallow lakes are eutrophic and hypereutrophic. Their range of TP and TN concentrations are consistent with the findings of Diovisalvi et al. (2015), who reported Pampean shallow lakes as extreme points in the trophic-state continuum of a worldwide broad database of shallow lakes ($N = 2,727$ lakes). The Chla of the 58 studied shallow lakes were not significantly correlated with TP, which is aligned with the lack of positive relationship reported by Phillips et al. (2008) and Prairie et al. (1989) for lakes with ranges of TP concentration similar to our study lakes. This result supports the idea that in eutrophic and hypereutrophic lakes there are other factors regulating the phytoplanktonic biomass. However, it is important to recognize that when considering TP as a potential driver of Chla, it is not only the dissolved phosphorus in the water, but also the phosphorus contained in the organisms (autotrophs and heterotrophs) and sediments (APHA, 2009) that could result in a different relationship between Chla and TP. For example, a lake with a high input of allochthonous organic material - which leads to high TP concentration in water - can sustain a plankton community dominated by heterotrophic organisms with relatively low Chla (del Giorgio and Gasol 1995). In this way, lakes with similar TP concentrations could have different proportions of autotroph: heterotroph organisms, resulting in a lack of relationship between Chla and TP.

For the 58 studied shallow lakes, the best model selected indicated that the presence of submerged macrophytes, TN concentration and Perc_Agr were key factors in shaping the phytoplankton biomass (Table 3). We observed that macrophyte presence exerted a significant and negative effect on the LN_Chla (Table 3). On the other hand, TN and Perc_Agr were positively and significantly related to the phytoplankton

biomass in this set of lakes (Table 3). When we split-up the data set and focused on lakes with submerged macrophytes ($N = 8$), TP was positively related to LN_Chla (Table 3). For the subset of lakes without submerged macrophytes ($N = 50$), agriculture was the most important factor (Table 3). These results are in agreement with the paradigm that when submerged macrophytes dominate a lake, they negatively affect the phytoplankton biomass. On the other hand, increasing TN and the percentage of agriculture in the surrounding area of each lake both enable higher concentrations of planktonic Chla. This finding is in line with what was observed by Søndergaard et al. (2017), where they showed that at high TP concentrations, TN explained most of the variability in Chla and its increment has a negative effect on lake water quality. A possible ecological mechanism explaining this finding is that many species of phytoplankton are co-limited by nitrogen and phosphorus and under high phosphorus concentration the increase in nitrogen redounds in an increment of this community (Müller and Mitrovic, 2015; Søndergaard et al., 2017). Concomitantly, TN concentration is increased by loadings of nutrients and biocides received from the agricultural activities in the basin. Agriculture can change the flow of organic matter to water bodies, modify the surrounding areas of lakes (Meerhoff and González Sagrario, 2021) and provoke physical disruption - by drainage and canalization - which also negatively affects the water quality of inland waters (Moss, 2008), threatening the aquatic biodiversity (Sala et al., 2000).

Submerged macrophytes play a key role in stabilizing clear regimes by different mechanisms (Scheffer, 2009 and cites therein). In particular, macrophytes act as a sink of nutrients (phosphorus and nitrogen) in the growing season by reducing their availability in the water column, which could limit phytoplankton development (Carpenter and Lodge, 1986; Søndergaard and Moss, 1998). In accordance with the alternative regimes theory proposed for shallow lakes (Scheffer et al., 1993) some pampean shallow lakes have been shifting from clear to turbid regimes and *vice versa* (Cano et al., 2008; Izaguirre et al., 2022). However, eutrophication provokes a shortening of the macrophyte growing season by favoring the increase of summer phytoplankton abundance (Phillips et al., 2016), preventing the switch back from a turbid to a clear regime. In eutrophic and hypereutrophic lakes this process causes, in advanced phases, the collapse of submerged plants with a simplification of the habitat complexity and a dominance of high phytoplankton biomass (Meerhoff and González Sagrario, 2021). Currently, the presence of submerged macrophytes is restricted to a small number of Pampean shallow lakes that although their eutrophic conditions remain in a clear regime. When we focused the analysis only on the subset of shallow lakes with submerged macrophytes, we found that the LN_Chla of these water bodies exhibited a classic positive relation with TP (e.g. Wetzel 2001). This also could be related to the stabilization mechanisms of

Table 2
Best fit models for the different data set studied (all lakes N = 58, lakes with macrophytes N = 8 and lakes without macrophytes N = 50) with the coefficient values of the variables and their significance. DV: dependent variable, TP: total phosphorus, DO: dissolved oxygen, TN: total nitrogen, Macro: presence of macrophytes, Cond: conductivity, LN_Chla: LN_chlorophyll a, Perc_Agr: percentage of agriculture, Random factor (Subregion): in the models that include subregion as a random factor, it indicates the proportion that this factor explained from the residual variance (proportion of the unexplained variance of the fixed factors), mR²: marginal R² is the variation explained by the fixed factor, cR²: conditional R² is the variation explained by the entire model, R²: is the variance explained in linear models. The symbol (-) indicates that in the model there is no such fixed and/or random factor included. Significance code: *** 0.001, ** 0.01, * 0.05, " 0.1, NS: non significant.

Model	Data set	Fixed factor										Random factor (Subregion)	mR ²	cR ²	R ²
		Limnological					Interaction								
		DV	Intercept	TP	DO	TN	Macro	Cond.	Perc_Agr						
1	All lakes (N = 58)	LN_Chla	3.7014***	-	-	-	-2.0383***	-	-	42.7 %	0.24	0.56	-		
2		LN_Chla	2.6816***	-	-	0.2152*	-1.6576***	-	-	44.7 %	0.26	0.59	-		
3		LN_Chla	2.8425***	-	-	0.1798	-3.2245*	-	-	45.0 %	0.27	0.60	-		
4		LN_Chla	3.3092***	-	-	-	-1.8854***	-	0.019*	37.7 %	0.33	0.58	-		
5		LN_Chla	2.4181***	-	-	0.1949	-1.5562***	-	0.018*	38.5 %	0.34	0.59	-		
6	With macrophytes (N = 8)	LN_Chla	1.2785***	3.0517***	-	-	-	-	-	-	-	-	0.76		
7		LN_Chla	2.7674	-1.1832 ^{NS}	-0.1186 ^{NS}	-	-	-	-	-	-	-	0.89		
8		LN_Chla	1.2785**	3.0516*	-	-	-	-	-	2.1x10 ⁻⁰⁸ %	0.73	0.73	-		
9	Without macrophytes (N = 50)	LN_Chla	3.3336***	-0.05104 ^{NS}	-	-	-	-0.0035 ^{NS}	0.01981**	-	32.1 %	0.13	0.41	-	
10		LN_Chla	3.2643***	-	-	-	-	-	0.02029**	-	36.4 %	0.11	0.43	-	

Table 3

Equations of the final selected models for the different data sets studied. In parentheses: model number selected from Table 2. LN_Chla: LN_chlorophyll a, TN: total nitrogen, Perc_Agr: percentage of agriculture, TP: total phosphorus.

Data Set	Final Selected models
All Lakes (N = 58)	LN_Chla ~ 2.4181 - 1.5562 Macrophytes + 0.1949 TN + 0.018 Perc_Agr Subregion (37.7 %) (model 5)
With macrophytes (N = 8)	LN_Chla ~ 1.2785 + 3.0517 TP (model 6)
Without macrophytes (N = 50)	LN_Chla ~ 3.2643 + 0.020 Perc_Agr Subregion (36.4 %) (model 10)

submerged macrophytes which diminish the TP concentration in the water column, making it less available for phytoplankton (Søndergaard and Moss, 1998); in fact, these lakes had lower concentrations of TP and Chla than those without macrophytes (Fig. S1). It is important to point out that the number of lakes with submerged macrophytes included in this study was low (N = 8) because of, as we mentioned before, currently it is difficult to find lakes in a clear regime. Besides, the studied shallow lakes are in a relatively narrow range of nutrients (all of them were eutrophic or hypereutrophic) which partially limited the reach of the developed models. Future research on models that include more lakes with submerged macrophytes may provide more information about the underlying mechanism shaping the TP-Chla relationships in Pampean shallow lakes.

Agriculture provokes – among other disturbs – an increase in nutrient concentrations, causing an increase in algal biomass, which in combination with other factors can favor the occurrence of Cyanobacteria blooms (Paerl 2008). In fact, Doubek et al. (2015) reported that growing levels of agriculture and developed land use were not only positively related to phytoplankton biovolume, but also to cyanobacterial biovolume and dominance. Cyanobacteria blooms have been reported in several lakes of the Pampean region (Izaguirre et al., 2015; O'Farrell et al., 2019; O'Farrell et al., 2021), which strongly suggests a relationship between the agricultural development, together with other anthropogenic activities in the lake basins and the proliferation of these frequent blooms events. Another recent study of Pampean shallow lakes demonstrated the direct and indirect effects of LULC on phytoplankton structure, which affect the morpho-functional groups that are present in these lakes (Sánchez et al., 2021).

Other studies have found that the impact of agriculture on nutrients and planktonic communities varies depending on the spatial scales considered (Soranno et al., 2015; de Mello et al., 2020), highlighting the need for multiscale studies that cover this range of variation (Soranno et al., 2015) and the inclusion of lake and landscape variables. In fact, our study found that Subregion membership explained a high proportion of the variance for the whole data set and for the subset of lakes without submerged macrophytes, meaning that there were regional drivers of the relationship of TP-Chla. The high number of lakes present in the Pampean Plain is the result of a low drainage and the flat topography of the region. However, there is heterogeneity in the climate and geology across the region and there were particular mechanisms acting that originated different groups of lakes: natural dams provoked by barriers of sand and shells, relictual oxbows of rivers and streams, segmentation of great water bodies occasioned by climate change, among others (Morello et al., 2012). Hence, the climatic conditions and geological characteristics of the Subregions have direct implications on the current physical and chemical features of the Pampean shallow lakes (Miretzky et al., 2001), making it key to consider the different subregions when studying and managing lakes of the Pampean region.

Paleolimnological studies of shallow lakes in the Pampean region

have shown the existence of a pristine clear regime dominated by macrophytes that changed recently towards a turbid regime (Stutz et al., 2014, González Sagrario et al., 2020, Sánchez Vuichard et al., 2021). Most of these changes were probably related to the intensification of agriculture in the region, canalization and changes in water levels (Quirós et al., 2002a, b, 2006, Sánchez et al., 2015, Izaguirre et al., 2022). These historical records, along with the results of our study, reveal the deterioration of these shallow lakes driven mainly by increasing nutrients concentrations, highlighting the key role of TN, and a decrease of submerged macrophytes concomitantly with the increase of agriculture in the surrounding areas. The few Pampean shallow lakes that remain in a clear-vegetated regime are probably near the boundary of the hysteresis situation and, if the turbidity increases - provoked for example by a strong water level decrease- a turnover to the turbid regime could be triggered (Sánchez et al., 2015). If this change occurs and the system is pushed out of the limits of alternative states, the return to the previous state is neither easy nor direct. In restoration experiences, the effect of reducing nutrient loads on the recovery of macrophytes was not uniform: while some lakes experienced a macrophyte increase (in abundance, coverage or depth distribution) other lakes exhibited no changes (Jeppesen et al., 2005). Therefore, once the lake shifts to a turbid regime, reestablishing the previous regime demands a strong effort and the combination of different strategies (Scheffer, 2004). All these difficulties along with our results highlight the importance of directing efforts to conserving shallow lakes with submerged macrophytes that are still in a clear regime in the Pampean region as well as in designing management strategies to preserve the surrounding areas of lakes in order to diminish the impact of anthropic activities from the catchment.

5. Conclusions

Our regional study extent and our inclusion of continuous and categorical factors acting at multiple scales (local and regional) allowed us to incorporate a new perspective into the study of the Pampean shallow lakes constituting an important contribution to the study of these aquatic systems in South America. We determined the influence of different factors to better understand the main drivers of phytoplankton biomass in clear and turbid shallow lakes in this highly anthropically-impacted region, moving us toward a more comprehensive understanding of the dynamics of these systems. Our models provide evidence of the role of submerged macrophytes as one of the main drivers of phytoplankton biomass in Pampean shallow lakes, probably acting as stabilizers of clear regimes. On the other hand, our results showed the positive effect of TN and agriculture on algal biomass. Therefore, measures for improving water quality of these shallow lakes should conserve macrophytes as well as to regulate the agriculture in the area surrounding each water body.

Author contribution

This paper was conceived during an internship of MLS in the “Data Intensive Landscape Limnology Lab” from Michigan State University headed by KSC. MLS led the conceptualization, investigation, manuscript writing, data curation, formal analyses and visualization. SB participated in the visualization creating the “Graphical Abstract”. MCB collaborated with the visualization making the final versions of Figs. 2, 3 and 4. MSV drafted Table 1. II, HZ, MRS, GC, MSV, SB, MCB, LL and MLS contributed with data curation providing the original data for the models. II, HZ, MRS and KC provided resources. All authors helped to conceptualization, re-defining the manuscript idea and questions, made corrections in the statistical analyses and interpreted the results. All authors conducted critical reviews of the manuscript drafts and approved the final version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Thanks to Dr. Lucía Babino for her statistical assistance and to Maggie Haite for their connectivity analysis. We are also thankful to the Fulbright Fellowship program and CONICET for their financial support to allow Dr. Sánchez internship at Michigan State University and to the US National Science Foundation (NSF) Macrosystems Biology Program [EF-1638679]. Data used in this study belong to different projects and were supported by the following funds: PAMPA² project (REDES-CONICET), Proyecto de Unidad Ejecutora CONICET-IEGEB, PICT 2017-2498, PICT 2017-0891, PICTO 0006/2019, SIB 575/2019, National Geographic (grant # 9736-15).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109834>.

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