

RESEARCH ARTICLE

Rise of toxic cyanobacterial blooms is promoted by agricultural intensification in the basin of a large subtropical river of South America

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Abstract

Toxic cyanobacterial blooms are globally increasing with negative effects on aquatic ecosystems, water use and human health. Blooms' main driving forces are eutrophication, dam construction, urban waste, replacement of natural vegetation with croplands and climate change and variability. The relative effects of each driver have not still been properly addressed, particularly in large river basins. Here, we performed a historical analysis of cyanobacterial abundance in a large and important ecosystem of South America (Uruguay river, ca 1900 km long, 365,000 km² basin). We evaluated the interannual relationships between cyanobacterial abundance and land use change, river flow, urban sewage, temperature and precipitation from 1963 to the present. Our results indicated an exponential increase in cyanobacterial abundance during the last two decades, congruent with an increase in phosphorus concentration. A sharp shift in the cyanobacterial abundance rate of increase after the year 2000 was identified, resulting in abundance levels above public health alert since 2010. Path analyses showed a strong positive correlation between cyanobacteria and cropland area at the entire catchment level, while precipitation, temperature and water flow effects were negligible. Present results help to identify high nutrient input agricultural practices and nutrient enrichment as the main factors driving toxic bloom formation. These practices are already exerting severe effects on both aquatic ecosystems and human health and projections suggest these trends will be intensified in the future. To avoid further water degradation and health risk for future generations, a large-scale (trans-boundary) change in agricultural management towards agroecological practices will be required.

KEYWORDS

crops, cyanobacterial blooms, health risk, land use, precipitation, temperature

1 | INTRODUCTION

The occurrence of massive toxic blooms of cyanobacteria is an environmental and public health problem worldwide. Most blooms produce metabolites that are toxic to animals and humans, which

are collectively referred to as cyanotoxins (Chorus & Welker, 2021; Preece et al., 2017; Svirčev et al., 2019). These cyanotoxins can lead to sickness and cause deaths of aquatic animals, including negative impacts on human health and other activities (Azevedo et al., 2002; Giannuzzi et al., 2011; Vidal et al., 2017; Zhang et al., 2015). Over

the past few decades, an upsurge in the frequency, geographic distribution and severity of such blooms has recurred in many areas of the planet (Preece et al., 2017) and forecast models indicate that both bloom frequency and intensity will continue to increase (Fang et al., 2022). Therefore, disentangling the main driving causes to define management actions is of fundamental importance (Suknik & Kaplan, 2021).

1.1 | Cyanobacterial bloom forcings

Understanding cyanobacterial toxic bloom dynamics is a complex issue and there are several driving forces linked to their occurrence and toxicity. However, there is a 50-year consensus in the scientific community about the fundamental role that the input of nutrients to water bodies (due to cultural eutrophication) plays in driving algal biomass increment and cyanobacterial dominance (Huisman et al., 2018; Paerl et al., 2018). The identification of nutrient enrichment as a relevant driver can be traced back to early empirical studies (e.g. Trimbee & Prepas, 1987; Vollenweider & Kerekes, 1982), including manipulative experiments at the ecosystem scale (Schindler, 1977) and has most recent support in cross-system field and laboratory studies of large data sets at different latitudes (Downing et al., 2001; Kosten et al., 2012). These studies demonstrate that bloom-forming cyanobacteria benefit over other phytoplankton groups under high nutrients and low turbulence conditions (e.g. Kim et al., 2017; Scheffer et al., 1993).

Cultural eutrophication originated through multiple human activities including agriculture, cattle raising and poorly treated sewage water from human settlements (Fang et al., 2022), which were traced back by paleolimnological studies (Bueno et al., 2021). Among the multiple human-related driving forces, agriculture is a prominent and persistent cause of diffuse nutrient loads and the world's largest source of both phosphorus and nitrogen pollution to water bodies (Bennett et al., 2001; Chakraborty et al., 2017; MacDonald et al., 2011; Withers et al., 2014). A strong linkage has been identified between the industrialized cutting-edge production of crops and the emergence of toxic cyanobacteria outbreaks (Chakraborty et al., 2017; Massey et al., 2020).

There are other drivers that also promote cyanobacterial blooms and might exert synergistic effects with eutrophication (Meerhoff et al., 2022). Most cyanobacterial organisms have relatively low specific growth rates and thus toxic populations are not able to proliferate under low to moderate flushing (Bakker & Hilt, 2016; Kruk, Martínez, et al., 2021; Kruk, Piccini, et al., 2021). Therefore, in eutrophic rivers, dam construction favors blooms by increasing water residence time (Massey et al., 2020; Paerl & Huisman, 2009). High temperatures also accelerate cyanobacterial metabolism, promoting their growth, the formation of blooms under stratified waters (Paerl & Huisman, 2008) and the stimulation of toxin production (Martínez de la Escalera et al., 2017; Massey et al., 2020). Changes in precipitation modify water residence time and geographical distribution of cyanobacterial blooms (Kruk, Martínez, et al., 2021; Kruk, Piccini,

et al., 2021; Massey et al., 2020). Moreover, the replacement of natural land cover with crops and the modification of trophic food webs accelerates the effects of eutrophication and climate change (Alcántara et al., 2022; Meerhoff et al., 2022). Thus, understanding the importance of individual drivers and potential synergies among them are both relevant to provide management actions to stakeholders at different levels (Alcántara et al., 2022; Fang et al., 2022; Kosten et al., 2012).

1.2 | Watersheds in southern South America

South America is one of the regions most affected by global agriculture, where large-scale cash crops have replaced natural vegetation (Doughty, 2010; Graesser et al., 2018; Pérez, Barreiro, et al., 2021; Pérez, Crisci, et al., 2021; Tucci & Clarke, 1998). Large proportions of land are dedicated to agricultural production with annual crops, such as soybean, maize, wheat and rice (Giller et al., 2021). These large-scale cash crop areas have transformed land use dynamics with important implications for food security, biodiversity conservation and revenues (Bueno et al., 2021; Graesser et al., 2018; Tucci, 2001; Tucci & Clarke, 1998).

Within South America, the Uruguay river is a major and vital ecosystem (ca. 1900 km long) with a transboundary catchment area of 365,000 km² shared by three countries (Brazil, Argentina and Uruguay). This river supports key ecosystem services, drinking water for human consumption, recreation and tourism, navigation, as well as biological production at different trophic levels including fisheries (de Vasconcelos et al., 2014; Tucci & Clarke, 1998). It integrates the Río de la Plata basin, the second largest in South America (Guerrero et al., 1997; Milliman et al., 2008) and represents an important region for agriculture and livestock production in the world (de Vasconcelos et al., 2014; Tucci, 2001; Tucci & Clarke, 1998). During the last decades, natural grasslands supporting extensive livestock production have been replaced with large-scale croplands, causing degradation of ecosystem services (de Vasconcelos et al., 2014; Modernel et al., 2016). High-resolution palaeoceanographic studies in the Río de la Plata demonstrated the effect of continental human activities on the aquatic ecosystems (Pérez, Barreiro, et al., 2021; Pérez, Crisci, et al., 2021) attributed to land-use intensification and dam construction leading to significant soil erosion and transport/deposition into the inner shelf, enhanced by the El Niño Southern Oscillation (ENSO) events (Bonachea et al., 2010; Pérez, Barreiro, et al., 2021; Pérez, Crisci, et al., 2021). The Uruguay river holds 10 large dams (>10 km²), and there are more than 90 further dams either planned or under construction (<http://globaldamwatch.org>) (Pérez, Barreiro, et al., 2021; Pérez, Crisci, et al., 2021), which cause strong modifications to its hydrological cycle (Depetris & Pasquini, 2007a, 2007b; Milliman et al., 2008; Tucci & Clarke, 1998).

Toxic cyanobacterial blooms are frequently registered in the Uruguay River (Bordet et al., 2017; Debastiani Júnior et al., 2016; O'Farrell & Izaguirre, 2014) and exported to the Río de la Plata

Estuary (Kruk et al., 2017; Martínez de la Escalera et al., 2017; Nagy, Gómez-Erache, Lopez, & Perdomo, 2002; Segura et al., 2017). These blooms negatively impact health, including human intoxications (Giannuzzi et al., 2011; Vidal et al., 2017), local economies, tourism and related recreational activities (Kruk, Martínez, et al., 2021). Long-term records of toxic cyanobacterial blooms and the analysis of their forcings are not common in large watersheds worldwide (Doubek et al., 2015; Salk et al., 2022), and particularly in the Southern Hemisphere, where these types of analysis are scarce (Silvarrey Barruffa et al., 2021). The objective of this study was to disentangle the contribution of different environmental drivers in determining cyanobacterial abundance. With this aim, we analyzed temporal trends which showed an increase in the frequency and severity of cyanobacterial blooms over a 60-year period in a large subtropical river basin (Uruguay river basin). In addition, causal path models were used to evaluate the relative importance of each driving forcing (land use change, urban sewage, river flow and climate variability [temperature, precipitation]) in explaining cyanobacterial abundance at the entire-basin level.

2 | METHODS

2.1 | Study area

The Uruguay river basin lies between 28°10'S and 37°08'S (Di Persia & Neiff, 1986) and it is shared by Brazil (percentage of surface area: 50.1%), Uruguay (32.5%) and Argentina (17.4%) (Figure 1). The river origin is located in Brazil at 200m above mean sea level and its main tributary is the Negro River (500 km long). Together with the Paraná River are the main tributaries of the Río de la Plata Estuary.

The Uruguay river hydrographic basin climate is located in a humid subtropical (*sensu* Köppen) and is set upon sedimentary and volcanic soils. It comprises mainly three dominant biomes from headwaters to the Río de la Plata: (i) upper basin: mixed agro-eco-region, (ii) middle basin: Campos biome and (iii) lower basin: South American Pampas biome (Argentina, Uruguay) (Saurral et al., 2008; Viglizzo & Frank, 2006). The upper river is steep (43 cm km^{-1}), comprises 750 km, has a maximum average flow of $9387 \text{ m}^3 \text{ s}^{-1}$ and exhibits large annual variations in water level. The Itá Hydroelectric Power Plant is the largest reservoir in this area (lake area: 141 km^2 , basin area: $45,800 \text{ km}^2$) and it became operative in 2000. Additionally, eight dams are now built in the river, and other 89 are planned for the next few years (<http://globaldamwatch.org>, Mulligan et al., 2020) (Figure 1). The middle zone of the river is 800 km long, has a 9 cm km^{-1} slope, and does not contain large reservoirs. The lower river is 350 km with a slope 3 cm km^{-1} and its hydrology is strongly influenced by the Salto Grande (SG) reservoir, constructed for hydroelectricity production (Concordia, Salto, $31^{\circ}16'29''\text{S } 57^{\circ}56'18''\text{W}$). SG became first became operative in 1979 with a catchment area of $224,000 \text{ km}^2$ and a lake surface area of 783 km^2 . Finally, at Nueva Palmira, the Uruguay river

flows into the Río de la Plata Estuary, and then into the Atlantic Ocean (Figure 1).

2.2 | Cyanobacterial abundance and limnological variables

Cyanobacterial information including abundance and blooms presence was compiled for the lower Uruguay river from different data sources, attaining a total number of 1712 cases from 1963 to 2019. From the total number of cases, 1424 were retrieved from sampling sites located either upstream or in the SG dam and 288 from sites downstream of this dam. The largest part of the data set was obtained from publicly accessible reports of the Uruguayan Government Water Institution (i.e. *Obras Sanitarias del Estado*, OSE, 2009), for the period between 1963 and 2008. This information included cyanobacterial cells abundance (cells ml^{-1}) in surface water, dominant cyanobacterial species and the presence of blooms in six sites next to three water treatment plants: (1) upstream SG reservoir: Bella Unión, (2) in the SG reservoir: Belén and Constitución and (3) downstream the reservoir in Salto, Fray Bentos, Paysandú and Bassotti. From 2008 until 2019, we gathered information from other institutional sources, including the Argentina-Uruguay Administrative Commission (CARU, 2019, <https://www.caru.org.uy/web/>), SG Joint Technical Commission (CTM, Argentina-Uruguay, <https://www.saltogrande.org/>) and the National Environmental Observatory of Uruguay (MVOTMA-OAN, 2019; <https://www.ambiente.gub.uy/oan/>). These data sources included cyanobacterial cell abundance, cyanobacterial species, and fecal coliform abundance (as fecal indicator bacteria, FIB) in 16 sites from Bella Unión (Artigas) to the SG reservoir main channel next to the dam. Total phosphorus concentration in water (mg L^{-1}) was retrieved for the same sites for the period 2008–2019, including information from CTM ($N = 245$), CARU ($N = 25$) and our own monitoring program (Kruk et al., 2015; $N = 72$).

In all cases, surface water samples were taken with bottles and fixed with Lugol solution. Cyanobacterial and other phytoplankton species were counted with comparable methods with Sedgwick Rafter or Utermöhl counting chambers using a light microscope and estimating the cell abundance (cell ml^{-1}) using the settling technique (Utermöhl, 1958). Utermöhl chambers were used for counting samples with low phytoplankton abundances, while Sedgwick chambers were used for high abundance samples including those dominated by cyanobacteria and with the presence of blooms. The abundance of cyanobacteria was also used to determine alert levels following (Chorus & Welker, 2021; level 1: $2000\text{--}100,000 \text{ cell ml}^{-1}$, level 2: higher than $100,000 \text{ cell ml}^{-1}$, vigilance stage: cell abundance higher than 200 cell ml^{-1}).

The effects of human settlements were estimated based on the abundance of FIB. Samples for FIB detection and quantification were taken from surface water in the same area as cyanobacteria but with a higher frequency from 1987 to 2020, attaining a total number of 2127 cases. For the 1987–2005 period, the information was retrieved from the binational Procon-CARU project (<https://www.caru.org>).

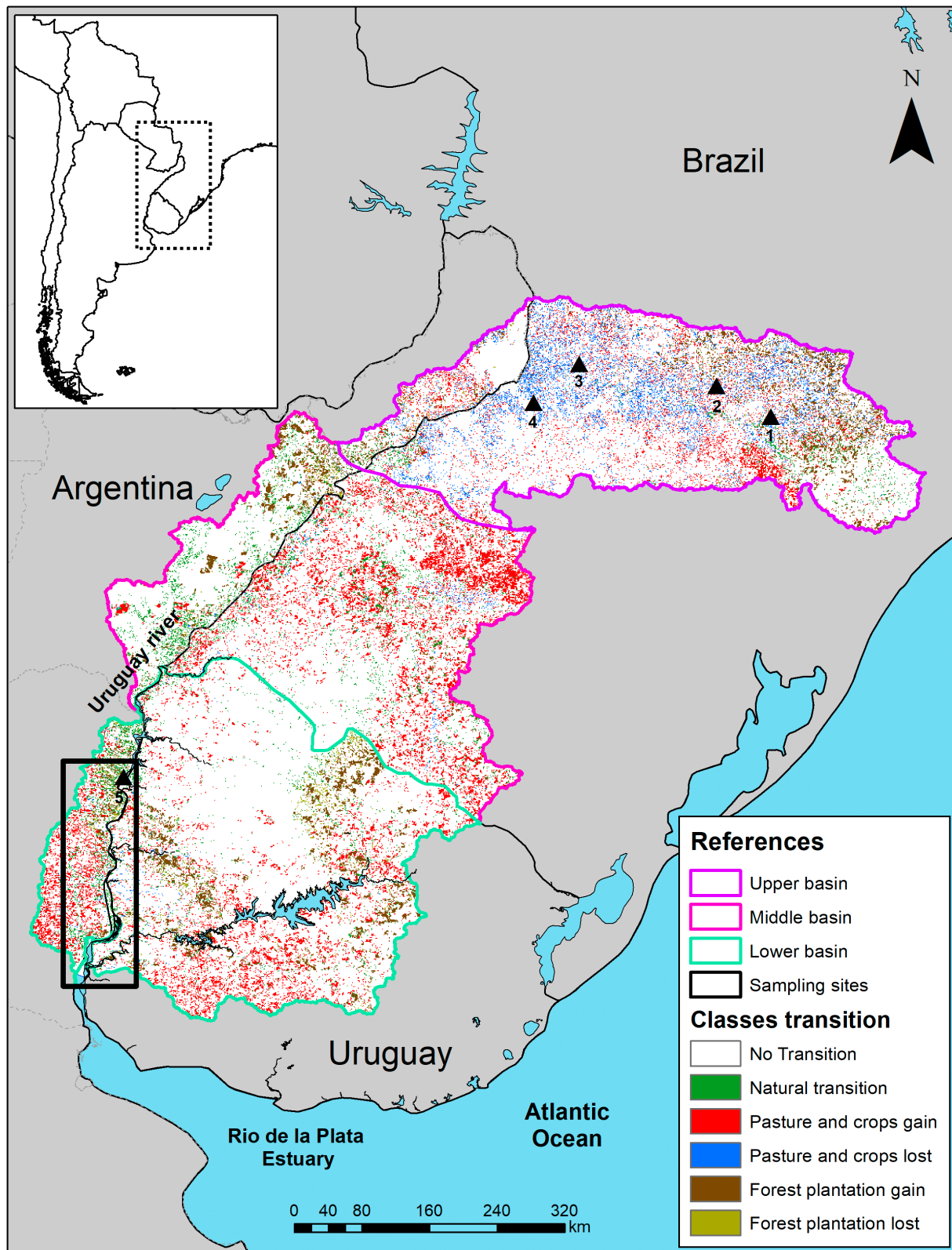


FIGURE 1 Uruguay river basin and its main tributaries in Brazil, Argentina and Uruguay. Location of the basin in South America, delimitation of the main areas of the basin (upper, middle and lower) and location of sampling sites. Land uses and land covers transitions between 2000 and 2019 and main dams (black triangles) are shown. In the upper basin: (1) Barra grande dam, (2) Machadihno dam, (3) Ita dam and (4) Foz de Chapecó dam. In the lower basin: (5) Salto Grande Dam. 'Pasture and crops lost' indicate the transition from crops and pasture to natural cover. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

uy/web/2020/05/programa-procon-caru-1987-2005-recopilacion-validacion-de-datos/). For the 2014–2020 period, the information source was the Uruguay National Environmental Observatory (OAN) (<https://www.ambiente.gub.uy/oan/>).

2.3 | Climatological and hydrological variables

Temperature and precipitation data in the Uruguay river watershed from 1963 to 2020 were obtained from the historical climate database produced by the Climatic Research Unit (CRU) of the University of East Anglia and provided by the World Bank climate knowledge portal, corresponding to the number 252 watershed (<https://climateknowledgeportal.worldbank.org/watershed/252/climate-data-historical>). The information included annual average values of maximum, minimum and average daily temperatures (°C) and the average annual precipitation (mm). Historical data on Uruguay river flow rates were retrieved from the Argentinian National System of Information (<https://snih.hidricosargentina.gob.ar>) and corresponded to station 3802 in Paso de los Libres. Monthly average water flow ($\text{m}^3 \text{s}^{-1}$) was selected from 1963 to 2020 and expressed as the maximum value and the accumulated flow per year.

2.4 | Land use

Annual land use and land cover maps from 2000 to 2019 for the entire Uruguay river basin were obtained from an assembly of classifications generated by MapBiomias initiatives (Table 1). The MapBiomias project is an international multi-institutional initiative whose goal is to generate annual land use and land cover maps based on the use of satellite images provided by Landsat 4, 5, 7 and 8 and automatic classification processes of images. These included MapBiomias Pampa (Baeza et al., 2022) and Atlantic Forest Tri-national initiatives (Souza et al., 2020).

Land use and land cover were grouped into six classes natural forest, forest plantation, grasslands and wetlands, farming, non-vegetated areas (that include bare soil and urban infrastructure)

and water bodies and rivers (Souza et al., 2020). Farming includes annual crops (i.e. maize, soybean, wheat, etc.) and sown pastures. Information for a longer period (from 1989 to 2019) was only available for the Brazilian portion of the basin. Collection 6 of MapBiomias Brazil was used to separate the composition of the class 'annual crops and pasture' into different land-use covers, such as pastures, soybeans, other summer crops and a 'mosaic of pastures and annual crops'.

2.5 | Data analysis

Cyanobacterial abundance was \log_{10} transformed for most analyses and graphical representations. Linear models were performed to evaluate the change in cyanobacterial abundance and total phosphorus yearly average with time and were compared using the differences in the Akaike information criteria (ΔAIC). The fit of the segmented models followed a well-developed technique based on a linearization of the problem that allows to estimate slopes and intercepts before and after a breakpoint, as well as a confidence interval for the breakpoint (Muggeo, 2003), which is implemented in the {segmented} package (Muggeo, 2008) in the R software. The relationships between total phosphorus and cyanobacterial abundance, and between total phosphorus and land use areas were explored with correlations and linear models. Due to the lack of sufficient available data points and the heterogeneity in the methodological approaches applied to estimate nitrogen in water, this nutrient was not included in the analysis.

To evaluate the effect of the unequal sample size and the increasing sampling effort with time on the estimation of cyanobacterial abundance (Hallegraeff et al., 2021), we conducted different strategies (Material S1): (i) aggregating the information as yearly average both including and excluding the periods with less data (between 1995 and 2003), (ii) aggregating the information every 5 years and performing unweighted and weighted regressions (weights proportional to the number of data points per period) and (iii) using bootstrapping type of re-sampling to produce 250 smaller samples of 15 cases and then producing 250 temporal

TABLE 1 Uruguay river (UR) basin and sub-basins areas, countries, MapBiomias (MB) collections and temporal period of the information used (MapBiomias Pampa: Baeza et al., 2022, Atlantic Forest Tri-national initiatives: Souza et al., 2020). Refer to Figure 1 for visual location. Land uses and land cover were grouped into six classes: natural forest, forest plantation, grasslands and wetlands, farming (annual crops and sown pastures), non-vegetated areas (that include bare soil and urban infrastructure) and water bodies and rivers.

Basin	Area (km ²)	Country	Information origin	Temporal period	Type of information
Total UR basin	329.003	Brazil, Argentina and Uruguay	MB Brazil Collection 5, MB Atlantic Forest Collection 1 and MB Pampa Collection 1	2000–2019	Six classes
Upper and middle	167.130	Brazil	MB Brazil Collections 5 and 6	1985–2019	Six classes and composition of 'annual crops and pasture'
Lower	161.875	Argentina and Uruguay	MB Atlantic Forest Collection 1 and MB Pampa Collection 1	2000–2019	Six classes

linear models with the yearly average in each period. In (iii) the number of significant models with positive slopes was registered. The models with similar response variables were compared using AIC (Material S2).

Temporal trends in temperature (average, maximum, minimum), precipitation average, river flow (accumulated and maximum) and \log_{10} cyanobacterial abundance were explored for each data set. The presence of white noise was evaluated in the residuals of the segmented regression on yearly clustered information, using Ljung-Box and turning points tests. The results did not allow to discard white noise and, therefore, specific time series analyses were not necessary. Spearman non-parametric rank correlation and the variance inflation factor (VIF) were used to evaluate multicollinearity among variables, including climatic, hydrological and land use.

Causal path models were constructed to evaluate the relative contribution as well as the interactions of the different potential driving factors of the annual average of \log_{10} (cyanobacterial abundance+1) (\log_{10} Cya) using {'Lavaan'} package. This model framework is specially designed to evaluate competing models representing hypothesis based on theoretical arguments (Petraitis et al., 1996). We a priori introduced eight path models, including the effect of climate (precipitation: PP, maximum temperature: T_{\max}), hydrology (accumulated river flow: Qacum) and land use (area of land with annual crops and pastures and natural area) (Figure 2). Covariates were standardized to 0–1 prior to the analysis. To evaluate the existence of multicollinearity among the explaining variables, we inspected the VIF. No significant multicollinearity was retrieved as VIF values were in all cases lower than four. Competing models

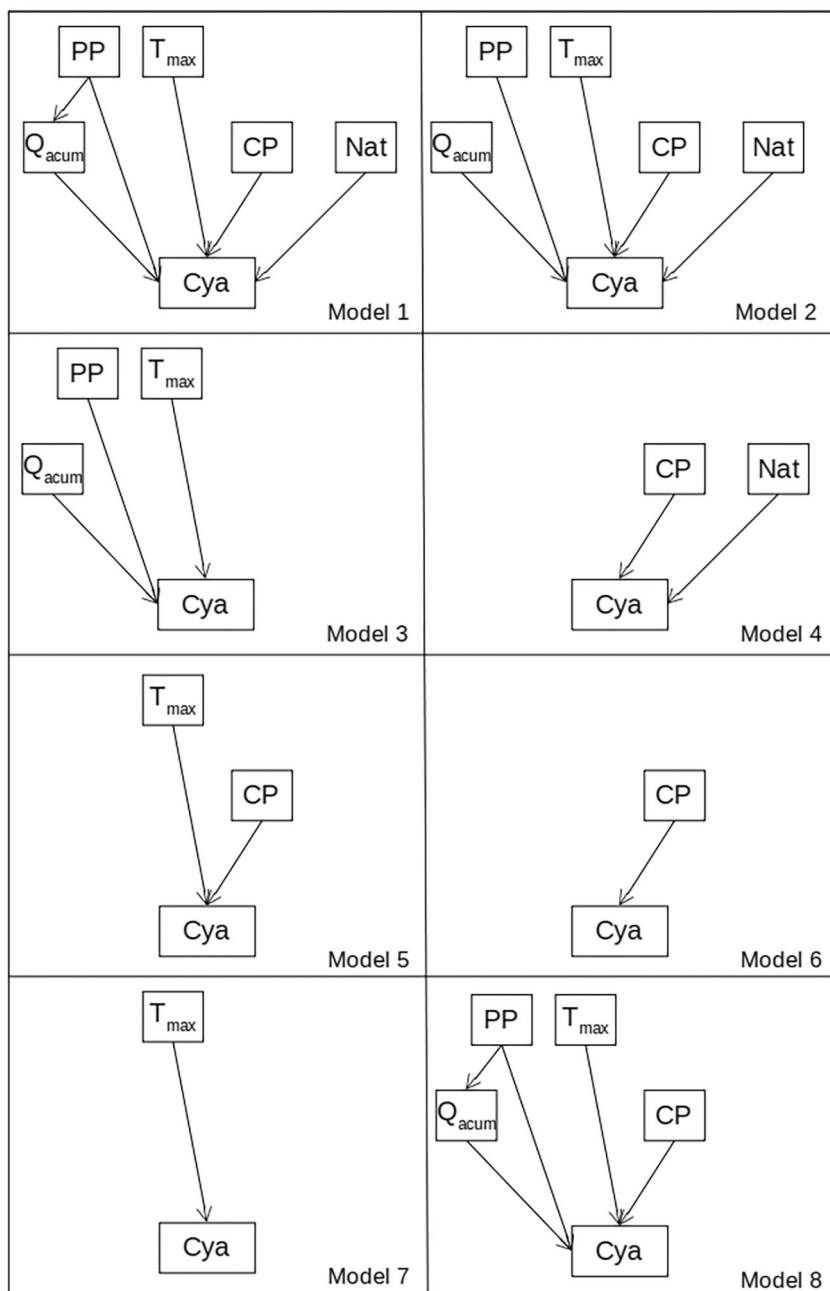


FIGURE 2 Graphical representation of the path models (1–8) constructed and tested based on the hypothetical causal relationships between climatic (precipitation: PP, maximum temperature: T_{\max}), hydrological (river water flux: Q_{acum}) and land use (crops and pastures: CP, natural forests: Nat) forcing variables of \log_{10} cyanobacterial abundance (Cya).

were compared based on the AIC and path coefficients were estimated including their standard error (SE), z statistics and the associated p -value. The Fisher's C statistic was calculated to evaluate whether the data follow the causal hypothesis specified in the dyacyclic aggregated paths. For the selected model, the root mean square error of approximation (RMSEA), the explained variance (R^2) and the comparative fit index (cfi) were estimated. Models were performed for the 1985–2019 period using land use covariates from the Brazilian catchment area.

3 | RESULTS

3.1 | Temporal changes in cyanobacterial abundance and composition

Total abundance of cyanobacterial cells in the SG reservoir and downstream increased by 4–5 orders of magnitude from 1963 to 1970 (average 33 cell L^{-1} , maximum = 53 cell L^{-1}) to 2010–2020 (average $21,281 \text{ cell L}^{-1}$, maximum = $1.69 \times 10^6 \text{ cell L}^{-1}$; Figure 3) and phytoplankton communities shifted from either diatom- or chlorophyte-dominated to cyanobacteria-dominated. The dominant cyanobacterial genera shifted from the first decades when *Merismopedia*, *Lyngbya*, *Planktothrix* and other genera from the Oscillatoriales order dominated, to *Dolichospermum* and *Microcystis* after the 2000s. In recent years, blooms were in most cases dominated by members of the *Microcystis aeruginosa* complex.

After 2000, blooms became highly frequent along with an exponential increase in both maximum and average cell abundance (Figure 3). Surface scums (i.e. water discoloration events) became

frequent from 2000 to 2007, particularly in the lower Uruguay river (Figure 1). Furthermore, the risk level alerts also increased with time, from no risk to vigilance (cell abundance higher than 200 cell mL^{-1}) in the period between 1963 and 2005, then from vigilance to at least one level 1 alert ($2000\text{--}100,000 \text{ cell mL}^{-1}$) per year, and since 2006 at least one level 2 alert ($100,000 \text{ cell mL}^{-1}$) per year was observed. During the last decade (2010–2020), 155 and 46 alerts of levels 1 and 2, were respectively reported. In addition, the temporal persistence of blooms throughout the year increased from isolated occasions in summer to continuous presence, including even the cold seasons (winter and autumn). Between 1960 and 2000 no winter or autumn blooms occurred; between 2000 and 2010, 24 cases of level 1 alert and one case of level 2 alert were observed in winter. In the last decade, 65 level 1 and 16 level 2 alerts developed during winter and autumn.

Temporal dynamics of yearly average cyanobacterial abundance, presented two different periods and was well characterized by a segmented log-linear model: (I) a first period (1963–2000) where average cell abundance remained constant with time (slope [95% CI] = -0.02 [-0.05 to 0.01]), a breakpoint after the year 2000 [CI 95% = 1995–2005], and (II) a second period characterized by an exponential increase (slope [95% CI] = 0.21 [0.13 – 0.30]) (Figure 3). The results remained similar either by including or excluding years with less data (between 1995 and 2003) or aggregating the information into 5-year periods. Linear weighted regressions also provided similar trends and coefficients and thus we decided to keep the simpler approach. In addition, when data were aggregated in 5-year bins, and the lineal model was performed 250 times, the fitted temporal models indicated a positive trend of cyanobacterial abundance increase in 100% of the cases, being significant in 93% of the cases (Material S2).

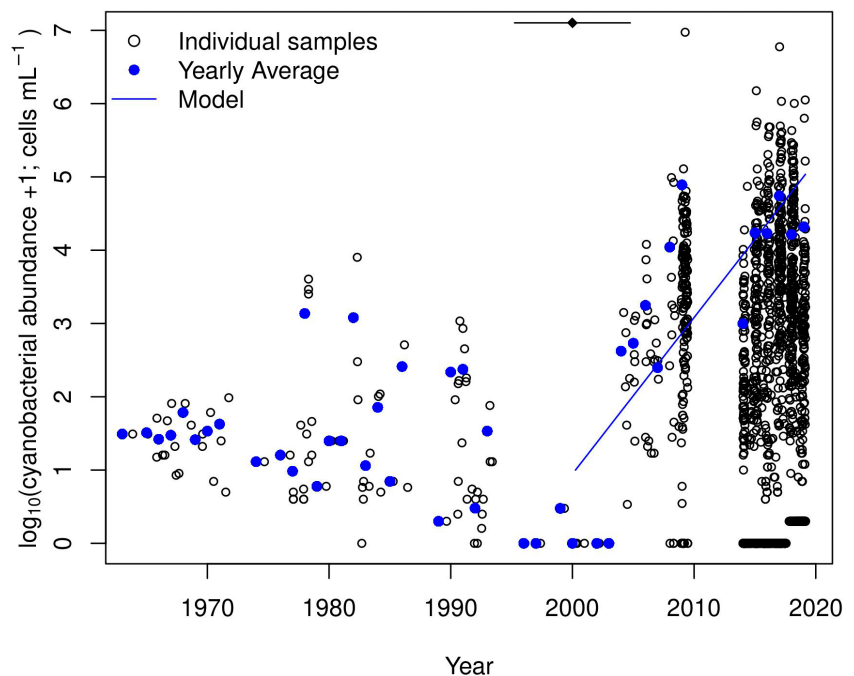


FIGURE 3 Temporal changes in the abundance of cyanobacterial cells in the Uruguay river and the significant fitted slope of the segmented model applied to cyanobacteria yearly average. Segmented model (I) period = 1961–2000 average cell abundance remained constant (slope [95% CI] = -0.02 [-0.05 – 0.01]) and (II) period = 2000–2020 with an exponential increase (slope [95% CI] = 0.21 [0.13 – 0.30]), breakpoint = 2000 [CI 95% = 1995–2005].

3.2 | Climate and hydrological changes observed in the Uruguay river basin

Average, maximum and minimum annual temperature at the watershed level were significantly correlated (minimum vs. mean temperature: $r = 0.93$; maximum vs. mean temperature: $r = 0.84$; minimum vs maximum temperature: $r = 0.58$; $N = 60$, all $p < .01$; Figure 4a). Minimum annual temperatures presented significant positive temporal linear trends since the beginning of the time

series ($T_{\min} = -22.11 + 0.018 \text{ year}$; $N = 60$, $R^2 = 0.32$, $p < .01$). A simple linear trend was chosen with respect to the more complex segmented model as the difference in AIC was low ($\Delta\text{AIC} < 2$).

Precipitation (PP) in the watershed showed an apparent linear temporal trend in the period 1963–2020 but this trend was not significant ($p > .05$; $R^2 = 0.05$) and no breakpoints were detected (Figure 4b). Neither the accumulated flow nor the annual maxima of the Uruguay river flow presented temporal trends ($p > .05$; $R^2 = 0.004$ and $p > .05$; $R^2 = .025$ respectively) (Figure 4c).

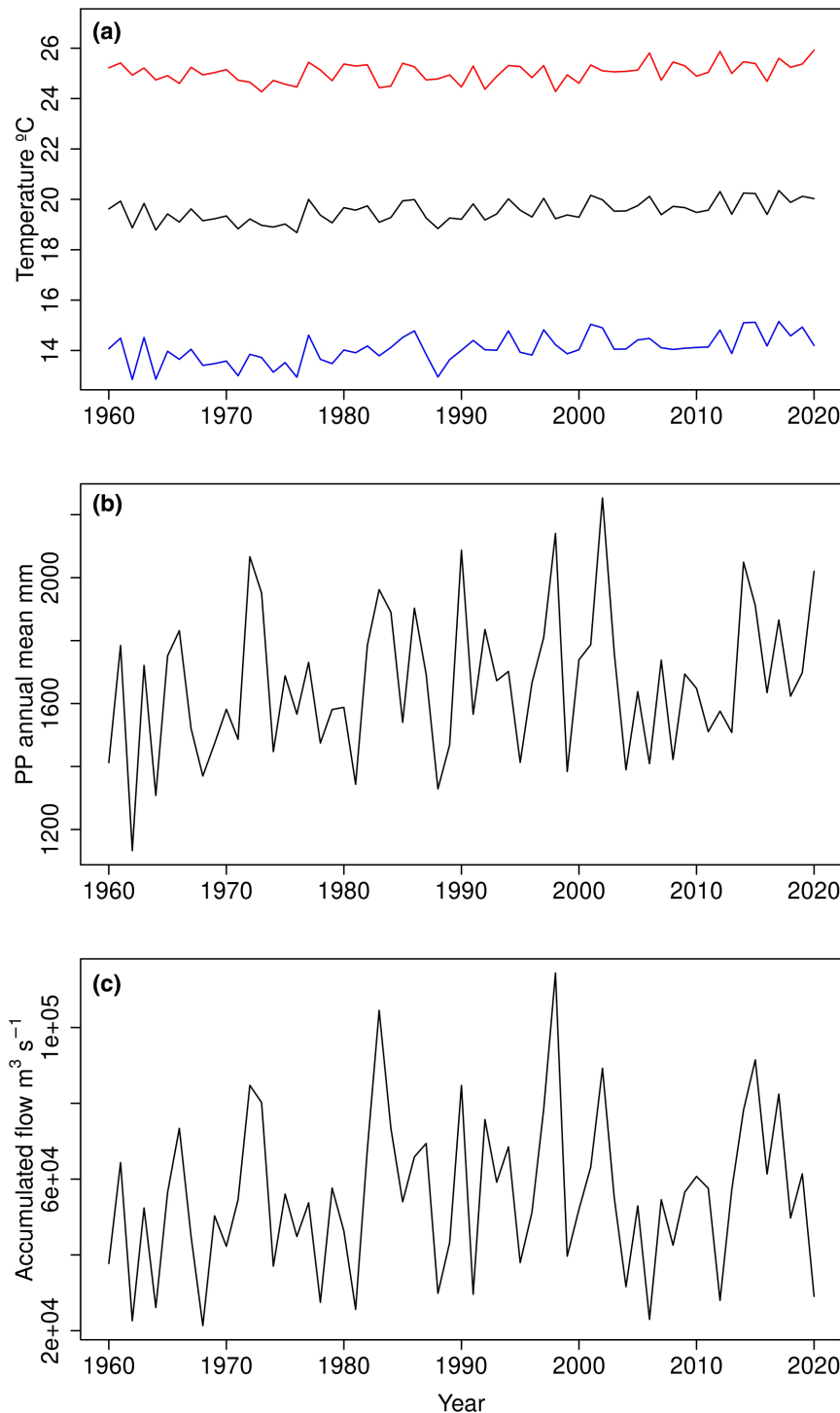


FIGURE 4 Temporal trends for the entire Uruguay basin in (a) temperature ($^{\circ}\text{C}$) including annual average (T_{ave}), maximum (T_{max}) and minimum (T_{min}) temperatures and in (b) annual average precipitation (PP). In (c) Uruguay river accumulated and maximum month average flows are included. Annual temperatures are correlated with maximum and minimum temperatures, temperature and precipitation are not correlated, and precipitation annual mean is correlated with accumulated and maximum river flows.

Correlation analyses between climatic variables for the period 1963–2020 indicated that average annual precipitation and minimum temperature had a weak positive linear correlation ($r = 0.52$, $p < .01$). Precipitation presented a strong correlation with water flow, either accumulated ($r = 0.83$, $p < .01$) or maximum flow ($r = 0.73$, $p < .01$). Minimum temperature exhibited a weak but significant correlation with yearly precipitation and water flow ($r_{pp} = 0.52$; $r_{Q_{max}} = 0.42$; $r_{Q_{acum}} = 0.4$; all $p < .01$) while maximum yearly temperature displayed a negative weak correlation with accumulated water flow ($r_{Q_{acum}} = -0.35$). Maximum and accumulated water flow were strongly correlated (Material S3).

3.3 | Changes in indicators of human and cattle effects

From 1987 to 2020 the collected FIB exhibited a variability of six orders of magnitude, ranging from undetectable to 2×10^6 UFC 100ml^{-1} , a median value of 160 and a mean of 5875 UFC 100ml^{-1} (Figure 5). A negative temporal trend in FIB concentration was described by a log-linear model (slope [95% CI] = -0.017 [-0.02 to -0.013]) with a low but significant explained variance ($R^2 = 0.04$, $p < .001$, $N = 2119$).

3.4 | Temporal trends in land-use change in the Uruguay river basin

The Uruguay river watershed displayed a marked transition in land use from 2000 to 2019 (Figures 1 and 6). The most conspicuous patterns were a 17% increase in land use dedicated to crops and pastures ($23,842\text{ km}^2$), a 97% increase in the forestation area ($10,047\text{ km}^2$), a decrease in 6% of natural forest (3004 km^2) and a decrease in 17% of

natural grasslands ($23,842\text{ km}^2$). This last change represents a loss of ~8% of natural grasslands replaced with intensive agricultural land use, including crops and forestation. Pastures and crops, as well as forestation gains, occurred along the entire basin, with larger proportions in the middle and lower areas (Figure 1). In the upper basin, the loss of pastures and crops was mainly detected in the littoral zones of the river (Figure 1). Data recorded in the upper and middle basins, available for 1985 to 2020, presented the same trend and were highly correlated with the changes registered in the lower basin for the 2000–2020 period (Table 2; Material S4). In addition, the proportion of land uses remained similar throughout most of the study, therefore, representing a proxy for total watershed changes (Table 2).

A major increase in land use dedicated to soybean production occurred along with a large decrease in other crops together with depleted pastures and the class 'mosaic of pastures and annual crops'. Soybeans were first introduced in 2000 but nowadays account for nearly 45% (4114 km^2) of the annual cropland area (Figure 7). Pastures, other crops and the 'mosaic of pastures and annual crops' decreased by 34%, 24% and 48%, respectively.

3.5 | Importance of drivers explaining cyanobacterial abundance

The causal path model indicated that changes in the area dedicated to crops and pastures (CP) displayed the strongest and most significant positive relationship with cyanobacterial abundance ($\log\text{Cya}$) (Table 3 and Figure 8). Model 8 presented the larger difference in AIC ($\Delta\text{AIC} > 35$) with the remaining models and included only the path between CP and $\log\text{Cya}$ as significant (Table 3, Figure 8). A positive relationship between annual precipitation and accumulated flow was also observed, but this relationship did not affect cyanobacterial

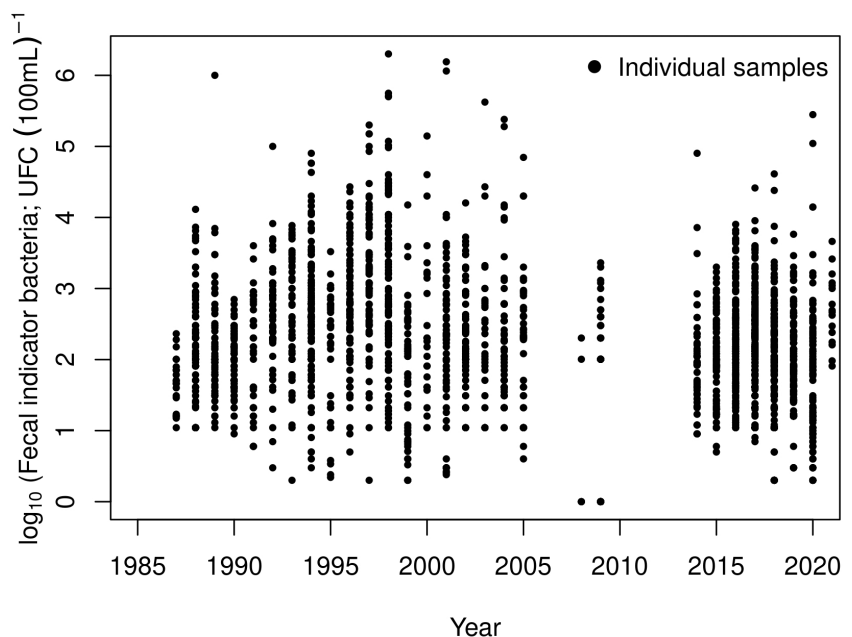


FIGURE 5 Temporal changes in the abundance of fecal indicator bacteria in the Uruguay river.

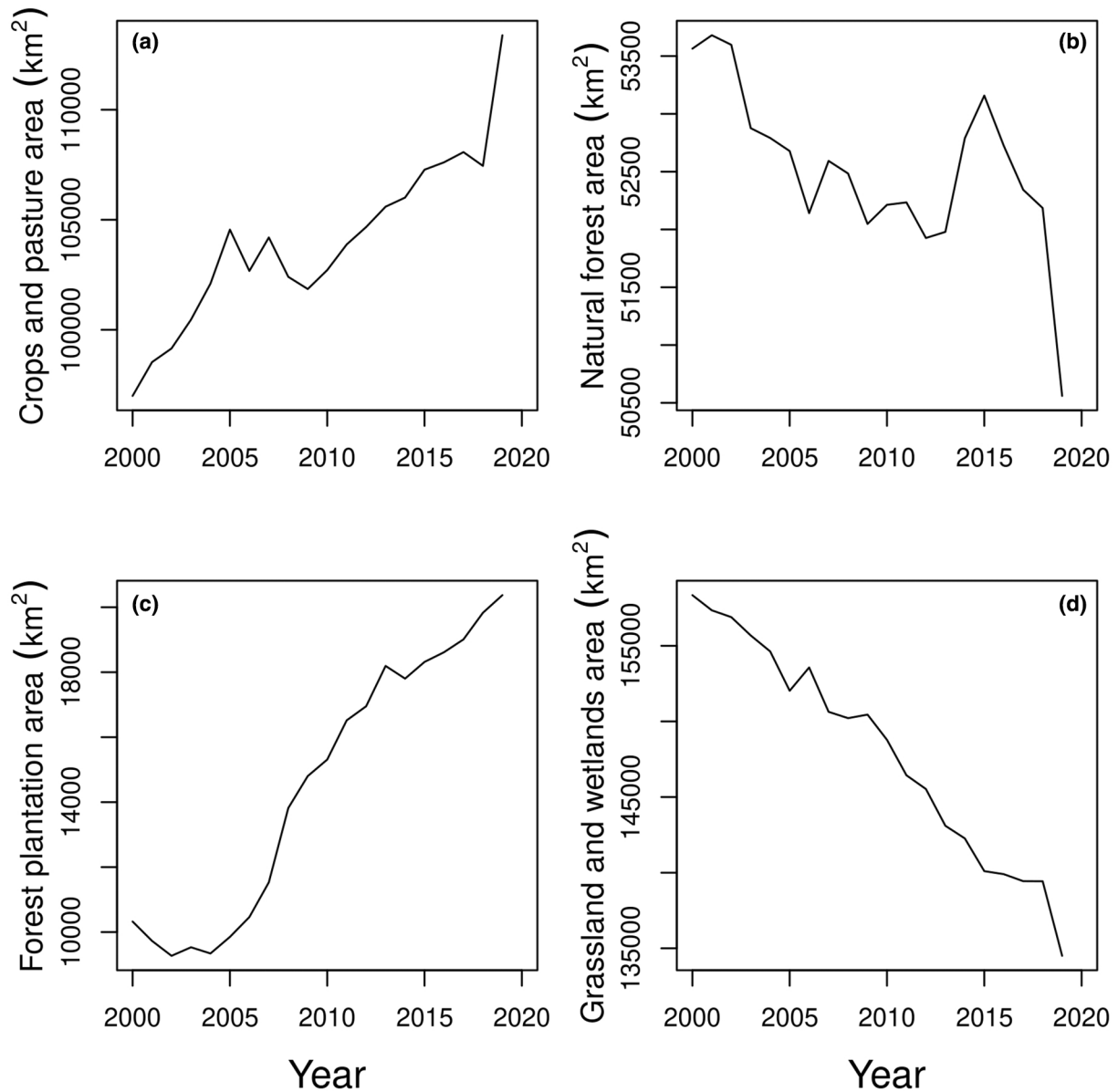


FIGURE 6 Temporal land use changes over the whole Uruguay river watershed. (a) Crops and pasture, (b) natural forest, (c) forest plantation and (d) grassland and wetlands areas.

	CP low	CP UM	Gras low	Gras UM	For low	For UM	Nat low
CP Low							
CP UM	0.73**						
Gra Low	-0.84**	-0.91**					
Gra UM	-0.72**	-0.98**	0.96**				
For Low	0.56*	0.86**	-0.91**	-0.94**			
For UM	0.67**	0.94**	-0.94**	-0.98**	0.96**		
Nat Low	-0.45*	-0.58**	0.53*	0.59**	-0.61**	-0.59**	
Nat UM	-0.54*	-0.77**	0.49*	0.68**	-0.40	-0.67**	0.52*

TABLE 2 Correlation between annual values of land use area from 2000 to 2019 between the lower area (LOW) and the combination of upper and middle areas (UM) of the Uruguay river basin.

Note: Land uses included were: crops and sown pastures (CP), natural forests (Nat), grasslands and wetlands (Gra), and forest plantation (For). The symbol indicates the significance level of Spearman correlation (* $p < .05$, ** $p < .01$).

abundance (Table 3). The selected model Fisher's C statistic was not significant ($C = 1.50$, $df = 2$, $p = .47$) supporting the hypothesis that data were generated following the causal relations specified in the dyacyclic aggregated path (Model 8, Table 4). The RMSE of approximation was low (95% confidence interval $[-0.36]$, $p = .49$) while the comparative fit index was high ($cfi = 1.00$) as well as the explained variance ($R^2 = 0.52$). Precipitation accounted for a high amount of variance from the accumulated water flow ($R^2 = 0.79$). Similar results were obtained when T_{min} was included in the model instead of T_{max} (Material S5).

3.6 | Relationship with total phosphorus concentration in water

An increase in average total annual phosphorus in water (TP) was observed with time ($TP_{mean} = -5.98 + 0.003 \text{ year}$; $R^2 = 0.66$, $p < .005$).

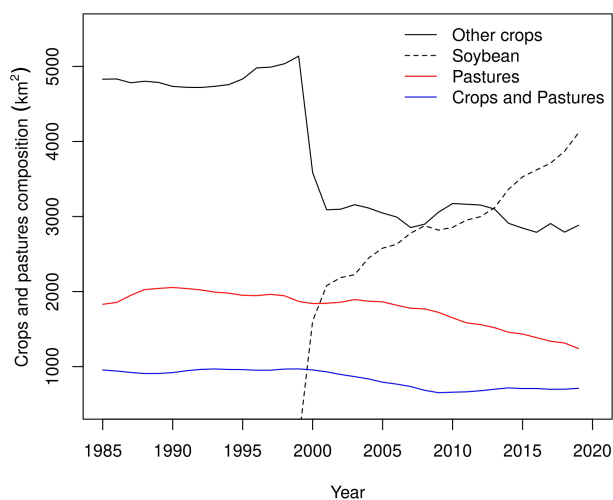


FIGURE 7 Temporal changes in the composition of crops and pasture class over the upper and middle Uruguay river watershed.

TABLE 3 List of the causal path models constructed to explain cyanobacterial abundance ($\log Cya$) sorted according to Akaike information criteria (AIC).

Model	ΔAIC	Paths					
		CP \rightarrow $\log Cya$	$T_{max} \rightarrow \log Cya$	PP \rightarrow Qacum	Qacum $\rightarrow \log Cya$	PP $\rightarrow \log Cya$	Nat $\rightarrow \log Cya$
8: All except Nat	0	0.61	ns	0.89	ns	ns	–
1: All variables	2	0.55	ns	0.89	ns	ns	ns
5: CP and T_{max}	41	0.61	ns	–	–	–	–
6: Only CP	41	0.70	–	–	–	–	–
4: CP and Nat	43	0.72	–	–	–	–	ns
2: All except effect of PP in Qacum	47	0.55	ns	–	ns	ns	ns
7: Only T_{max}	52	–	0.46	–	–	–	–
3: Climatic	55	–	0.46	ns	ns	ns	–

Note: Significant paths and their coefficients ($p < .05$) are shown for each model. We recall that temperature was significant only when land uses were not included as a possible path in the model. ns: path included but with non-significant coefficients, '–': path not included in the model.

Abbreviations: CP, crops and pastures area; Nat, natural class; PP, precipitation, Qacum, accumulated water flow; T_{max} , maximum annual temperature.

Cyanobacterial cells abundance (Cya) was significantly related with TP values higher than 0.2 mg L^{-1} ($N = 46$, Pearson correlation: 0.46; $\log_{10}(Cya + 1) = 2.22 \times TP \text{ mg L}^{-1} + 1.96$; $df = 44$, $R^2 = 0.18$, $p < .005$; Figure 9). For TP values lower than 0.2 mg L^{-1} no significant correlation was obtained. Finally, we also obtained a positive relationship between average annual TP concentration in water and area dedicated to annual crops and pastures ($TP \text{ mg ml}^{-1} = 1.79 \times \log_{10}(\text{Annual crops and pasture area}) - 8.93$, $R^2 = 0.54$, $p < .05$; Figure 10a) and a negative relationship with natural grassland area ($TP \text{ mg ml}^{-1} = -1.70 \times \log_{10}(\text{Grasslands area}) + 8.79$, $R^2 = 0.63$, $p < .05$; Figure 10b).

4 | DISCUSSION

In this manuscript, we evidenced the exponential increase in cyanobacterial abundance and number of blooms in a relevant subtropical aquatic ecosystem of South America. A comprehensive geographical long-term analysis confirmed that the increase of intensive agriculture land use was the main driver. Climatic and hydrological effects on cyanobacterial abundance, otherwise, were rather marginal. Moreover, results indicate that models not including the effect of land-use change would incorrectly point to temperature as a relevant variable, but under a causal path analysis, we demonstrated that its effect was negligible when compared with land-use change. Anthropogenic drivers of eutrophication other than land use, such as sewage or contamination by cattle were discarded as the temporal trend of fecal contamination was opposite to that observed for cyanobacterial abundance. Previous field studies suggest that anthropogenic factors (e.g. fertilizer, gross domestic product, population) are stronger than climatic drivers (e.g. temperature, rainfall; Fang et al., 2022). In addition, nutrients and not temperature were identified as the key drivers for cyanobacterial biomass in lakes from America (Bonilla et al., 2023).

The global trend towards the replacement of natural areas by cropping and pastures was validated for the Uruguay basin. A drastic

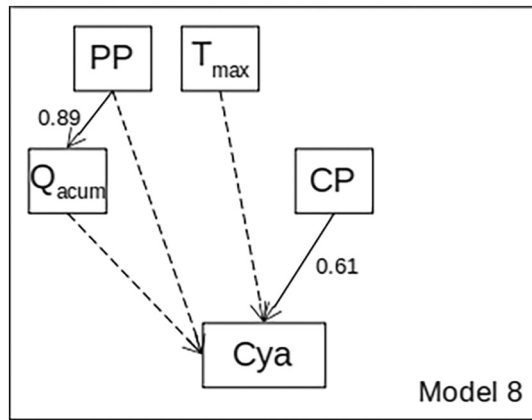


FIGURE 8 Path diagram of the selected model showing the expected links between climatic (PP, T_{max}), hydrological (Q_{acum}) and upper basin land use (crops and pastures: CP, natural forests: Nat) variables with the logarithm of cyanobacterial abundance (CYA). Significant coefficients ($p < .05$) are shown while non-significant relationships are presented as dashed lines.

TABLE 4 Coefficients estimated in the path analysis of the selected model to explain cyanobacterial abundance with climatic, land use and hydrologic variables.

Variable	Coefficient	SE	z	p
PP	-0.14	0.30	-0.47	.64
T_{max}	0.23	0.16	1.39	.17
Q _{acum}	0.13	0.30	0.42	.67
CP	0.55	0.22	2.32	.02
Nat	-0.06	0.22	-0.27	.79
PP~Q_{acum}	0.89	0.03	9.55	<.001

Note: Their standard error (SE), the z-statistics (z) and the associated p values are included. The significant variable was crop and pasture area (CP in bold) and the relationship between precipitation (PP) and accumulated flow (Q_{acum}). The remaining variables showed non-significant relationships ($p > .05$).

Abbreviations: Nat, natural forests class; Q_{acum}, accumulated water flow; PP, precipitation; T_{max} , maximum annual temperature.

change in the type of farming and crops occurred in the new millennium (Giller et al., 2021; Schlindwein et al., 2021) with a large expansion of soybean production (Figure 7). These practices can trigger large phosphorous releases to water bodies, due to increased phosphate fertilization and no-till practices, stratification of phosphorous content in surface soil horizons and facilitation of phosphorous runoff (Carver et al., 2022). These mechanisms were confirmed here with linear positive relations between total phosphorous and area of crops and sown pastures, as well as between total phosphorous and cyanobacterial abundance. In future analyses, nitrogen inputs should also be evaluated (Paerl et al., 2016; Wurtsbaugh et al., 2019).

In the middle and lower Uruguay basin, soybean expansion was at expense of the deterioration area of natural grasslands previously devoted to cattle ranching, which shows lower phosphorous exports (Goyenola et al., 2020; Modernel et al., 2016; Viglizzo et al., 2001). This resulted in increased nutrient loads and a reduced capacity of

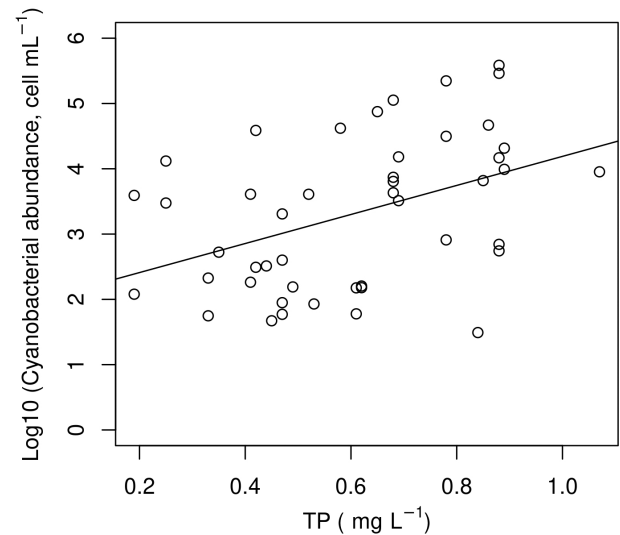


FIGURE 9 Relation between cyanobacterial cell abundance (CYA) and total phosphorus in water (TP). The adjusted linear model is included ($\log_{10}(\text{Cya} + 1) = 2.22 \times \text{TP mg L}^{-1} + 1.96$, $df = 44$, $R^2 = 0.18$, $p < .01$).

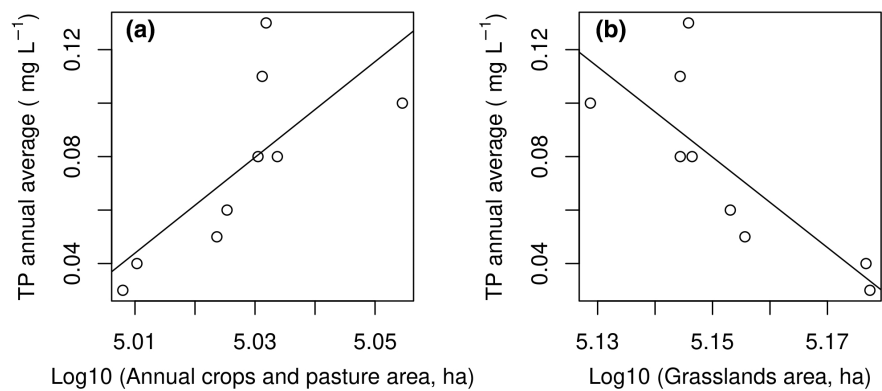
natural vegetation for filtering the contaminated water runoff from land (Goyenola et al., 2020). The gain in secondary forest in the northern basin (Rosa et al., 2021) was not able to counteract the increment in agricultural area promoting cyanobacterial abundance and toxic blooms.

4.1 | Climatic and hydrological variables affecting cyanobacteria

In general terms, temperature, precipitation and river flow modulate ecosystem's eutrophication (Meerhoff et al., 2022; Salk et al., 2022). In this study, these variables did not present a significant contribution to explain major historical changes in cyanobacterial abundance in the Uruguay river. Temperature values were never limiting for cyanobacterial growth (Reynolds et al., 2002; Segura et al., 2018), and blooms occurred throughout the year including the coldest months (Kruk et al., 2017). Furthermore, it has been recently shown that different toxic cyanobacterial ecotypes exhibiting different temperature optima exist (Martínez de la Escalera et al., 2022) sustaining potential toxicity production along the entire year in the studied system.

The obtained positive relationship between precipitation and water flow is coincident with studies evaluating larger periods (1900–2020) in the lower reaches of the basin (Barros et al., 2015; Díaz et al., 2020; Saurral et al., 2008; Ungerovich et al., 2021). In addition, previous studies described how water flow modulates cyanobacterial blooms (Adloff et al., 2018; Ferrari et al., 2011; Mitrovic et al., 2011; O'Farrell & Izaguirre, 2014). However, our results evidenced that in the long run (years-decades), land use change and its effect on eutrophication were hierarchically more important than hydrology. Hydrological variability is expected to modulate cyanobacteria at

FIGURE 10 Relation between (a) average annual total phosphorus concentration in water (TP) and area dedicated to annual crops and pastures and (b) between TP and grassland area. The fitted models are included (a) $TP \text{ mg ml}^{-1} = 1.79 \times \log_{10}(\text{Annual crops and pasture area}) - 8.93$ ($R^2 = .54$, $p < .05$). (b) $TP \text{ mg ml}^{-1} = -1.70 \times \log_{10}(\text{Grasslands area}) + 8.79$ ($R^2 = .63$, $p < .05$).



shorter time scales (days-months), promoting blooms by biomass accumulation (Bowling et al., 2013) and long-range transport (Kruk, Martínez, et al., 2021; Kruk, Piccini, et al., 2021).

An increase in more than four orders of magnitude in the abundance of cyanobacteria took place between 1963–2000 and 2000–2020. This type of catastrophic shift is commonly observed in elsewhere aquatic ecosystems (Scheffer et al., 1993) and specifically in reservoirs (Yang et al., 2017). Phytoplankton community shifts driven by human activities, particularly nutrient enrichment, changes rapidly from species-rich communities experiencing good water quality into cyanobacteria-dominated communities with toxin production (Scheffer et al., 1993). These drastic shifts are non-linear and reversing such a process could take far longer than it takes to arrive to degraded quality ecosystems. A clear evidence of a regime shift can be traced to the extreme of the closure of three potabilization plants (years 2005, 2006 and 2008; OSE, 2009), the persistence of blooms throughout the year, the dramatic increase in the number of health alerts from bi-national authorities (especially after 2000), and the occurrence of acute human intoxications in the river and downstream (Giannuzzi et al., 2011; Vidal et al., 2017). These bloom events reached a climax in 2019, when an unprecedentedly large and persistent bloom of *Microcystis* reached the Río de la Plata (Aubriot et al., 2020; Kruk, Martínez, et al., 2021; Kruk, Piccini, et al., 2021).

4.2 | Future scenarios and land-use changes on demand

Land use changes are affected mainly by economical drivers (Bueno et al., 2021; Modernel et al., 2016; Schlindwein et al., 2021). Brazil, Argentina and Uruguay are major producers of agricultural commodities that increased substantially in the last years to supply the demand of the world market (Bueno et al., 2021; Schlindwein et al., 2021). As a result, the expansions of monocultures such as soybean or eucalyptus were performed in absence of adequate conservation strategies and environmental impact assessments (Bueno et al., 2021; Modernel et al., 2016; Viglizzo & Frank, 2006). Along with this escalation in world demand for crops, warming, increased precipitation and increased

river flow are expected (Díaz et al., 2013; Vera et al., 2006) with synergistic effects modulating water quality, pollution and biodiversity loss (Wilkinson et al., 2022; Zabel et al., 2019). Some of the areas that currently experience restrictions on cultivation will become productive regions depending on supplementary irrigation by constructing dams. Dams modulate river discharge and sequester sediments (Bonachea et al., 2010; Depetris & Pasquini, 2007a), thus favoring eutrophication and allowing reproduction and accumulation of cyanobacteria, increasing their toxin production and diversity (Martínez de la Escalera et al., 2017, 2022) as reported for the upper reaches (Debastiani Júnior et al., 2016) and at the lower stretches (O'Farrell & Izaguirre, 2014) of the river. Increases in extreme precipitation events, allow rapid nutrient transport from soils into rivers (Ockenden et al., 2017) and then to dams, where blooms will continue to increase in frequency and magnitude. Extreme events will help transport blooms to coastal and marine ecosystems along with their negative effects (Alcántara et al., 2022; Kruk, Martínez, et al., 2021; Kruk, Piccini, et al., 2021; Preece et al., 2017).

The first and more important step to limit the increase in cyanobacterial blooms is to reduce the external anthropogenic loading of nutrients at the entire basin level as well as limiting dam construction. Otherwise, local actions will have little chance of being effective (Chorus & Welker, 2021). Major changes in agricultural practices will be required to mitigate phosphorus losses and cyanobacterial blooms under a climate change scenario (Ockenden et al., 2017) especially at the catchment-to-coast transboundary continuum (Paerl et al., 2018; Wurtsbaugh et al., 2019). Large river basins include international territories over several countries and their management requires coordinated regional actions in terms of river water use and land-use policies, which are still far from being implemented in the current settings (Saguier et al., 2021). As current results suggest, the increase of surface area dedicated to high nutrient input agricultural practices and the intensification of these practices in the basin will intensify the present situation of toxic cyanobacterial blooms in this subtropical river.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at <https://doi.org/10.5061/dryad.6t1g1jx3d>.

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