Indicadores de eutrofización cultural en ecosistemas acuáticos continentales subtropicales y modelos predictivos de cianobacterias planctónicas

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Índice general

Prefacio.....3
  Resumen gráfico de la tesis.....4
  Resumen.....5
  Abstact.....7
  Lista de artículos y presentaciones en congresos.....9
1. Introducción general.....11
  1.1 Eutrofización cultural de los cuerpos de agua límnicos.....12
  1.2 Sinergia entre la eutrofización y forzantes climáticos.....13
  1.3 Cianobacterias planctónicas y su éxito en los ambientes límnicos eutróficos.....15
  1.4 Modelos predictivos de eutrofización y de cianobacterias planctónicas.....16
  1.5 Eutrofización en los ecosistemas límnicos de Uruguay.....18
  1.6 Justificación.....19
2. Hipótesis e objetivos.....21
  2.1 Hipótesis.....22
  2.2 Objetivo general.....23
  2.3 Objetivos específicos.....23
3. Resultados.....24
  I: Influence of land use changes and hydrology on freshwater eutrophication, Uruguay.....25
  II: The chlorophyll-nutrient relationship varies with lake type and seasonality in subtropical lakes.....62
  III. Temperature and precipitation shape the distribution of harmful cyanobacteria in subtropical lotic and lentic ecosystems.....88
  IV: Predicting cyanobacterial biovolume from water temperature and conductivity using a Bayesian compound Poisson-Gamma model.....100
4. Discusión general y conclusiones.....117
5. Perspectivas.....124
6. Bibliografía.....126

Prefacio

Resumen gráfico de la tesis

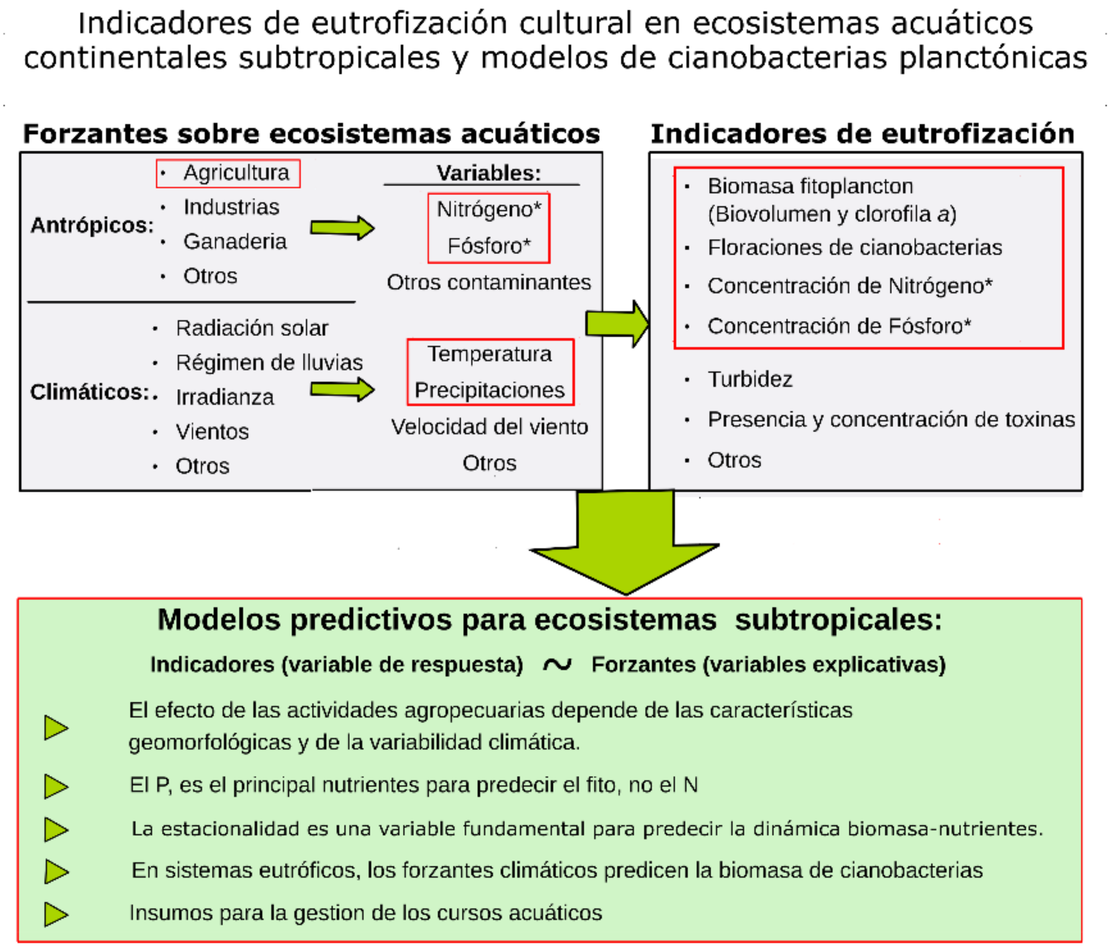


Figura 1: Resumen gráfico que destaca los aspectos centrales analizados en la tesis (contornos en rojo) y los nuevos conocimientos generados sobre la eutrofización en ecosistemas subtropicales a partir de los modelos predictivos.

*considerados tanto variables forzantes como indicadores de la eutrofización.

Resumen

La eutrofización cultural es un fenómeno global que causa deterioro de la calidad del agua. Las floraciones de cianobacterias, como respuesta directa del proceso de eutrofización, son cada vez más frecuentes en todo el mundo, limitando el uso del agua con distintos fines. A pesar de décadas de estudios, sobre las causas y los efectos de la eutrofización, aún falta más información para los ecosistemas de climas cálidos. Además, los modelos predictivos de las cianobacterias son un gran desafío dada la alta asimetría en la distribución de su biomasa, desde estar prácticamente ausentes a alcanzar valores extremos (floraciones). Por otro lado, dentro de los grupos que forman floraciones frecuentemente se asume la predominancia de las formas coloniales de gran tamaño de tipo acumulativas (ejemplo *Microcystis*), pero esto no es claro en ecosistemas subtropicales. El objetivo general de la tesis fue determinar los efectos de los forzantes climáticos y antrópicos sobre la distribución y biomasa del fitoplancton y de las cianobacterias planctónicas en una región subtropical. Se recopiló y utilizó una matriz de datos históricos (1982 a 2020) de Uruguay (latitud 30 to 35ºS, longitud 53 to 58ºW). Se realizó un análisis sinóptico para evaluar la tendencia temporal de eutrofización a nivel país, basado en fósforo total en el agua. Se seleccionaron y muestrearon subcuencas del país para analizar los efectos de cambios en los usos de suelo y en su interacción con las precipitaciones acumuladas sobre indicadores de eutrofización. Se desarrollaron nuevos modelos predictivos de indicadores de eutrofización y de la biomasa de cianobacterias planctónicas utilizando herramientas innovadoras de la estadística Bayesiana. El estado trófico general aumentó en las grandes cuencas del país desde 2002 a 2020. Asimismo, se pudo evidenciar una relación entre el aumento del fósforo total en cursos de agua en el tiempo con el aumento del uso de suelo destinado a la agricultura y efectos directos de las precipitaciones sobre la concentración de este nutriente, en las subcuencas analizadas. El fósforo (y no el nitrógeno) fue el nutriente principal para predecir la concentración de la clorofila *a* fitoplanctónica en ecosistemas naturales y artificiales, cuestionando paradigmas sobre el papel de los nutrientes en lagos de climas cálidos. Contrariamente a lo esperado, *Dolichospermum* fue el género de cianobacterias más distribuido y más frecuente en el país, incluso en los ecosistemas lóticos, lo cual está en línea con las predicciones globales de aumento de este grupo de cianobacterias (Nostocales) y alertan sobre la presencia de toxinas que no han sido aún estudiadas en el país. En ecosistemas

eutróficos, la temperatura en interacción con las precipitaciones y con la conductividad, fueron buenos predictores de la biomasa de cianobacterias planctónicas en lagos y ríos y en zonas costeras, respectivamente. La aproximación Bayesiana utilizada es novedosa y permitió superar desafíos vinculados a la modelación de cianobacterias. Los resultados de esta tesis aportan conocimiento sobre la eutrofización y la ecología de las cianobacterias planctónicas en regiones subtropicales, y son un insumo directo para mejorar la gestión de los recursos acuáticos.

Abstact

Cultural eutrophication is a global phenomenon that causes the deterioration of freshwaters. Cyanobacterial blooms, often a direct response to the process of eutrophication, are becoming more frequent around the world, limiting the use of water for different purposes. Despite decades of studies on the causes and effects of eutrophication, information for warm-climate ecosystems is still limited. In addition, developing predictive models for cyanobacteria is a great challenge due to the high asymmetry in their biomass distribution, from near absences to extreme values (blooms). Within bloom-forming cyanobacteria, the predominance of large colonial forms (e.g., *Microcystis*) is frequently assumed, but this trend is not clear for subtropical ecosystems. The general objective of this thesis was to determine the effects of climatic and anthropic factors on the distribution and biomass of phytoplankton and planktonic cyanobacteria in a subtropical region. A matrix of historical data (1982 to 2020) for Uruguay (latitude 30 to 35ºS, longitude 53 to 58ºW) was created. Using total phosphorus, a synoptic analysis was carried out to evaluate temporal trends of eutrophication in the country. Small watersheds of the Santa Lucia River were then selected and sampled to analyze the effects of land use changes and their interaction with accumulated rainfall on eutrophication indicators. New predictive models of eutrophication indicators and cyanobacterial biomass were also developed using Bayesian statistics. The trophic status of large basins generally increased between 2002 and 2020, toward eutrophic and hypereutrophic conditions, which poses a serious threat to water use. In the selected watersheds, there was a positive relationship between total phosphorus and the percent of agriculture in the catchment, as well as a direct effect of rainfall on the P concentration. Phosphorus (and not nitrogen) was the main nutrient that predicted the concentration of phytoplankton chlorophyll *a* in natural and artificial ecosystems, questioning paradigms about the role of nutrients within warm climates lakes. Somewhat surprisingly, *Dolichospermum* was the most distributed and most frequent genus of cyanobacteria, even in lotic ecosystems. This is consistent with predictions of a global increase of Nostocales and also serves as a warning about the probable presence of toxins, that have yet to be analyzed in the country. In eutrophic ecosystems, water temperature, in interaction with rainfall and conductivity, was a good predictor of planktonic cyanobacterial biomass. The novel Bayesian approach used in this study enabled us to

overcome challenges related to modeling cyanobacterial biomass. The results of this thesis provide knowledge about eutrophication and the ecology of planktonic cyanobacteria in subtropical regions that can be directly applied to the management of inland waters.

Lista de artículos y presentaciones en congresos

<u>Esta tesis ha generado los siguientes artículos:</u>

- **Haakonsson S.,** Rodríguez M.A., Aubriot L., Chalar G., Rodríguez-Gallego L., Bonilla S.

The chlorophyll-nutrient relationship varies with lake type and seasonality in subtropical lakes.
Manuscrito sometido

- **Haakonsson S.**, Rodríguez-Gallego L., Somma A., Bonilla S. 2017

Temperature and precipitation shape the distribution of harmful cyanobacteria in subtropical lotic and lentic ecosystems
Science of the Total Environment, 609.

- **Haakonsson S.**, Rodríguez M.A., Carballo C., Pérez M.C., Arocena R., Bonilla S. 2020

Predicting cyanobacterial biovolume from water temperature and conductivity using a Bayesian compound Poisson-Gamma model
Water Research, 176

<u>Presentaciones en congresos internacionales:</u>

- **Haakonsson S.**, Rodriguez M.A., Rodríguez-Gallego L., Arocena R., Carballo C., Bonilla S.

Predicting cyanobacterial biovolume in a subtropical estuary through a Bayesian Compound Poisson-Gamma approach (2018).
IFHAB, 2nd Interdisciplinary Freshwater Harmful Algal Blooms Workshop, Toronto, Canada.
Modalidad: Presentación oral

- **Haakonsson S.**, Rodriguez M.A., Rodríguez-Gallego L., Arocena R., Pérez M., Carballo C., Bonilla S.

Predicting planktonic cyanobacteria through a novel Bayesian approach (2019).
11th International Conference on Toxic Cyanobacteria (2019), Cracovia, Polonia
Modalidad: Póster

Parte de los resultados de la tesis ha contribuido a la generación de los siguientes artículos:

- **Haakonsson S.**, Maciel F., Rodríguez M. A., Ponce de León L., Rodríguez-Gallego L., Arocena R., Pedocchi F., Bonilla S.

Improving cyanobacteria monitoring in estuaries combining Bayesian modeling and remote sensing
Manuscrito en preparación

- Bonilla S., Aubriot A., **Haakonsson S**., Illarze M., Díaz I., Brena, B. 2021

Las floraciones de cianobacterias tóxicas comprometen el uso del agua del Río Negro, Uruguay
INNOTEC No. 22 (e577)

1. Introducción general

1.1 Eutrofización cultural de los cuerpos de agua límnicos

El aumento de la carga de nutrientes en el agua conduce a mayores tasas metabólicas alterando la estructura y la función de los ecosistemas acuáticos, proceso denominado eutrofización. Si bien esto ocurre naturalmente, es acelerado por las actividades humanas que aportan nutrientes que llegan a los cuerpos de agua, y se denomina eutrofización cultural (de ahora en adelante eutrofización) (Dodds y Whiles, 2010; Paerl y Paul, 2012). Los principales nutrientes en causar la eutrofización son el fósforo y el nitrógeno, dado que son los que generalmente controlan el crecimiento de los organismos autotrófos (Conley et al., 2009).

Los aportes excesivos de estos nutrientes pueden proceder de fuentes puntuales (industrias y saneamiento urbano) o difusas (agricultura y ganadería principalmente). Dentro de los diferentes tipos de uso de suelo, la agricultura es la actividad principal asociada a la eutrofización, debido a la aplicación de fertilizantes y a las prácticas de manejo empleadas (Carpenter et al., 1998; Moss, 2008). Su área incluso, puede tener una relación lineal directa con los nutrientes en los cuerpos de agua de la misma (Kronvang et al., 1995; Varanka y Luoto, 2015). La carga de nutrientes que llega a los cuerpos de agua depende, además del tipo de uso del suelo (actividades productivas, grado de urbanización, cobertura vegetal, etc.), de las variables físicas y estructurales (geomorfológicas y climáticas-meteorológicas) generando un escenario complejo para el manejo (McFarland y Hauck 2001; Jeje, 2006). La relación entre el uso de suelo y los nutrientes en el agua, por lo tanto, puede presentar gran variación según las características de cada cuenca y también de los patrones climáticos de cada región (Andersson y Nyberg, 2009; Varanka et al., 2015).

Durante décadas ha habido un debate basado en numerosos estudios científicos que evaluaron cuál de los nutrientes, si el P o el N, era la variable más importante para causar eutrofización de los cuerpos de agua límnicos (Canfield, 1983; Lewis y Wurtsbaugh, 2008; Paerl et al., 2016; Prairie, 1989). De manera muy general existen dos grandes hipótesis: la que sostiene que el P es el nutriente crítico en causar eutrofización, mientras el N juega un papel secundario y es solo es limitante en ecosistemas ya eutróficos (Schindler et al., 1974, 1977, 2008; Sterner, 2008; Vollenweider, 1968) y la que argumenta que ambos nutrientes, N y P,son importantes para la eutrofización de los lagos

(Elser et al., 2007; Lewis et al., 2011; Paerl et al., 2016; Wurtsbaugh et al., 2019). En particular para climas cálidos (tropicales y subtropicales), se ha propuesto que el N podría ser más importante que el P (Lewis, 2000, 2002; Talling y Lemoalle, 1998) por factores asociados a diferencias climáticas. Esta postura ha sido debatida por algunos resultados empíricos. Por ejemplo, Huszar et al., 2006, no encontraron que el N fuera más prevalente en limitar la producción primaria en su estudio con 192 lagos y embalses subtropicales y tropicales. Mientras otros estudios han concluido que sin importar región ni clima, los lagos pueden ser limitados tanto por P o por N dependiendo de factores locales como la morfometría del ecosistema acuático y las características de la cuenca hidrográfica (Abell et al., 2012; Elser et al., 2007; Kosten et al., 2009). Por lo tanto, el debate sigue abierto y es necesario contar con más estudios para saber cuál de los nutrientes es el más importante en la eutrofización de los cuerpos de agua límnicos en climas subtropicales.

Los efectos causados por la eutrofización cultural son diversos, e incluyen la reducción en la diversidad biológica y de la transparencia del agua, problemas para la potabilización por mal sabor y olor del agua y por las floraciones de algas nocivas (FAN) (Smith y Schindler, 2009). Las FAN por lo tanto pueden ser considerados como un efecto indirecto de la eutrofización o como “síntoma secundario” de la misma. Particularmente las floraciones de cianobacterias, han generado mayor preocupación, por el aumento en su frecuencia registrada y por la presencia de toxinas altamente toxicas, generando efectos directos sobre la salud humana y animal limitando o impidiendo el uso del agua (Chorus y Welker, 2021; Hart et al., 1999).

1.2 Sinergia entre la eutrofización y forzantes climáticos

Los patrones climáticos, precipitaciones, vientos y las variaciones térmicas, afectan directamente la productividad y el funcionamiento de los ecosistemas acuáticos continentales. Las precipitaciones afectan indirectamente la magnitud de los aportes de nutrientes que llegan a los cuerpos de agua desde las cuencas hidrográficas por el escurrimiento, así como a la dilución de los nutrientes presentes en el sistema. Según sea la duración e intensidad de las precipitaciones, las mismas pueden favorecer el crecimiento de la biomasa del fitoplancton y el desarrollo de FAN (Paerl y Huisman, 2009; Paerl y Paul, 2012).

El efecto sinérgico entre las precipitaciones y la eutrofización influye de manera diferencial entre las diferentes regiones climáticas y a lo largo del tiempo. Por ejemplo, en las regiones templadas, el crecimiento del fitoplancton es fuertemente estacional, con dos picos máximos de biomasa, uno en primavera y otro en el verano (Dodds y Whiles, 2010). En condiciones de exceso de nutrientes, estos máximos pueden prolongarse transformándose en uno solo pico y con los efectos del cambio climático (precipitaciones y aumento de temperatura) esta tendencia se puede agravar (De Senerpont Domis et al., 2013; Jeppesen et al., 2009). Sin embargo, para las regiones subtropicales y tropicales, el conocimiento sobre la dinámica entre la eutrofización y las forzantes climáticas es más limitado que en los ambientes de climas templados (De Senerpont Domis et al., 2013; Reichwaldt y Ghadouani, 2012). Hay estudios que indican que los ecosistemas límnicos de las regiones cálidas son más variables y por eso menos predecibles que los de zonas templadas (Havens et al., 1999; Huszar et al., 2006; Lewis, 1996). Por ejemplo, para ecosistemas de climas subtropicales el factor viento introduce grandes variaciones en las relaciones entre la biomasa del fitoplancton y las concentraciones de nutrientes en el agua (Crisci et al., 2017; Havens et al., 1999), mientras que en los climas tropicales los cambios en la profundidad de la columna de agua, dado por época seca versus época lluviosa, también es un factor clave en esta relación (Hoyer et al., 2005; Lewis, 2000). Por otro lado, las predicciones climáticas globales pronostican que las precipitaciones disminuirán en la mayoría de las zonas geográficas con climas subtropicales (Meehl et al., 2007). Eso generará mayores tasas de evotranspiración y menor escurrimiento, por lo que se espera que los efectos del cambio climático sean menores en comparación con otras regiones climáticas (De Senerpont Domis et al., 2013). Sin embargo, las predicciones de cambio climático pronostican un aumento de las precipitaciones y de los eventos extremos en algunas zonas geográficas con climas subtropicales como la zona sur oeste de América del Sur, donde se encuentra Uruguay (Díaz, 2018). Esto implica que los modelos generales globales no son adecuados para estas zonas y destaca la importancia de realizar estudios en cada región para poder estimar los efectos combinados de los forzantes climáticos y la eutrofización.

1.3 Cianobacterias planctónicas y su éxito en los ambientes límnicos eutróficos

Las cianobacterias son procariotas que realizan fotosíntesis oxigénica y evolucionaron hace más de 2.900 millones años (Fournier et al., 2021; Schirrmeister et al., 2016). Actualmente son un grupo de gran diversidad morfológica y funcional particularmente en ecosistemas límnicos donde tienen un enorme impacto en los ciclos bio-geoquímicos (carbono y nitrógeno) de la biosfera (Whitton, 2012).

El aumento de nutrientes proveniente de actividades antrópicas es reconocido como el principal causante del aumento y gravedad de las floraciones de cianobacterias a nivel mundial (Glibert y Burkholder, 2006; Huisman et al., 2018; Wurtsbaugh et al., 2019). A medida que la concentración de nutrientes aumenta, ocurre muchas veces un cambio en la comunidad fitoplanctónica hacia la dominancia de cianobacterias (Dokulil y Teubner, 2000; Dolman et al., 2012; Pick y Lean, 1987). Los rasgos que contribuyen al éxito de las cianobacterias en cuerpos de agua eutrofizados incluyen, la capacidad de formar vesículas de gas regulando la flotabilidad, la capacidad de fijar N_2 cuando disminuye el nitrógeno inorgánico disuelto disponible, alta eficiencia para incorporar el CO_2 aún a bajas concentraciones gracias a los CCM (CO_2-concentrating mechanism) entre otros (Pierce y Omata, 1988).

En los cuerpos de agua eutrofizados donde las condiciones para las floraciones son las adecuadas, los forzantes climáticos juegan un papel fundamental sobre la proliferación de cianobacterias planctónicas (Bormans et al., 2005; O'Neil et al., 2012; Reichwaldt y Ghadouani, 2012). Por un lado, el aumento de la temperatura favorece su crecimiento, dado que muchas, pero no todas tienen su temperatura óptima de crecimiento por encima de de 25 ºC, mayor a la óptima de la mayoría de las algas eucariotas (Huisman et al., 2018). El aumento de la temperatura además puede favorecer la persistencia de las floraciones por mayor tiempo por causar un periodo prolongado de estratificación donde las cianobacterias que forman vesículas de gas se benefician regulando su posición en la columna de agua (mayor acceso a la luz) (Deng et al., 2014; Wagner y Adrian, 2009).

El efecto de los cambios en los patrones de las precipitaciones sobre las poblaciones de cianobacterias es más impredecible. Por ejemplo, las precipitaciones tienen un efecto de dilución sobre las concentraciones de nutrientes en el agua y directamente sobre la biomasa de los organismos, impidiendo su acumulación y desarrollo (Reichwaldt y Ghadouani, 2012). Sin embargo, cuando las precipitaciones extremas son seguidas por períodos de sequía se favorece el desarrollo de las cianobacterias, debido a que hay un aporte importante de nutrientes que sufre un proceso de concentración debido a la evaporación (Jeppesen et al., 2011; Reichwaldt y Ghadouani, 2012). A pesar de estas generalidades las cianobacterias son un grupo de organismos altamente diverso a nivel evolutivo (reflejado en los órdenes y familias) y pueden responder de manera muy diferente a cambios ambientales.

En particular las cianobacterias tienen respuestas dispares frente a diferentes condiciones de luz, mezcla y disponibilidad de nutrientes (Dolman et al., 2012; Reynolds et al., 2002; Whitton, 2012). Por ejemplo, los individuos del género *Microcystis,* son sensible a la mezcla y baja intensidad de luz, mientras que los de otros géneros como *Planktothrix* y *Raphidiopsis* toleran mejor estas condiciones (Reynolds, 2006; Whitton y Potts, 2002). Los géneros de cianobacterias también difieren en las toxinas que pueden producir, por ejemplo, especies del género *Dolichospermum* pueden producir microcistinas (hepatoxinas), saxitoxinas (neurotoxinas) o anatoxinas (neurotoxinas) según la especie (Li et al., 2016). El género *Microcystis* es ampliamente conocido por producir microcistinas, mientras existen pocos registros sobre su capacidad de producir otros tipos de toxinas (Hart et al,. 2016). Aunque estas características son ampliamente conocidas, aún faltan estudios que profundicen en las respuestas de los grupos cianobacterianos, por ejemplo, frente a los efectos causados por cambios en los patrones climáticos como las precipitaciones. Para cada región climática, es entonces fundamental conocer cuáles son los géneros prevalentes en los cuerpos de agua, y ampliar el conocimiento sobre cómo responden a los cambios ambientales para poder predecir y evaluar potenciales riesgos en diferentes escenarios.

1.4 Modelos predictivos de eutrofización y de cianobacterias planctónicas

Para medir el grado de eutrofización de los cuerpos de agua límnicos se usan diferentes tipos de indicadores incluyendo variables químicas, físicas y biológicas. La producción primaria refleja el estado trófico de los cuerpos de agua, por lo que las variables de abundancia o biomasa de microalgas y cianobacterias son considerados indicadores directos de la eutrofización (Ferreira et al., 2011; Nürnberg, 1996). La concentración de la clorofila *a* (chla), pigmento universal de los autótrofos, es el bioindicador más comúnmente utilizado por ser una variable robusta y fácilmente estimada en el laboratorio (OECD, 1982). Ha sido utilizada durante décadas como variable clave para definir los niveles críticos de carga de fósforo que aceleran la eutrofización (Nürnberg, 1996; Søndergaard et al., 2011). Otras veces se utilizan las concentraciones del fósforo total (PT) y/o del nitrógeno total (NT) como indicadores de eutrofización y/o determinación del estado trófico de los cuerpos de agua (OECD, 1982; Salas y Martino, 2001).

Para evaluar y predecir el grado de eutrofización de los cuerpos de agua a su vez se han utilizado diferentes aproximaciones metodológicas (Vollenweider, 1968; Watson, et al., 1992; Zhang et al., 2013). En la década del ’60 surgieron, para ecosistemas lénticos templados, los primeros modelos predictivos lineales de la clorofila *a* fitoplanctónica utilizando los nutrientes principales (fósforo total (PT) y nitrógeno total (NT) como variables explicativas (Carlson, 1977; Vollenweider, 1968). Más adelante se publicaron nuevos estudios que también predecían la concentración de la clorofila *a* y si bien surgieron modelos no-lineales, la mayoría de los modelos más recientes encuentran robustas relaciones lineales entre la concentración de la clorofila a y los nutrientes (Basu y Pick, 1996; Beaulieu et al., 2013; Van Nieuwenhuyse y Jones, 1996; Van Nieuwenhuyse, 2007; Søndergaard et al., 2011). En las regiones más cálidas (tropicales y subtropicales), se ha encontrado menor poder predictivo (Abell et al., 2012; Canfield, 1983; Huszar et al., 2006), atribuido a que la limitación por luz es más prevalente, por ser más turbios (Abell et al., 2012) y por tener redes tróficas más complejas (Abell et al., 2006; Huszar et al., 2006).

Para los ecosistemas lóticos, solo en pocos casos se ha logrado un buen ajuste entre la concentración de la clorofila *a* y los nutrientes (N y P) (Basu y Pick, 1996; Van Nieuwenhuyse y Jones 1996; Van Nieuwenhuyse, 2007), debido a que las variables hidrológicos y climáticas, en particular el caudal y las precipitaciones, tienen mayor efecto sobre esta relación, generando un desacoplamiento entre las variables (Ha et al., 1999). Por este motivo, en los ecosistemas lóticos, las concentraciones de nutrientes, más que la clorofila *a*, son utilizados como indicador de eutrofización en los modelos predictivos y para estimación del estado trófico (Dodds y Smith, 2016; Soares et al., 2007)

Para la predicción de biomasa y abundancia de cianobacterias también se han utilizado una gran variedad de aproximaciones, tales como modelos de regresión lineal y no lineal (Downing et al., 2001; Kosten et al., 2012; Persaud et al., 2015), modelos aditivos (Elliott, 2010) y redes artificiales neuronales (Ahn et al., 2010; Yang et al., 2016). Más recientemente, se han comenzado a utilizar aproximaciones estadísticas Bayesianas, tanto en modelos predictivos de indicadores de eutrofización, como en modelos para cianobacterias, tales como los redes Bayesianas (Johnson et al., 2010; Rigosi et al., 2015) y las regresiones Bayesianos (Cha et al., 2014; Hamilton et al., 2009; Obenour et al., 2014). La principal diferencia de la estadística Bayesiana con la estadística frecuentista (clásica) es que hace uso explícito de la probabilidad para estimar los efectos e incertidumbres para la inferencia. Esto permite una inferencia más lógica y flexible, comparado con el uso del P-valor para rechazar o aceptar hipótesis, método muy afectado además por el tamaño muestral (Amrhein et al. 2019; Burnham y Anderson 2002). El trabajo en un marco Bayesiano tiene además una serie de otras ventajas frente a la estadística frecuentista, entre las cuales se destaca que permite: ajustar modelos más complejos más fácilmente, alcanzar estimaciones más exactas cuando el tamaño de muestra es pequeña y una interpretación más fácil y más directa de los resultados (Gelman et al. 2013; Krusch 2015). A su vez, los modelos ajustados en este marco, tienen alto poder predictivo y permiten una cuantificación realista de la incertidumbre y separación del error de medición del error del proceso (Franks, 2018; Hamilton et al., 2009). Sin embargo, aún han sido poco aplicados para la predicción de indicadores de eutrofización (Cha et al., 2016; Malve y Qian, 2006;) y para las FAN en general (Obenour et al., 2014).

1.5 Eutrofización en los ecosistemas límnicos de Uruguay

Aunque las praderas naturales constituyen el ecosistema terrestre dominante del país (59%, 2015), ha disminuido drásticamente en las últimas décadas (71%, 2000) (Dinot, 2016), mientras la agricultura, junto a otras actividades productivas, han aumentado. Solo entre los años 2005 y 2012 la superficie destinada a praderas artificiales aumentó en un 70 % y el cultivo de cereales 61 % (MGAP-DIEA, 2013). Estas actividades productivas tienen alto consumo de fertilizantes nitrogenados y fosforados. A esto se suma que el tratamiento del agua de saneamiento no incluye remoción de nutrientes, en gran parte del país, siendo una importante fuente puntual de nutrientes a los cursos de agua (Goyenola et al., 2015; Rodríguez-Gallego et al., 2017), al igual que sucede con efluentes industriales. Como consecuencia, a lo largo de varias décadas estudios científicos del país, incluso de nuestro grupo de trabajo, han evidenciado alto grado de eutrofización en lagos, embalses, ríos y estuarios del país (Alonso et al., 2019; Arocena et al., 2008; Bonilla et al., 2015; Conde y Sommaruga, 1999; Conde et al., 2002; Chalar, 2006; Díaz, 2013; Goyenola et al., 2009, 2021; Nagy et al., 2002). La cuenca del Río Santa Lucía, está particularmente afectada siendo una de las más productivas del país (Arocena et al., 2018; Aubriot et al., 2017; Díaz, 2013). A la vez es la fuente de agua potable para 60% de la población del país teniendo de esta manera importantes conflictos entre intereses. Las cianobacterias potencialmente tóxicas, a su vez, están ampliamente distribuidas y forman floraciones en todos los tipos de ecosistemas, incluso en sistemas lóticos donde generalmente son menos propensas a ocurrir (Bonilla, 2009; Bonilla et al., 2015; Haakonsson et al., 2014). El primer registro de una floración tóxica en el país fue en 1999 (De Leon y Yunes, 2001) y posteriormente han habido registros en todo tipo de agua (Bonilla et al., 2015; Pírez et al., 2013). Asimismo han habido registros de dos casos de intoxicación aguda en humanos. Un adulto en el embalse Salto Grande (Giannuzzi et al., 2011) y una niña de dos años en la playa de Carrasco, Montevideo (Vidal et al., 2017), lo que evidencia la problemática de la eutrofización y las floraciones de cianobacterias en el país.

1.6 Justificación

Es fundamental ampliar el conocimiento sobre la eutrofización cultural y las floraciones de cianobacterias potencialmente tóxicas para las regiones subtropicales ya que la información disponible es fragmentada y la problemática es creciente (Bonilla et al., 2015; Goyenola et al., 2021; Rodell et al., 2018). Para Uruguay, localizado en una región subtropical, los estudios existentes ya alertan sobre los efectos de la eutrofización en las cuencas principales del país. Si bien existen evidencias para la región que demuestran que las actividades productivas promueven la eutrofización (Barreto et al., 2017; Chalar et al., 2017; Gorgoglione et al., 2020; Goyenola et al., 2015), hay diferentes visiones sobre sus contribución relativa en promover las floraciones de cianobacterias (Alcántara et al., 2021; Berreta y Carrasco 2021). Por otro lado, aun se necesitan más evidencias emipircos para evaluar si el nitrógeno juega un papel más importante que el fósforo en el control de la biomasa del fitoplancton como propuesto en modelos teoricos-conceptuales (Lewis 2000; Lewis 2002; Talling y Lemoalle, 1998). Estudios recientes sugieren que las diferencias dada por la morfometría y origen de los lagos (Abell et al., 2012; Elser et al., 2007; Kosten et al., 2009) podrían ser más importantes que los factores regional/climáticos. Por estos motivos, es necesario ampliar el conocimiento sobre la eutrofización en latitudes intermedias a través de datos empíricos y modelos predictivos, que permitan inferir la importancia relativa de los nutrientes (N vs P) y demostrar su relación con las actividades productivas en las cuencas hidrográficas. Las tendencias climáticas generales indican que en las regiones subtropicales disminuirán las precipitaciones (promedio anual) (IPCC, 2007), sin embargo este no es el caso para la región suroeste de América del Sur (Cabré et al., 2015; Díaz 2018). En esta región particular se espera un aumento de las precipitaciones para verano y otoño (Cabré et al., 2015), época con mayor ocurrencia de floraciones. Esto implica que son necesarios estudios a nivel regional para evaluar adecuadamente los efectos causados por las variaciones climáticos. Esto es aún más importante al tomar en cuenta que la región de estudio está cubierta por una densa red hidrográfica de ecosistemas lóticos que presentan una relación más inmediata con las precipitaciones comparado con, por ejemplo, los sistemas lénticos. Finalmente, es conocido que las cianobacterias planctónicas dominan en los ambientes acuáticos eutrofizados (Dolman et al., 2012; Pick y Lean, 1987), mientras que, el papel de las variables relacionadas con el clima (temperatura y precipitaciones) son menos estudiadas, particularmente en regiones subtropicales (De Senerpont Domis et al., 2013; Reichwaldt y Ghadouani, 2012). Para esto se deben instrumentar más estudios que profundicen en identificar, por ejemplo, cuáles son las cianobacterias más frecuentes y las biomasas que alcanzan. Es también necesario avanzar en el desarrollo de modelos matemáticos flexibles que permitan determinar las variables más importantes y mejorar la predicción de la biomasa fitoplanctónica y de las floraciones de cianobacterias.

2. Hipótesis e objetivos

2.1 Hipótesis

Hipótesis 1:

Los ecosistemas lóticos subtropicales son sensibles a la eutrofización mediada por los efectos combinados de la agricultura y las precipitaciones resultando en aumentos en los niveles de nutrientes.

Predicción 1:

El aumento de la concentración de fósforo total y nitrógeno total en el agua en ecosistemas lóticos se relacionan positivamente con el aumento de la superficie de tierra destinada a la agricultura y con las precipitaciones acumuladas.

Hipótesis 2:

En los lagos subtropicales, el aumento de las concentraciones de nutrientes favorece el crecimiento del fitoplancton en forma diferencial según el tipo de ecosistema en cuanto a la morfometría y el origen.

Predicción 2:

Se puede predecir la concentración de clorofila *a* fitoplanctónica a partir de los nutrientes del agua si se tiene en cuenta el tipo de ecosistema (morfología y origen).

Hipótesis 3:

En los ecosistemas subtropicales eutróficos la biomasa de las cianobacterias planctónicas responde positivamente con el aumento de la temperatura en interacción con variables hidrológicas.

Predicciones 3 y 4:

La temperatura y las precipitaciones son predictores de la biomasa y de la composición de las cianobacterias siendo la respuesta diferente entre ecosistemas lénticos y lóticos.

Se puede estimar la probabilidad de ocurrencia de floraciones de cianobacterias utilizando la temperatura del agua y variables hidrológicas en condiciones de eutrofia.

2.2 Objetivo general

Determinar y predecir los efectos de forzantes climáticos y antrópicos sobre la distribución y biomasa del fitoplancton y de las cianobacterias planctónicas en una región subtropical.

2.3 Objetivos específicos

1: Determinar el efecto de los cambios en el uso del suelo sobre los indicadores de eutrofización (clorofila *a* y fósforo total) y estimar los efectos combinados de las precipitaciones sobre esta relación.

2: Evaluar el efecto del tipo de lago y el estado trófico en la predicción de la concentración de clorofila a a partir de los nutrientes, nitrógeno total y del fósforo total.

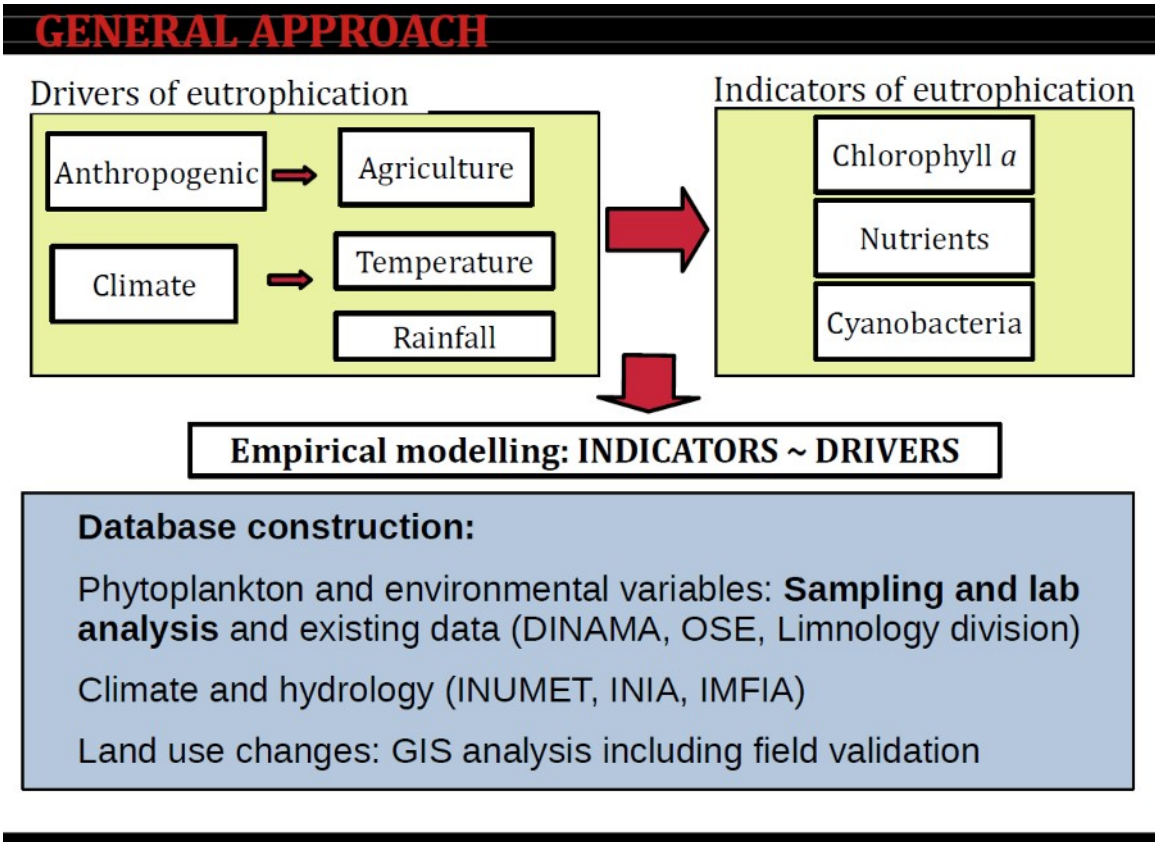
3: Establecer las diferencias en la distribución de los valores de los principales indicadores de eutrofización y de las cianobacterias formadoras de floraciones comparando ecosistemas lóticos y lénticos.

4: Determinar el efecto de las variables relacionadas a la hidrología y la temperatura del agua como factores clave para predecir la biomasa de cianobacterias en ecosistemas eutróficos.

3. Aproximación metodologica general

3. Aproximacion general

La aproximación general utilizada para alcanzar los objetivos planteados es la modelación empírica. Se desarollarán diferentes modelos para determinar los efectos de las variables forzantes (antrópicas y climáticas) sobre los indicadores de eutrofización y las cianobacterias planctónicas (figura 2). Los datos utilizados para los análisis provienen de muestreos propios realizados durante la tesis y de datos públicos de la OAN (Observatorio Ambiental Nacional) y de INIA (Instituto Nacional de Investigacion Agropecuaria). Además, algunos datos fueron brindados por INUMET (Instituto Uruguayo de Meteorología) e IMFIA (Instituto de Mecánica de los Fluidos e Ingeniería Ambiental, Facultad de Ingeniería). También se recopilaron datos históricos de diferentes informes técnicos, revistas científicas y datos no publicados de diferentes proyectos de investigación de la Sección Limnología de la Facultad de Ciencias (Proyecto ANII FCE6384). En particular, para el análisis de uso de suelo se usaron métodos de? sistemas de informacion geográfica (SIG) para obtener las áreas destinadas a cada uso de suelo en los tres periodos de tiempo analizados (2005, 2010 y 2016), que fuera validado posteriormente en el campo (muestreos realizados en 2016). La metodología y en particular los modelos empíricos desarrollados para alcanzar cada objetivo especifico son detallados en cada capítulo. En la figura 2 (en inglés) se resume de manera gráfica la aproximación metodológica empleada .



GENERAL APPROACH

Drivers of eutrophication

Anthropogenic → Agriculture

Climate → Temperature, Rainfall

Indicators of eutrophication

Chlorophyll *a*

Nutrients

Cyanobacteria

Empirical modelling: INDICATORS ~ DRIVERS

Database construction:

Phytoplankton and environmental variables: **Sampling and lab analysis** and existing data (DINAMA, OSE, Limnology division)

Climate and hydrology (INUMET, INIA, IMFIA)

Land use changes: GIS analysis including field validation

Figura 2: Resumen gráfico de la aproximación utilizada para comprender los efectos de las variables forzantes sobre los indicadores de eutrofización. El diagrama presentado fue utilizada durante la defensa oral de la tesis (15/03/2022).

4. Resultados

I: Influence of land use changes and hydrology on freshwater eutrophication, Uruguay

En este capítulo, presentamos las tendencias de los últimos 20 años en los niveles de fósforo en los cuerpos del agua del país y realizamos un análisis para evaluar las influencias de las actividades productivas utilizando los usos de suelo de las cuencas hidrográficas y el efecto de las precipitaciones. Para este último análisis seleccionamos la cuenca del río St. Lucía (área: 13.310 km²). Este río tiene gran importancia para el país siendo uno de los principales polos de producción de alimentos a escala nacional (Achkar et al., 2012) y ser fuente de abastecimiento de agua potable (Planta de Aguas Corrientes, OSE) a más de la mitad de la población del país (1.700.000 habitantes).

Influence of land use changes and hydrology on freshwater eutrophication, Uruguay

Highlights:

- Eutrophication is widespread in the main waterbodies of Uruguay.
- The most influential predictor of total phosphorus (TP) was agricultural land use/land cover.
- Rainfall had a positive effect on TP depending on catchment characteristics, major effects was found in catchments with low soils and steep slopes.
- Dairy farming is also an large source of phosphorus affecting freshwater quality.

Abstract

Changes in land use/land cover (LULC) due to anthropogenic activities can result in water quality deterioration, eutrophication and phytoplankton blooms, among other negative effects on freshwaters. Lotic water bodies are highly dependent on flow and thus on the precipitation regime, being the low plain lotic ecosystems particularly sensitive to the effects of LULC changes. However, the effects resulting from the interaction of LULC, catchment characteristics and climate are not completely understood in these ecosystems, particularly in the subtropical regions of South America, where major anthropogenic activities are ongoing. We conducted a survey to summarize the total phosphorus (TP) trends over the last 20 years in 67 aquatic ecosystems (n = 5900) of Uruguay. Next, we analyzed a case study of critical importance to drinking water in order to identify the effects of LULC changes, flow and rainfall on TP levels. For this purpose, we selected streams of four sub-catchments of the Santa Lucía River (SLR) and analyzed the main productive activities and LULC in three time windows (2005, 2010, 2016). Overall, our results indicated a clear trend towards eutrophication, with TP levels generally characteristic of eutrophic to hypereutrophic conditions in all major watersheds of the country. At the sub-catchment level, agriculture (in % of land use) was the most important predictor of TP, however in the most eutrophic stream dairy farming was as relevant as agriculture regarding the amount of P exported. Rainfall (7-day accumulated) had a positive effect on TP in one of the studied ecoregions with low levels of agriculture (< 5%) and no dairy production, suggesting a high vulnerability to climate change in that

area. Furthermore, the expected changes in rainfall patterns together with land use intensification can lead to a worsening of the current freshwater situation. There is an urgent need to implement effective management plans and measures to mitigate eutrophication and protect freshwater resources.

1. Introduction

Productive land use/land cover (LULC) has increased in the last decades to sustain the growing world population and consumption (Foley et al., 2005; Godfray et al., 2010). Natural ecosystems have been deeply modified by anthropogenic uses like agriculture, dairy farming and urbanization. These activities export significant nutrient loads, mainly phosphorus (P) and nitrogen (N), contaminating the waterbodies (Carpenter et al., 1998; Giri and Qiu, 2016; Vörösmarty et al., 2010). Main consequences include eutrophication, loss in ecosystem functioning, loss in biodiversity, algal blooms and taste and odor of water (Dodds, 2006; Dodds and Smith, 2016; Newbold et al., 2015; Wurtsbaugh et al., 2019). Contaminant exports from LULC are broadly classified into non-point sources, spread across large surface areas reaching freshwaters by runoff (e.g., agriculture), and point sources, which originate from a single discharge outlet (e.g., effluents of the milking parlor) (Carpenter et al., 1998). Nutrients from non-point sources are difficult to determine and to control due to the complex and diffuse nature of interaction between runoff and landscape (Carpenter et al., 1998; Chiwa et al., 2012, Delkash et al., 2018). Although nutrient levels from point sources are easier to confine and regulate, in practice, treatment and control measures are many times limited or insufficient, resulting in a large impact on freshwater nutrient levels (Davis and Koop, 2006). The direct access of dairy cattle to aquatic ecosystems is a particular case of point-non-point source of contamination, resulting in an increase of nutrient loading to freshwaters (Chalar et al., 2017; Conroy et al., 2016). Moreover, the influence of non-point and point contamination from both agriculture and animal production sources is tightly related and dependent on land characteristics, climate, rainfall patterns and local farming practices (Khan et al., 2020; Reddy et al., 2018). Therefore, to preserve global freshwater ecosystems and minimize eutrophication effects, studies that attempt to identify the relationship between LULC changes and regional catchment characteristics should be promoted.

Climate patterns are unique in each region and have a direct influence on river water quality and quantity (Macklin and Lewin, 2019). For instance, the interaction between rainfall and LULC may directly influence the water nutrient levels in rivers, particularly in regions with fertilized soils. In the review paper by Hart et al. 2004 this was clearly demonstrated. P loss by rainfall runoff was 4.5 times greater in fertilized compared to unfertilized fields. Comparing catchments with similar characteristics (LULC, size, lowland) in temperate Denmark (Europe) and subtropical Uruguay (South America), Goyenola et al. (2015) found that P exports to streams were explained by the different climatic rainfall patterns between countries (Goyenola et al., 2015). Therefore, studies on a region-by-region basis are needed to determine and predict the effect of LULC and its interaction with climate on water eutrophication.

Located in a lowland region of Southern South America, Uruguay (176.000 km^2, between 33° and 35° S) has a dense freshwater network. Eutrophication processes of both lotic and lentic freshwaters have been going on for decades (Alonso et al., 2019; Bonilla et al., 2015; Conde and Sommargua, 1999). Several large rivers and lentic ecosystems show signs of water deterioration in line with the increase in productive LULC activities (Goyenola et al., 2021). A clear example is the Santa Lucía River (SLR) system, the principal water source for 60% of the Uruguayan population. Intensive agro-industrial activities are carried out in the SLR basin generating an alarming situation regarding water quality, being one of the most threatened basins in the country (Achkar et al., 2012; Aubriot et al., 2017; Díaz, 2013; Gorgoglione et al., 2020; MVOTMA, 2020). Great social and political concern arose when a large cyanobacterial bloom event (*Dolichospermum* sp.) caused an unpleasant smell and taste in tap water in 2013 (Aubriot et al., 2017). The non-point sources account for ~ 80% of the nutrient contamination in this river system (Gorgoglione et al., 2020; MVOTMA, 2020). In several sub-catchments of this basin, though, dairy farming is responsible for a large part of the P exported to waters due to the lack of proper effluent treatment and direct access of livestock to streams, as demonstrated in recent studies (Chalar et al., 2017; MVOTMA, 2020). No-till farming may also accelerate nutrient exports due to the P stratification in the upper centimeters of the soil and the use of soluble fertilizers, making labile P more prone to transport via runoff (Sharpley, 2015; Piñeiro, 2021).

In this study, and for the first time, we carried out a combined spatial and temporal mapping of TP levels in the freshwaters of the country to visualize the general status and temporal evolution of eutrophication. Then, we analyzed TP levels of four catchments located in the upper SLR basin using three time frames of LULC classifications (2005, 2010 and 2016). The objectives of this study were to map TP trends in freshwaters of Uruguay and to determine the effect of LULC changes on TP levels in streams with contrasting LULC, including hydrology (flow and rainfall), and catchment characteristics (geomorphology). We hypothesized that TP levels of streams in the upper SLR watershed will be highly affected by the increase in agricultural land cover and that rainfall will positively interact with this effect.

2. Material and Methods

2.1 Study area

Uruguay is located on the Atlantic Coast of South America (Fig. 1) within a humid subtropical climate (Kottek et al., 2006). The seasonal distribution of rainfall is variable without distinctive rainy or dry periods, resulting in the occurrence of periods of drought at any time throughout the year with high spatial variability (Díaz et al., 2019). The predominant ecosystems are natural grasslands (Fig. 1), but in recent decades both large LULC changes and intensification of productive activities have increased, particularly in the south and southwest expanding towards the central region (Gazzano et al., 2019). Agriculture clearly expanded and intensified between 2000 and 2020, particularly for soybean and milk production (Fig. S1). As a result, the use of fertilizers (Kg/Ha arable land) showed an overall increase in the period (Fig. S1, Data sources: World Bank and DIEA (2006, 2012, 2020)).

Four sub-catchments, located in the upper SLR basin, were selected for this study (Fig. 1). The flow regimes of streams in this area were classified as “highly flashy” varying between 0.9-1.3 due to the R-B Index (Richards-Bakers Flashiness Index) (Goyenola et al., 2015). The R-B index characterizes the stream flow variability through measurements of the absolute day-to-day fluctuations of inflow relative to total discharge. The four sub-catchments are located within two ecoregions with different geomorphological characteristics (Table 1). The “Escudo Cristalino” ecoregion (sub-catchment 1) has mainly deep soils and the main LULCs are cultivated pastures and agriculture, while the “Sierras del Este” ecoregion (sub-catchments 2 to 4) has shallow soils and the main activities are livestock ranching on natural grasslands and afforestation.

2.2 Data sets and sampling

TP data was obtained from studies run by the University of the Republic (UdelaR) and the Ministry of the Environment (DINACEA) (compiled by Bonilla et al., 2015) and from the National Environmental Observatory (OAN) (https://www.dinama.gub.uy/oan/geoportal/; period 2015-2020). The final dataset includes TP from both lotic and lentic waterbodies and spanned from the year 2002 to 2020 (n = 5900, lotic = 73%, lentic = 27%). We then selected four sub-catchments (1-4) of the SLR basin for a more complete analysis. We defined a single sampling point in each sub-catchment that were sampled 3 to 4 times per year between 2005 and 2010 by the Ministry of the Environment of Uruguay as part of their monitoring program (n = 92). In 2016 we sampled the same four sub-catchments twice at the same sites (n = 8). In the sampling campaigns of 2016, temperature, pH, dissolved oxygen, conductivity, and turbidity were measured in the field, while total nitrogen (TN) (Valderrama, 1981), total phosphorus (TP) (Valderrama, 1981) and chlorophyll *a* (chla) (ISO, 1992) were estimated in the laboratory. For sub-catchment 1, stream flow data was estimated by the Uruguay National Water Board (DINAGUA), from water level measurements obtained three times a day at the hydrometric station located in Florida city, just downstream of the sampling station for sub-catchment 1 (Fig. 1). For catchments 2 to 4, flow was estimated by Santiago Narbondo and Christian Chreties using the GR4J rainfall-runoff model calibrated in the study region (Narbondo et al., 2020). Daily accumulated rainfall was obtained 30 days before each sampling date from three meteorological stations (“Minas”, “La Calera”, and “Florida”) belonging to the Uruguayan Institute of Meteorology (InuMet). Then, accumulated rainfall was estimated 3, 7, 15 and 30 days before each sampling date using the R packages “zoo” (Zeileis and Grothendieck, 2005).

2.3 LULC classification

The current national land use (2020-2021) was obtained from the Ministry of Livestock, Agriculture and Fisheries (MGAP) (MGAP, 2021). For the four selected sub-catchments of the SLR, the LULC determination was done using supervised classification of LANDSAT 5TM (2005 and 2010) and LANDSAT 8OLI (2016) satellite images. They were classified into seven categories: natural grasslands, agriculture (rain-fed crops: cereal, oil seed and forage, including grass and legume pastures), bare land for agriculture, afforestation (the conversion of grassland and shrubland to tree plantations, *sensu* Farley et al., 2005), bare land for afforestation, natural forest, and water. The bare lands were grouped according to their main use, agriculture and afforestation respectively for analysis. The 2016 classification was validated in the field with a confidence level of 90%.

To estimate the importance of dairy production in stream TP compared to agriculture we estimated the number of dairy cows per catchment and study year. The number of dairy cows was obtained from DICOSE ("División de Contralor de Semovientes") based on farmers' sworn statements. The total number of cows from farms that declared dairy farming as their main activity was used as estimator. To obtain the total number of animals per catchment, we assumed that the number of cows in each "DICOSE count section" (named police area) was proportional to the area of each section (the area of the DICOSE count section did not exactly match the area of the catchments).

2.4 Data analysis

2.4.1 TP spatial and temporal trends at a national scale

For the construction of the geo-referenced maps of the TP trends, the complete data set ($n = 5900$) was divided into three time periods (2002-2008, 2009-2014, 2015-2020). The data per site were afterwards classified by: 1) number of TP cases below 25 µg/L of the total for the period (%) and 2) number of TP cases above 75 µg/L of the total for the period (%). The first threshold is the maximum TP level in Uruguayan regulations (decree 253/79) for all types of water and the second indicates eutrophic-hypereutrophic conditions (Cunha et al., 2013; Lamparelli, 2004). Finally, sites were also classified due to maximum and average TP values for each time frame and 12 geo-referenced maps (four maps per period) were obtained using the GIS program ArcMap10.

2.4.2 Estimation of the effect of LULC on TP in SLR sub-catchments

We selected four sub-catchments of the SLR system to explore the effects and importance of different environmental variables on stream TP levels using a classification and regression tree analysis (CART) (Breiman et al., 1984). The variable selected first is the most important one or has the most effect on Chla (Qian and Anderson 1999). The environmental (explanatory) variables included: total area of afforestation (% of catchment), agriculture (% of catchment) and natural grasslands (% of catchment), river flow (m^3/s), accumulated rainfall (mm) 3, 7, 15 and 30 days before sampling (multiplied by the normalized catchment area, ha), number of dairy cows (normalized by the catchment area), water temperature (°C), and the catchment categorical variables (1 to 4) and year (2005, 2010, 2016). TP, flow, dairy cows and rainfall variables were log-transformed to stabilize variance and to make the variables symmetric (Qian and Anderson 1999). Subsequently, we performed a hierarchical model within a full Bayesian framework to estimate the effects of agriculture and rainfall on water TP. We also performed an initial model including flow, however only minor effects were estimated (data not shown). To accurately estimate the effects of the variables, catchment (space) and year (time) were modeled as random effects.

Our model assumes that the logarithm of total phosphorus (log(TP)) has a normal distribution, with mean μ, and standard error σ:

$\log(y_{ijk}) \sim \text{Normal}(\mu_{ijk}, \sigma)$

$\mu_{ijk} = \beta_0 + \beta_{1,j}\,\text{Agri}_{ijk} + \beta_{2,j}\,\text{Acc\_Rain}_{ijk} + \eta_k$

$\beta_{1,j} \sim \text{Normal}(0, \sigma_{\beta 1})$

$\beta_{2,j} \sim \text{Normal}(0, \sigma_{\beta 2})$

$\eta_k \sim \text{Normal}(0, \sigma_\eta)$

where $\log(y_{ijk})$ is the *i*th observed log(TP) value ($i = 1,\ldots, N_{jk}$) from catchment j ($j = 1, \ldots, 4$) in years k ($k = 1, 2$ y 3). β_o defines the intercept, $\beta_{1,j}$ defines the random slope for agricultural LU (Agri) and $\beta_{2,j}$ the random slope for the 7-days accumulated rainfall (Acc_Rain). η_k are temporal random effects given by year of sampling. Finally, the parameters $\sigma_{\beta1,}$ $\sigma_{\beta2}$ and σ_k are the standard deviation associated with catchments and year (i.e., model prediction error).

After fitting the model, posterior predictive plots were used to visualize the effect of agriculture on stream TP levels. For each catchment, the probability of exceeding 50 µg/L of TP due to agriculture was estimated within the range of our data set (0.05 to 35%). We used this threshold as an intermediate level (mesotrophic-eutrophic conditions) between the 25 µg/L accepted level and eutrophic-hypereutrophic conditions (75 µg/L) (Cunha et al., 2013; Lamparelli, 2004).

The model was fitted with the "rethinking" package in R (McElreath, 2020), which uses an MCMC algorithm to sample from the posterior distribution of parameters. We ran 4 chains for 10000 iterations, discarded 3000 (warmup) and the thinning was set to 1 to obtain a total of 2800 MCMC samples. Diffuse prior probability distributions (priors) were assigned to all parameter values. Posterior distributions of individual parameters were summarized as medians and 95% credible intervals. Posterior predictive checks were also conducted to examine model fit (McElreath, 2017). Convergence of the chains was assessed using visual inspections of trace plots and the rhat values for all parameters were assured to be below 1.1 (Gelman et al., 2014). All plots and statistical analyses were done in the R environment (R Core Team, 2020).

3. Results

The phosphorus concentration in Uruguayan freshwaters in general showed an increasing trend over time (Fig. 2). A significant aggravation can be observed in some regions of the country (I: Río Cuareim, II: Río Uruguay, III: Río Negro and IV: Coastal lagoons, see legend of Fig. 2). Furthermore, in the last time period (2015-2020), in most of the sites (60% of the total) TP were >75 µg/L in >50 % of the samplings (Fig. 2, second panel) indicating eutrophic to hypereutrophic conditions. In the SLR basin, hypereutrophic conditions (site mean >135 µg/L) were observed as early as the first period (2002-2008) (Fig. 2).

In the four selected SLR sub-catchments TP increased between 2005 and 2010 (Fig. 3), a trend that continued for catchment 1 up to 2016 (Fig. 3). This catchment also had the highest TP values observed during the study period (Fig. 3), while the TN levels were also the highest among these catchments (catchment 1 mean value= 1.0 ± 0.4 mg/L compared to catchments 2 to 4 mean value of 0.4 ± 0.2 mg/L; data only available from 2010 to 2016, data not shown). The sub-catchments located within the same ecoregion (“Sierras del Este”, catchments 2-4) had in general similar values in most variables (TP, TN and stream flow values, Fig. 3 and Fig. S2). The chla values were low (<4 µg/L) for all sub-catchments, except for two high values observed in catchment 1 (~12 µg/L) after extreme rainfall (7-days accumulated >400 mm) (Fig. S2). The “Sierras del Este” catchments were also distinctive in the rainfall patterns compared to sub-catchment 1, as lower values were registered. In addition, only catchment 1 received high to extremely high rainfall events (7-days accumulated >200 mm) before samplings (Fig. S2).

Agricultural LULC increased in all catchments from 2005-2016 (varying between +30% and +150%, Fig. 4, table S2). In catchment 1, dairy production, estimated by the number of dairy cows, was an important activity which also increased during the study period (+35%) (Table S2). However, this change was lower compared to the agricultural land use area which increased by 93% (Table S2). The number of dairy cows slightly increased in catchments 3 and 4 in 2010, although the number of dairy cows per hectare was very low in all three catchments (<0.01) located in the “Sierras del Este” ecoregion, thus this activity can be considered negligible (Table S2). In catchment 1 the area designated for artificial water bodies (reservoirs and cutwaters) increased by one order of magnitude in five years (from 0.2 to 2.2 km^2 between 2005 and 2010) (Table S2, Fig. 4). In catchments 2-4 an important increase of afforestation was observed, reaching its maximum percentage in catchment 4 (20.4%) and a total increase of +84% in catchment 2.

The CART exploratory analysis showed that agriculture together with accumulated rainfall (7 days) were important variables to explain TP levels in the studied streams (Fig. 5). Agriculture was the most important varaible (Fig. 5, R^2=0.65) and when it was above 10.5% of land use, the mean TP concentration in water exceeded 130 µg/L (Fig. 5, MSE=1704, obs=9). Rainfall (7 days accumulated), played a role for explaining differences between TP values only in the catchments where agriculture was below 10.5%, having a positive effect on TP in streams. To further explore and estimate the effects of TP and rainfall, we conducted a Bayesian hierarchical model accounting for both temporal and spatial effects. The results of the model were consistent with the CART analysis, as they showed a clear positive effect of agricultural surface area on TP in catchment 1 (Fig. 6). Accumulated rainfall (7 days) showed a minor positive effect on TP levels only in catchments 2 to 4 (Fig. 6). The effect of agriculture on streams was visualized by constructing probabilities of exceeding the TP threshold level of 50 µg/L (Fig. 7). The probability of exceeding the tier was highest in catchment 1 and only with 15% of agricultural land use the probability of exceeding this level was close to 1. For the catchments of the “Sierras del Este” ecoregion, the probability of exceeding the tier was lower. Again, these catchments showed a similar pattern among them (almost identical response in catchments 2 and 3) (Fig.7).

4. Discussion

4.1. General trends of total phosphorus

The overall global TP trends in Uruguayan freshwaters indicated eutrophic to hypereutrophic conditions and an aggravation over the last 20 years. This is consistent with previous synoptic articles which have revealed eutrophication of Uruguayan inland waters (Alonso et al., 2019; Bonilla et al., 2015; Conde and Sommaruga, 1999; Goyenola et al., 2021; Nagy et al., 2002). Although with differences in the amount of the existing data, we found an increment in TP towards hypereutrophic conditions in four regions of the country (Río Cuareim, Río Uruguay, Río Negro and the coastal lagoons of the Atlantic coast), with overall mean TP values above 75 µgL^{-1} and maximum values higher than 135 µgL^{-1} at the end of the studied period. This trend has taken place together with changes in productive activities, concurrently with an increase in the extension and intensification of agriculture (Baeza et al., 2014; Gazzano et al., 2017; Rama et al., 2018). The SLR basin showed signs of hypertrophy as early as 2002, being the region that has experienced the greatest LULC changes through time (Achkar et al., 2012; Aubriot et al., 2017). In the last two decades, LULC destined to soy bean has increased in the country ~ 16 times from virtually zero, while afforestation and milk production have increased ~

2.5 and ~ 1.8 times, respectively (see Fig. S1), a rising trend that is expected to continue (Torremorell et al., 2021; Zabel et al., 2019;). The intensification of productive activities is linked to the increase in the use of fertilizers and pesticides, resulting in loss of biodiversity and eutrophication of the waters (Aubriot et al., 2017; Gorgoglione et al., 2020; Soutullo et al., 2020).

Our study, for the first time, showed the temporal changes in the last 20 years of the main basins, highlighting hotspots that involved the main rivers (Río Negro, Río Uruguay and SLR) and coastal lagoons. We showed that monitoring efforts are recent and discontinuous in most of the country's watersheds making it a challenge for establishing long term trends and the response to further landuse change or management. Furthermore, most of the monitoring efforts are concentrated on large high order rivers within large basins. The inclusion of sampling sites of low order streams and rivers in monitoring programs could improve the cause-consequence identification in water quality and environmental management since these ecosystems rapidly respond to LULC changes (Stålnacke et al., 2004)

The high TP levels found in the water (> 75 μgL^{-1}) are a robust indicator of LULC uses and changes like agriculture, dairy farming and afforestation expansion and intensification among others, factors that have globally been identified as responsible for eutrophication (Jones and Downing, 2009; Liu et al., 2014). In the country's watersheds that have a low intensity of agro-industrial activities (extensive livestock ranching), total phosphorus and total nitrogen are respectively ~ 19 and 3 times lower than those water bodies located in regions with intensive and multiple productive activities (Goyenola et al., 2021). Although not included in our study, productive areas (dairy farming) with riparian forest and animal access restrictions to streams (low order streams, west region of SLR) showed lower levels of eutrophication than areas without this type of protection (Chalar et al., 2017), indicating that management measures and good practices are alternatives to allow high productivity without high impacts on water quality (Wilcock et al., 2013). In our study, the high levels of total phosphorus observed in the reservoirs of large rivers (Río Negro and Río Uruguay) may trigger phytoplankton blooms, a phenomenon frequently seen in those ecosystems (Aubriot et al., 2020; Bonilla et al., 2021; Ferrari, 2020; Kruk et al., 2019). Particularly, in the last analyzed period of our study (2015-2020), coastal lagoons located on the Atlantic watershed showed an increase in TP levels alerting to an eutrophication process. Although several natural coastal lagoons are biosphere reserves and RAMSAR sites due to their biodiversity and ecosystem relevance, they have also been subject to human impact and to occasional blooms (Bonilla et al., 2006; González-Madina et al., 2019; Pérez et al., 1999; Rodríguez-Gallego et al., 2017). Overall, eutrophication is a critical issue for Uruguayan freshwaters compromising their use and sustainable development.

4.2. Eutrophication and LULC changes in the Santa Lucía River basin

Unlike previous studies (Gorgoglione et al., 2020; Goyenola et al., 2015), our work on the RSL basin analyzed a long period (11 years) including three time windows of LULC, gaining in accuracy to clarify the effect of each LULC from other factors related to catchment characteristics. Our long-term data showed that when agriculture reached more than 10% of the catchment area, a clear effect on TP concentration in water was found. A similar result was also found in a nearby watershed of a coastal lagoon (Martínez, 2021). These findings suggest that 10% of the LULC can represent a threshold value, above which agriculture begins to have mayor impacts on water quality, regardless of catchment characteristics. Nevertheless, direct effects of agriculture are complex to isolate because agriculture also includes artificial and fertilized pastures used for grazing animals for meat and dairy production. In the RSL basin, dairy farming is a typical activity which has intensified in the last years (Errazola, 2021) and is a relevant P source to streams in many SLR catchments (Chalar et al., 2017; MVOTMA, 2019). Only catchment 1, among the four studied catchments, had a significant number of dairy cows. For this catchment we estimated similar values of P exported from dairy farming (export from milking parlors) compared to agriculture (Table S3), which demonstrated the importance of this productive activity on river P levels for this particular catchment. Even so, our results also indicated that the observed increase in river P may be more related to agricultural expansion than to the dairy production intensification. The number of dairy cows only increased by 35%, compared to a 95% increase in agricultural LULC. Overall, these results, together with previous ones, demonstrated that agriculture is a major source of P in streams of the SLR, and that whenever dairy production occurs, this point source should not be overlooked.

The four studied catchments of the SLR belonged to different ecoregions. While catchment 1 was located in soils suitable for crop cultivation in the “Escudo Cristalino” region, the other three (catchments 2 to 4) were located in the “Sierras del Este” ecoregion, which are suitable for afforestation due to the predominance of rocky and shallow soils, and where natural grassland still prevails (Table 1). In these latter catchments, dairy production was negligible, agriculture accounted for less than 5% of the LULC and no other important point sources of pollution were present, supporting the lower TP values found in water in comparison with the streams of catchment 1. In these catchments, with lower suitability for agriculture, TP levels in waters were shown to be more sensitive to hydrology, as accumulated precipitation had a positive effect on TP increase. In this kind of catchment, river flow is prone to respond more rapidly to rainfall due to its steeper slopes (Leopold et al., 1964) and runoff from other diffuse sources may explain the increase in P with precipitation, such as cattle ranching and afforestation. Even though no direct effect was found with the 7-day accumulated rainfall in catchment 1, larger and more extreme rainfall events may also have a great positive impact on TP exports from agricultural LULC to streams (Fig. S2), since the intensity of rainfall is an important factor on phosphorus exports, particularly from diffuse sources (Goyenola et al. 2015; Hart et al., 2004). Uruguay is among the countries which receive most rainfall in the world (FAO, 2010), much of which occurs during extreme events (storms or heavy rains). Moreover, climate change predictions for the region foresee increases in the frequency of extreme events (droughts and extreme rainfalls) (IPCC, 2021), with consequences on the hydrological regimes of streams and rivers (Barros et al., 2015; Van Vliet et al., 2013). Considering the synergic effect of rainfalls and phosphorus loads, more studies should be carried out in the region to quantify the impacts of rainfalls on freshwater eutrophication, even in less agricultural catchments, to implement adequate management plans to prevent future impacts of climate change. Moreover, increased vulnerability to extreme events and LULC intensification and expansion of agriculture can be expected in the “Sierras del Este” ecoregions (and others with similar geomorphologic characteristics).

Overall, catchments located within the same ecoregion showed similar effects due to agriculture and rainfall. Therefore, we suggest that studies based on ecoregion-focused analyses should be further explored as a tool to model effects of environmental stressors on water quality. Larger datasets, for longer periods and more catchments are needed to accurately understand the process involved in nutrient exportation to streams, allowing to understand the differences between LULCs in different ecoregions and their interaction with geomorphology and climate.

4.3 Responses of other eutrophication indicators: TN and Cha

Agricultural activities have also been related to high N concentrations in streams of the SLR watershed (Goyenola et al., 2020), a trend also supported by our results for all four catchments, but only in the period of available data (2010-2016, Fig. S2). Our results, therefore, supported that agriculture is the main cause of eutrophication, when exceeding a certain surface area. We also found the highest values of chla in the catchment with the highest nutrient values (Fig. S2), both TN (when data were available) and TP. Contrary to what is normally expected, these high chla values were recorded after very high rainfall events, usually attributed to a wash-out effect of phytoplankton biomass (Reichwaldt and Ghadouani, 2012). However, cyanobacteria in the SLR basin have been associated with high flow events, probably being transported from small- and medium-sized eutrophic reservoirs (Somma et al., 2021). In our study we found an increase in this type of reservoirs and therefore suggest that further studies investigate the possible impacts of the interaction between rainfall and reservoirs on water quality, in particular on the boosting of noxious cyanobacterial blooms transported downstream.

4.4. Implications for management

Our results demonstrated that Uruguayan freshwaters are in a critical situation and that greater efforts are urgently needed to mitigate the impact of LULC changes on eutrophication. Nutrients from dairy farming can be significantly reduced by installing effluent treatment plants at the milking parlor, and reducing the access of cows to streams (Chalar et al., 2017; Conroy et al., 2016). Diffuse P export from agriculture, including artificial pastures, may be more difficult to mitigate as it is highly dependent on farm management and soil and topography characteristics (Sharpley, 2015). However, implementing buffer zones between agricultural fields and water bodies can be an effective measure to prevent the loss of nutrients to water (Lescano et al., 2017; Rodriguez-Gallego et al., 2020), together with implementing best management practices for the prevention of P loss on farms (Cabrera, 2015). Nevertheless, our results further evidenced that eutrophication is highly dependent on the local characteristics of the sub-catchments. Therefore, management plans should be designed according to catchment characteristics in order to achieve effective mitigation measures. The identification of catchments sensitive to LULC changes and climate change is therefore a relevant task. We believe that it is necessary to implement high frequency and long-term monitoring programs, including meteorological and limnological data, to clarify the effect of temporal variations and extreme rainfall events.

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Figure 1. Left: Uruguay land use/cover (2020-2021) indicated with colors (see legend). Redrawn from: Ministry of Agriculture and Farming (MGAP, 2021). The large basins are delimited by solid black lines. Right: The Santa Lucia River basin. Gray areas indicate four sub-catchments selected for analysis.

Figure 2. Total phosphorus trends at freshwater system sampling sites (dots) over three periods (2002-2008, 2009-2014 and 2015-2020). From left to right the maps show different classifications: the percentage (%) of sites with: TP< 25 µg/L and TP>75 µg/L, the maximum and the average TP concentrations (µg/L). Colors indicate the levels of each classification. Areas with increased TP (between 2002-2020) are indicated in the second panel (I: Río Cuareim, II: Río Uruguay, III: Río Negro and IV: Coastal lagoons)

Figure 3. Temporal variations in total phosphorus for the selected sub-catchments (1-4, Fig. 1) within the Santa Lucía basin between 2005 and 2016 (black = catchment 1, red = catchment 2, green = catchment 3, blue = catchment 4).

Figure 4. Land use/land cover classification for the three years studied (2005, 2010, 2016) for sub-catchments 1 (upper), 2 (middle) and 3-4 (down). Colors indicate different land uses/covers (see legend).

Figure 5. Regression tree plot of observed TP (µg/L) partitioned by agricultural area (proportion of catchment) and accumulated rainfall 7 days before sampling (mm, multiplied by the normalized catchment area; 1.1, 1.8, 1 and 13.5 for the catchments 1-4 respectively) for the Santa Lucía River catchments.

Figure 6. Summary of posterior distributions (medians and 95% credible intervals) of regression coefficients, where β_0 and η (year) are intercepts. β_1 and β_2 are the random slopes for agriculture and rainfall, respectively, discriminated for each catchment (1 to 4 between square brackets). σ, $\sigma_{\beta1}$, $\sigma_{\beta2}$ and σ_η are the standard deviations.

Figure 7. Probability of exceeding TP level of 50 µg/L due to agricultural soil use (%). The predictions are shown for each sub-catchment (1 to 4) of the year 2016. (black = catchment 1, red = catchment 2, green = catchment 3, blue = catchment 4).

Figure 1.

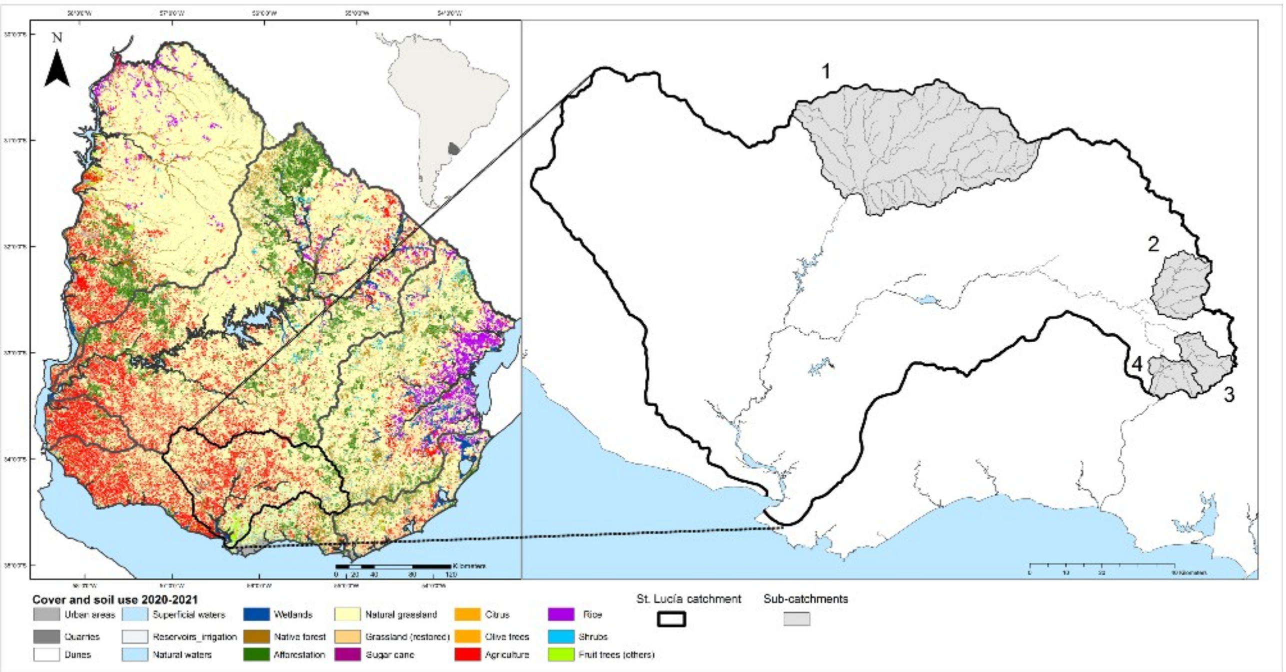

N
1
2
3
4
0 20 40 80 120
Kilometers
Cover and soil use 2020-2021
Urban areas
Quarries
Dunes
Superficial waters
Reservoirs_irrigation
Natural waters
Wetlands
Native forest
Afforestation
Natural grassland
Grassland (restored)
Sugar cane
Citrus
Olive trees
Agriculture
Rice
Shrubs
Fruit trees (others)
St. Lucía catchment
Sub-catchments

Figure 2.

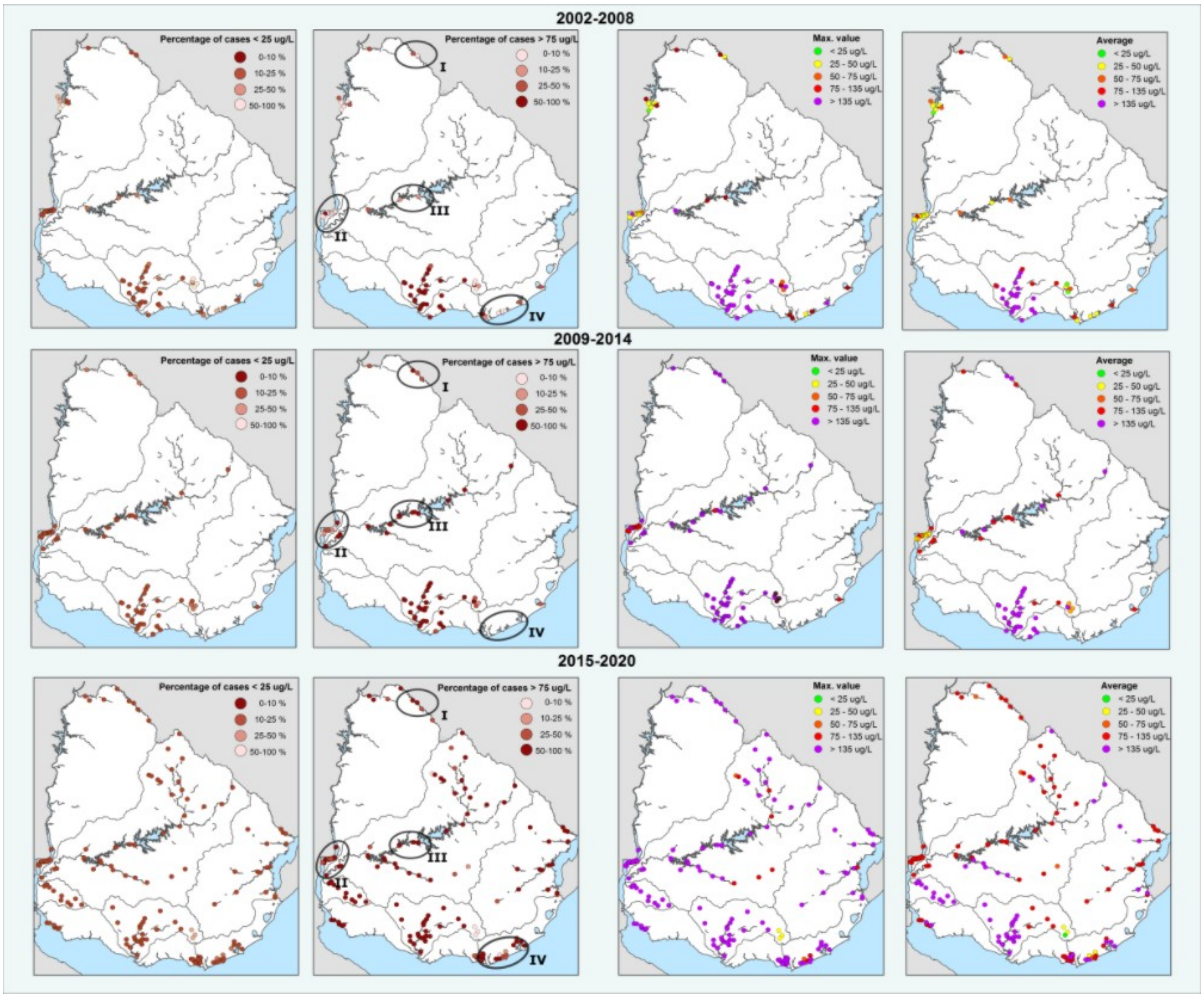

2002-2008
Percentage of cases < 25 ug/L
0-10 %
10-25 %
25-50 %
50-100 %
Percentage of cases > 75 ug/L
0-10 %
10-25 %
25-50 %
50-100 %
I
II
III
IV
Max. value
< 25 ug/L
25 - 50 ug/L
50 - 75 ug/L
75 - 135 ug/L
> 135 ug/L
Average
< 25 ug/L
25 - 50 ug/L
50 - 75 ug/L
75 - 135 ug/L
> 135 ug/L
2009-2014
Percentage of cases < 25 ug/L
0-10 %
10-25 %
25-50 %
50-100 %
Percentage of cases > 75 ug/L
0-10 %
10-25 %
25-50 %
50-100 %
I
II
III
IV
Max. value
< 25 ug/L
25 - 50 ug/L
50 - 75 ug/L
75 - 135 ug/L
> 135 ug/L
Average
< 25 ug/L
25 - 50 ug/L
50 - 75 ug/L
75 - 135 ug/L
> 135 ug/L
2015-2020
Percentage of cases < 25 ug/L
0-10 %
10-25 %
25-50 %
50-100 %
Percentage of cases > 75 ug/L
0-10 %
10-25 %
25-50 %
50-100 %
I
II
III
IV
Max. value
< 25 ug/L
25 - 50 ug/L
50 - 75 ug/L
75 - 135 ug/L
> 135 ug/L
Average
< 25 ug/L
25 - 50 ug/L
50 - 75 ug/L
75 - 135 ug/L
> 135 ug/L

Figure. 3

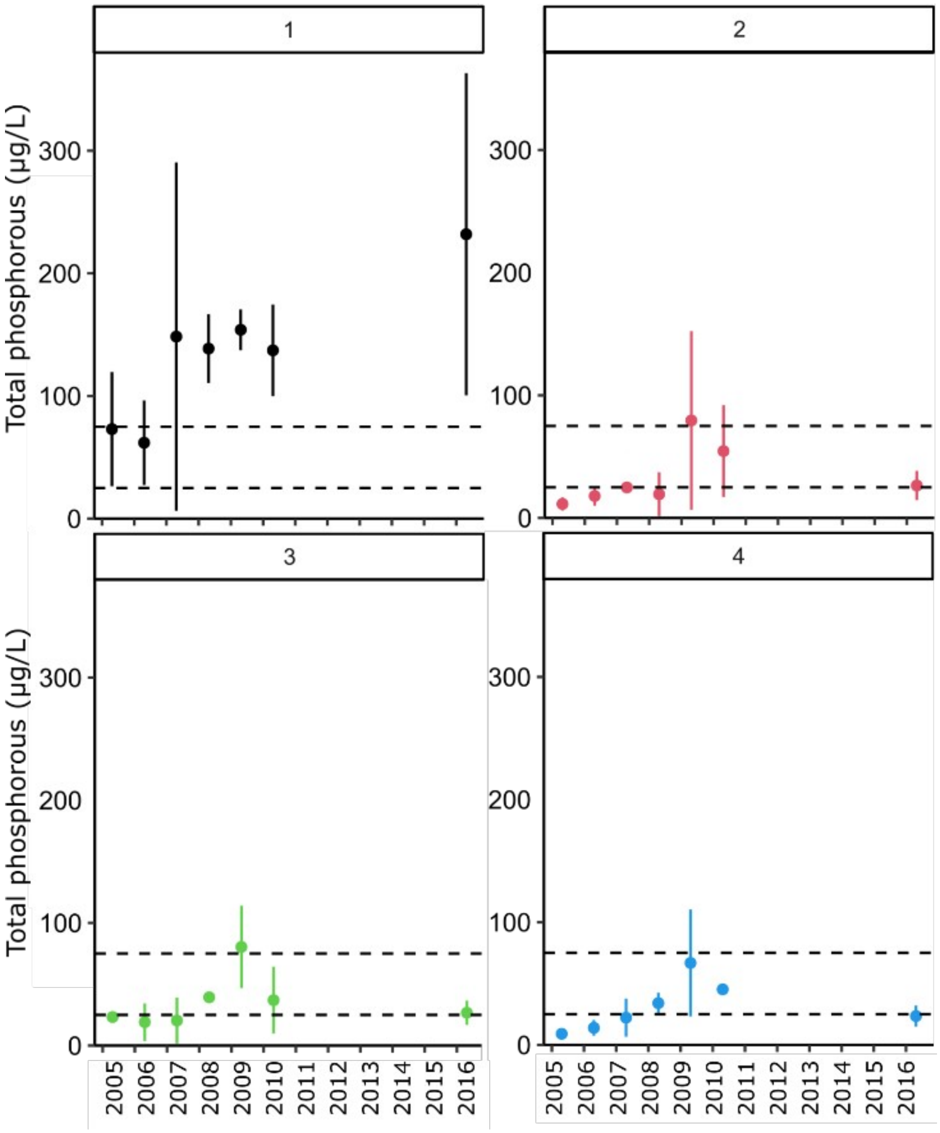

1
2
3
4
Total phosphorous (µg/L)
Total phosphorous (µg/L)
0
100
200
300
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016

Figure 4.

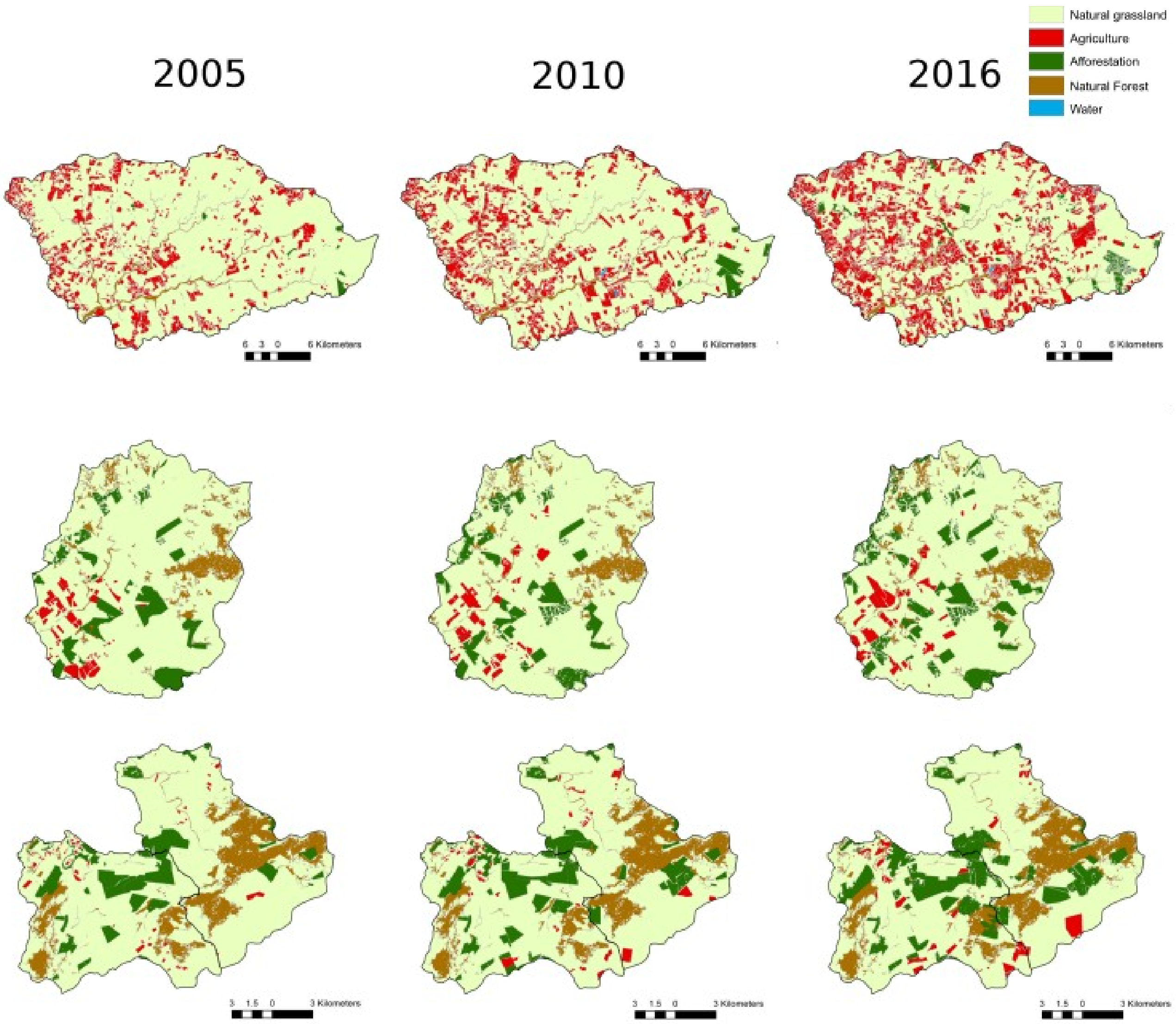

2005
2010
2016
Natural grassland
Agriculture
Afforestation
Natural Forest
Water
6 3 0 6 Kilometers
3 1.5 0 3 Kilometers

Figure 5.

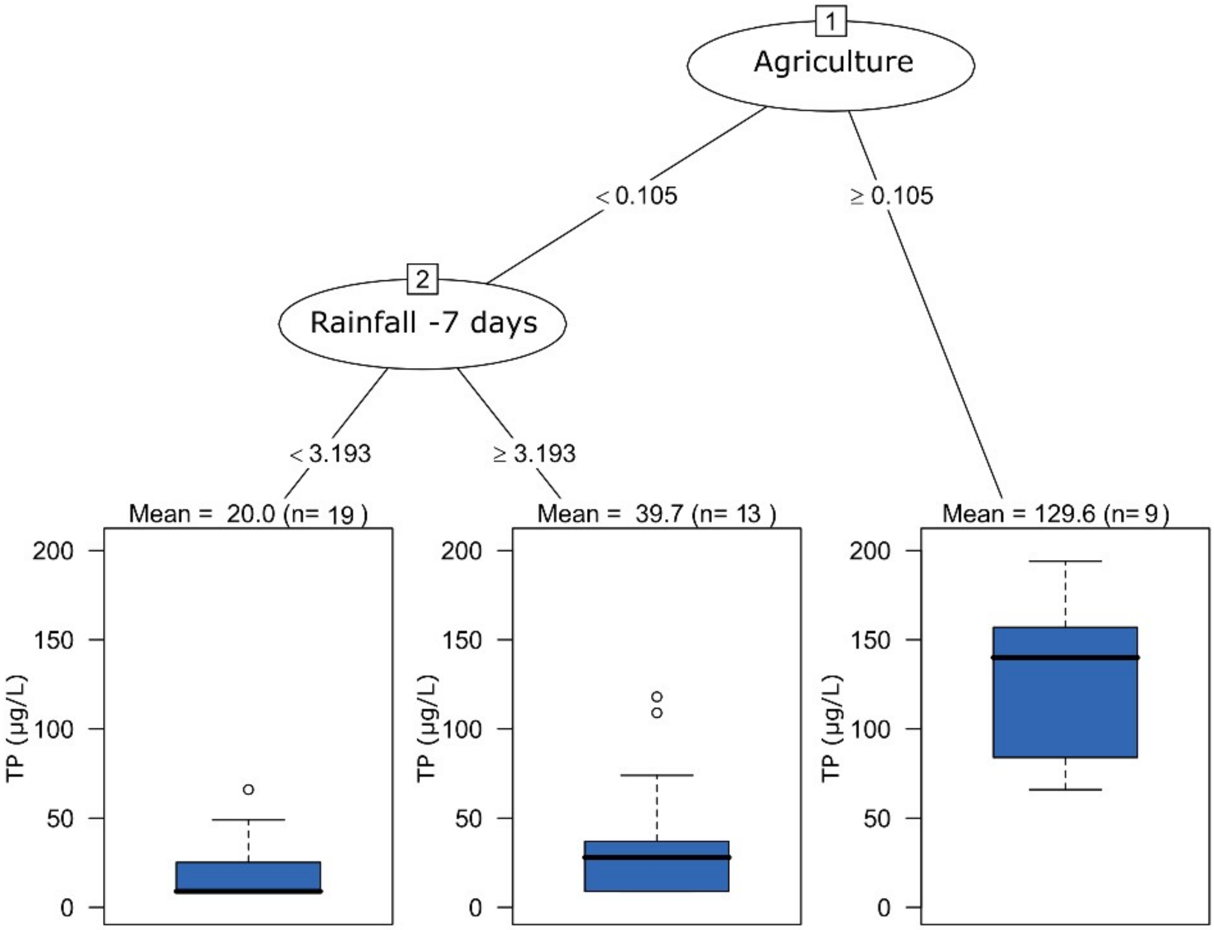

1
Agriculture
< 0.105
≥ 0.105
2
Rainfall -7 days
< 3.193
≥ 3.193
Mean = 20.0 (n= 19)
Mean = 39.7 (n= 13)
Mean = 129.6 (n= 9)
TP (µg/L)
0
50
100
150
200

Figure 6.

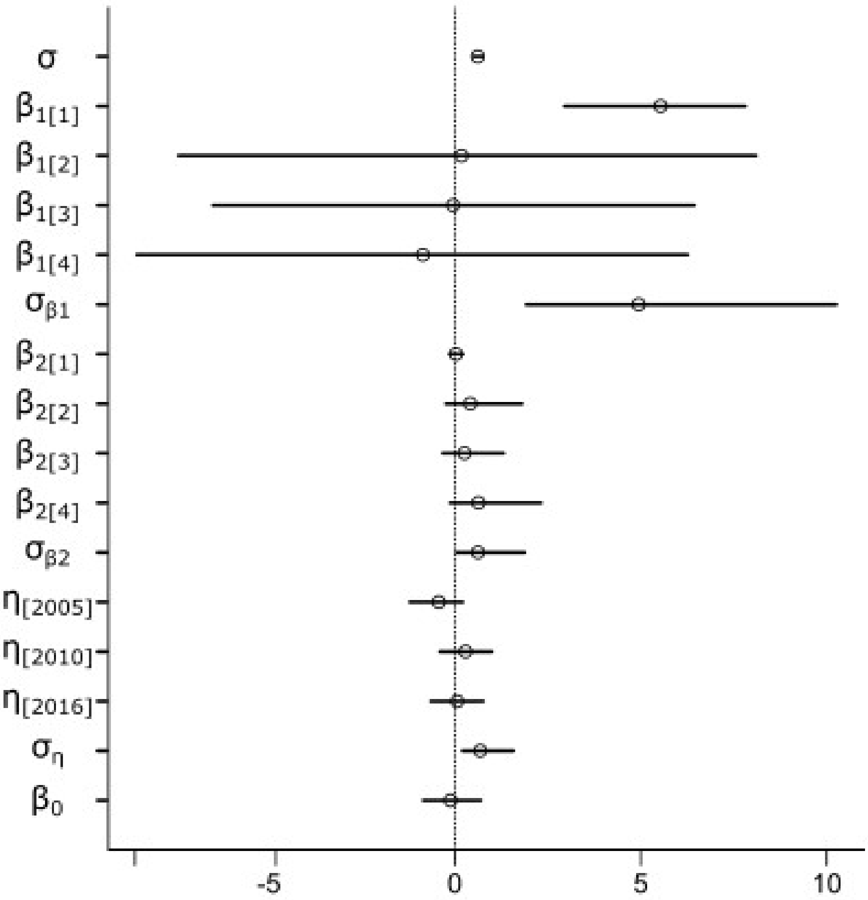
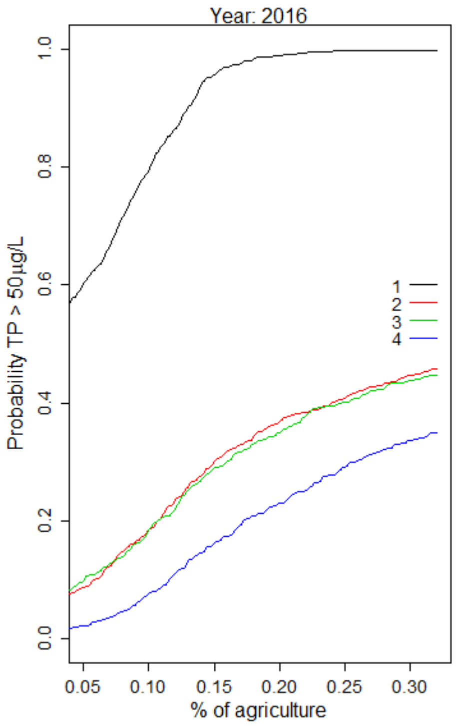

σ
β1[1]
β1[2]
β1[3]
β1[4]
σβ1
β2[1]
β2[2]
β2[3]
β2[4]
σβ2
η[2005]
η[2010]
η[2016]
ση
β0
-5
0
5
10

Figure 7.


Year: 2016
Probability TP > 50µg/L
1.0
0.8
0.6
0.4
0.2
0.0
0.05
0.10
0.15
0.20
0.25
0.30
% of agriculture
1
2
3
4

SUPPLEMENTARY

Table S1. Geomorphology and environment characteristics of the subcatchments of St. Lucía basin by ecoregions (Brazeiro et al. 2012).

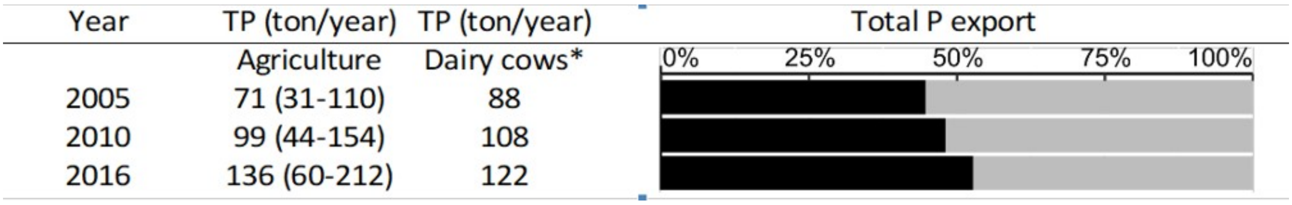
Catchment	Ecoregion	Dominant geo-form	Dominant soils	Depth of soils	Domiant land use
1	“Escudo Cristalino”	Small hills and smooth small hills	Brunisolic and vertisolic	Moderately deep	Planted pastures, agriculture, natural grasslands
2-4	“Sierras del del Este”	Hills	Brunisolic and litosolic	Moderately superficial and rocky	Planted pastures, afforestation, natural grasslands.

Table S2. Area (km^2), area of land use/cover (km^2, percentage between ()) and dairy cows (total number) in the four subcatchments of the St. Lucía River basin.

Catch.	Year	Area	Agriculture	Afforestation	Natural forest	Natural grasslands	Water	Dairy cows*
1	2005	1618	268 (16.5)	8.4 (0.5)	44.7 (2.7)	1297 (80.1)	0.2 (0)	19014
	2010	1618	375 (23.1)	28 (1.7)	44.3 (2.7)	1169 (72.2)	2 (0.1)	23156
	2016	1618	516 (31.9)	39.8 (2.4)	45 (2.7)	1015 (62.7)	2.2 (0.1)	26321
2	2005	133	1.1 (0.8)	8.8 (6.6)	28.4 (21.4)	94 (71)	0 (0)	1
	2010	133	2.6 (1.9)	13.5 (10.1)	28.5 (21.5)	88 (66.3)	0 (0)	1
	2016	133	2.8 (2.1)	16.7 (12.6)	28.9 (21.8)	84 (63.3)	0 (0)	0
3	2005	222	7.7 (3.5)	23.7 (10.7)	20 (9)	170 (76.7)	0 (0)	0
	2010	222	8.5 (3.8)	25.9 (11.6)	19.2 (8.6)	1678 (75.7)	0 (0)	132
	2016	222	9.9 (4.5)	30.8 (13.9)	20.3 (9.1)	160 (72.3)	0 (0)	45
4	2005	120	2 (1.6)	18.8 (15.6)	14.5 (12.1)	84.5 (70.4)	0 (0)	0
	2010	120	2.9 (2.4)	20.8 (17.4)	14.3 (11.9)	81.8 (68.2)	0 (0)	66
	2016	120	4.8 (4)	24.5 (20.4)	15.1 (12.6)	75.5 (62.9)	0 (0)	22

*Estimated number. See methodology for details on estimation.

Table S3: Estimation of the total amount of phosphorous (TP) (ton/year) exported due to agriculture soil use (total area) and dairy production (the number of dairy cows) for catchment 1 (tons/year) for each study year. The methodology used by DINAMA et al. 2019 and Perdomo 2013 were followed. For agriculture, the export coefficients (kg/ha/year) used were: 2.65 (mean), 1.16 (min.) and 4.11 (max.) (Reckhow, 1980 in Perdomo, 2013). For comparison of these two main contributors of P, the assumption that agriculture and dairy cows sums up the total P exported was taken (Right part of table). Black = agriculture export, gray = dairy cows export.



Year	TP (ton/year) Agriculture	TP (ton/year) Dairy cows*	Total P export
2005	71 (31-110)	88	
2010	99 (44-154)	108	
2016	136 (60-212)	122	

*Dairy cows. As the DICOSE count section did not have the exact same size as the catchment they were corrected considering that the number of cows were proportional to the surface area.

Figure S1. Global trends in the productive activities (soy bean, afforestation and milk production) in Uruguay. Data sources: World Bank, DIEA (2006, 2012, 2020).

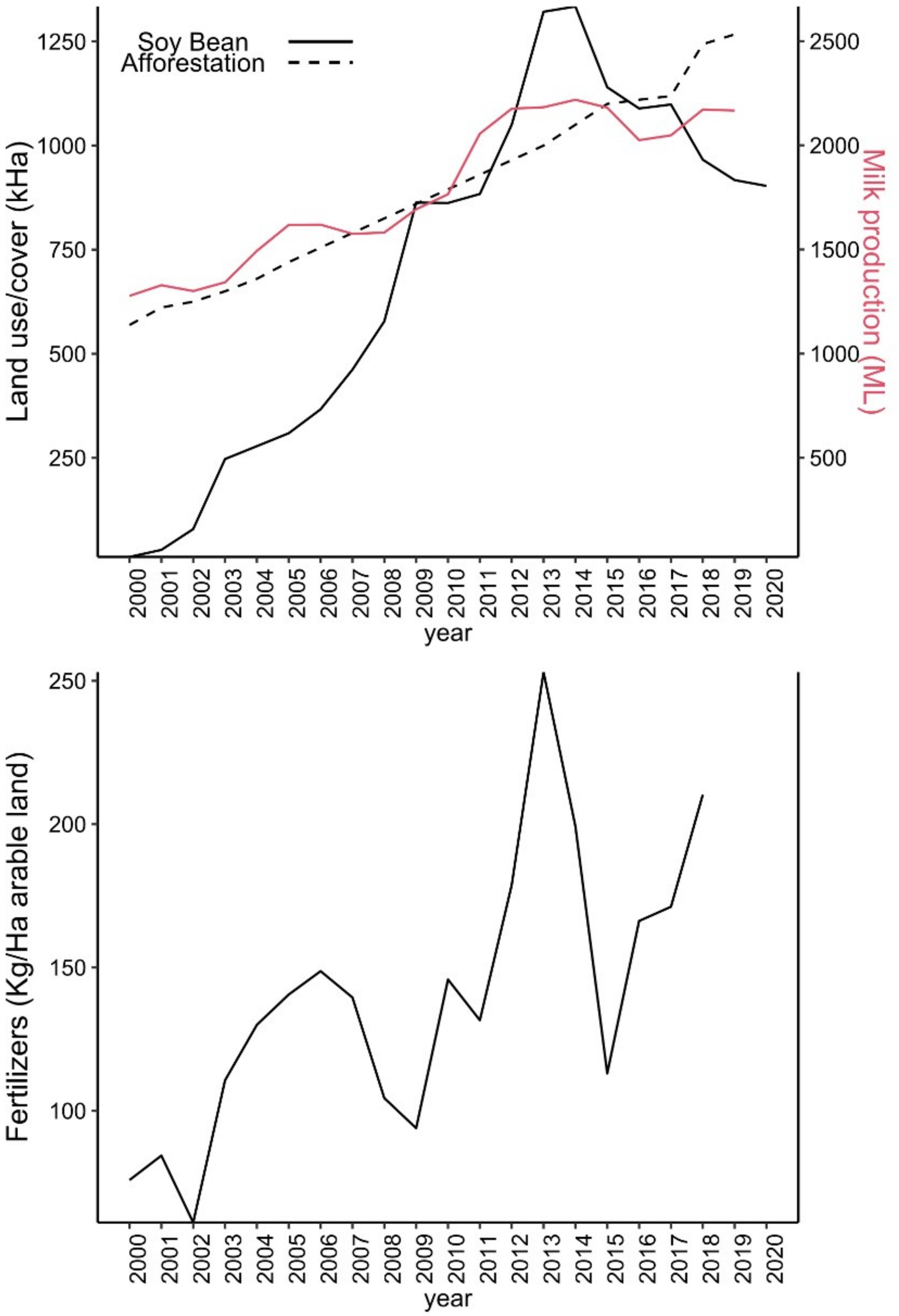


Figure S2. Scatterplot matrix and correlations (Spearman) among main variables for the years studied (2005, 2010 and 2016) for the subcatchments of the St. Lucía River basin. Water temperature, C° (Temp.), total phosphorus, µg/L (TP), total nitrogen, mg/L (TN), chlorophyll *a*, µg/L (Chla), 7-days accumulated rainfall, mm (Rain7Days), flow, mm³/s; in log (Flow_log), natural grassland, percentage (0-1) (LU_Natural), agriculture, percentage (0-1) (LU_Agriculture), afforestation, percentage (0-1) (LU_Afforestation), dairy cows, log + 1 (Dairy_cows_log). TN and chla available from year 2010. Black = catchment 1, red = catchment 2, green = catchment 3 and blue = catchment 4.

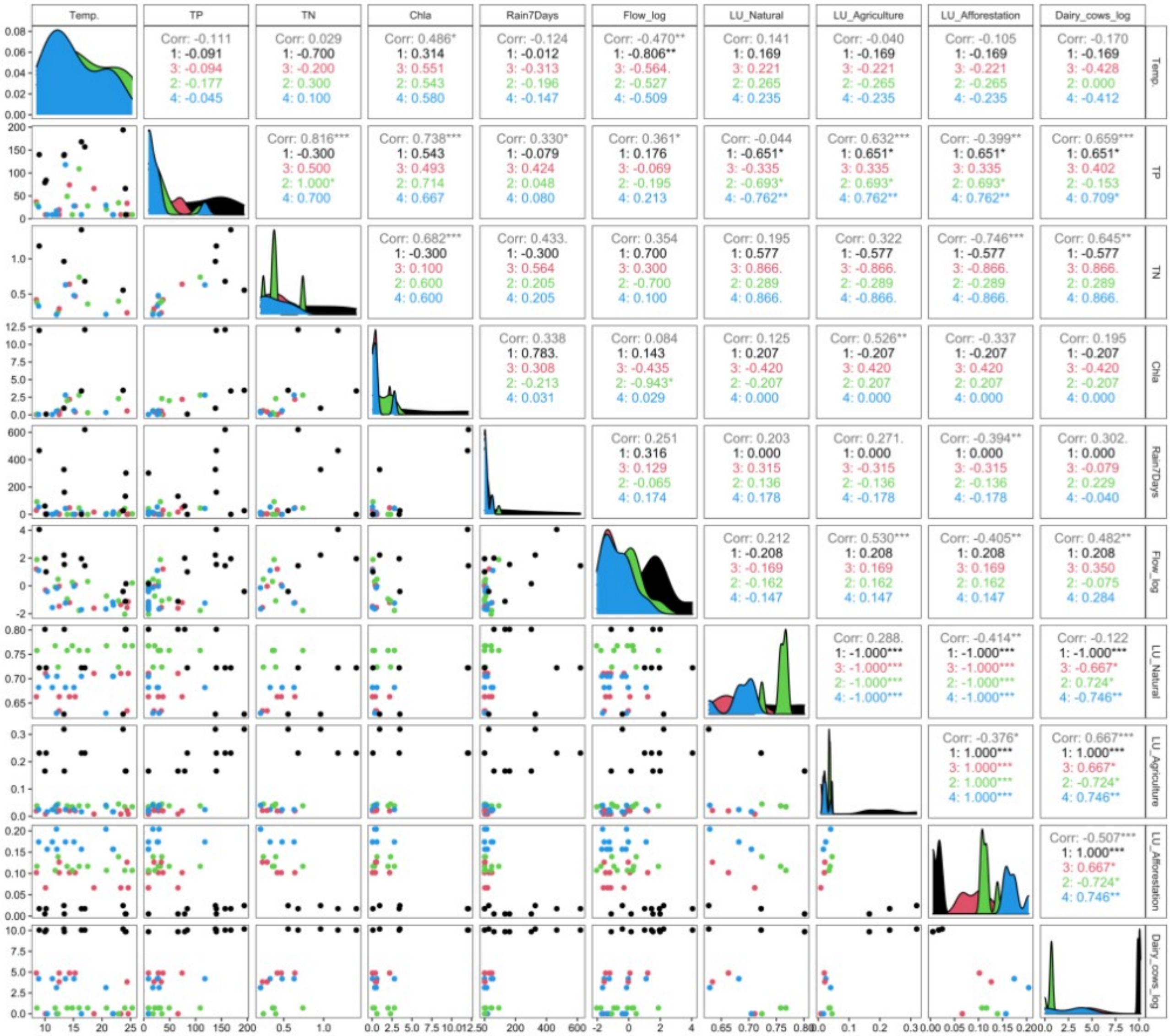
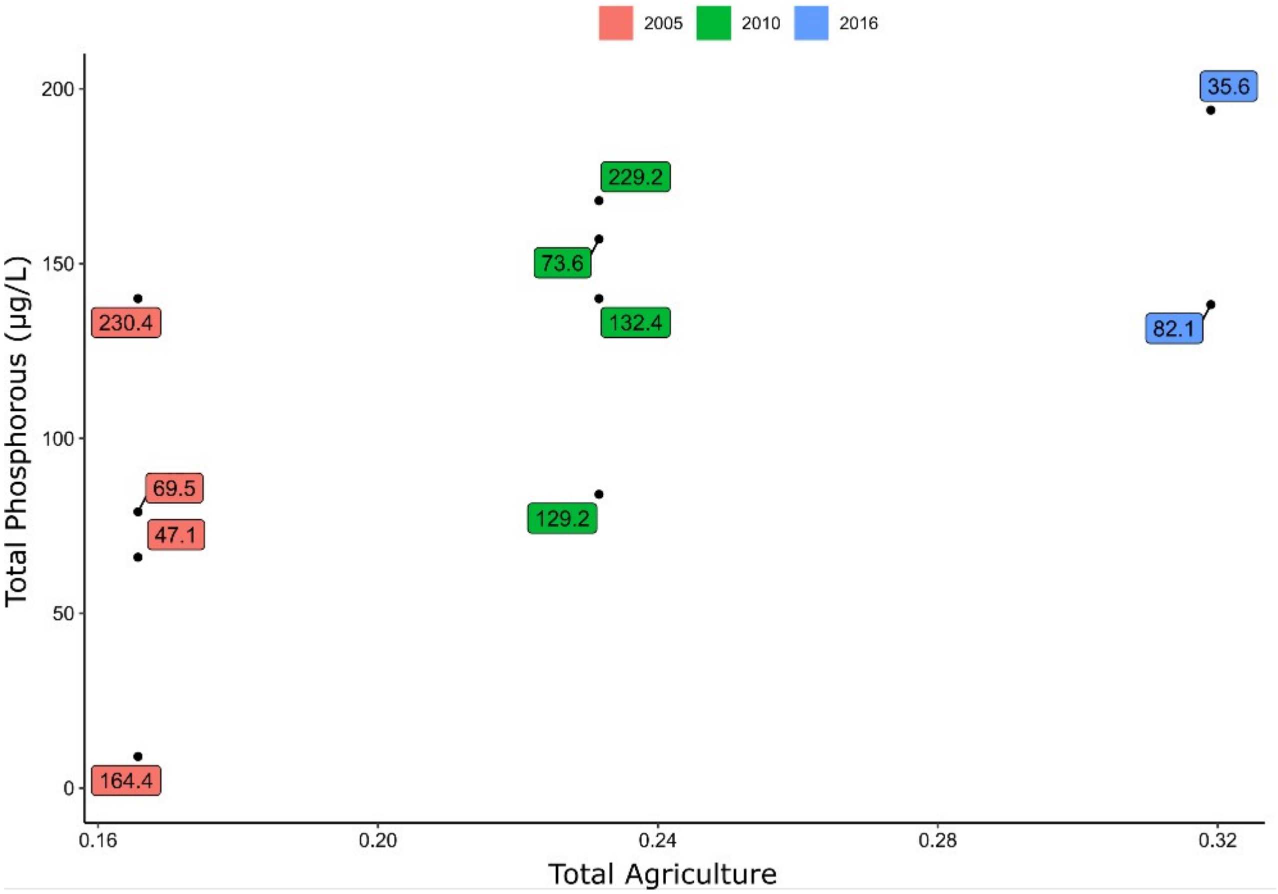


Figure S3: Relationship between the area of agriculture (in percentage of total catchment area, 0-1) and total phosphorus (µg/L) in the water at catchment 1. The colors indicate study years (red = 2005, green = 2010 and blue = 2016). The numbers within the boxes show the accumulated rainfall (mm) 30-days before each sampling. The highest intra-annual values of TP were registered when rainfall was very high to extreme (> 200mm; year 2005 and 2010).



II: The chlorophyll-nutrient relationship varies with lake type and seasonality in subtropical lakes

En el capítulo anterior vimos como la eutrofización es una gran problemática a nivel del país y como las actividades agropecuarias influyen directamente sobre los niveles de nutrientes en el agua. En este capítulo analizamos el efecto de los nutrientes (P y N) sobre la biomasa del fitoplancton (clorofila *a*) en los principales tipos de agua lénticos del pais (embalses, lagunas y lagos). Además buscamos determinar cual de los dos nutrientes es más importante en la predicción según el tipo de lago y la estacionalidad. Pretendemos aportar evidencias empíricas acerca del efecto de los nutrientes sobre el crecimiento del fitoplancton en climas subtropicales, buscando mejorar la predicción de la clorofila *a*.

The chlorophyll-nutrient relationship varies with lake type and seasonality in subtropical lakes

Authors

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Highlights

1. The effects of N and P on phytoplankton in warm climate lakes is poorly understood.

2. P was the main nutrient predicting chla in subtropical lakes.

3. Lake type and seasonality were key factors for the prediction of chla concentrations.

4. N was only of predictive value in eutrophic-hypereutrophic urban lakes.

Abstract

Nitrogen (N) and phosphorus (P) are the most common nutrients triggering freshwater phytoplankton blooms at a global scale, and current trends imply that eutrophication will continue to increase in the future. However, the influences of lake characteristics and seasonality have generally been overlooked in modelling warm lake data. We used a Bayesian hierarchical approach to (1) estimate the effects of P and N on phytoplankton chlorophyll *a* (chla) concentrations in 13 subtropical waterbodies, and (2) determine how these effects varied in relation to lake type (natural shallow lakes, urban artificial lakes, and impoundment reservoirs) and seasonality (warm and cold periods). P was the main nutrient predicting chla, with more pronounced effects found in warmer months. P was relatively more important in shallow natural lakes and N in urban hypereutrophic lakes, implying that the main control on chla was related to lake type and trophic state. Weaker nutrient effects were found in reservoirs, probably due to specific hydrodynamic characteristics in these ecosystems. Our results challenge the common use of annual averages in models applied to warm lakes and suggest that management programs should consider lake type and seasonality to improve their chla prediction capacity. More attention should be paid to nutrient pollution, especially of P, derived from anthropogenic activities in warm lakes, since cultural eutrophication and phytoplankton blooms occur independent of climate.

Keywords: phytoplankton, warm climate lakes, Bayesian framework, lake-type approach, cultural eutrophication, seasonality.

Introduction

Nutrient enrichment leads to the degradation of the aquatic ecosystem and phytoplankton blooms, thereby limiting access to clean water (Rodell *et al.*, 2018). Chlorophyll *a* (chla) concentration is widely used for being a simple and robust bioindicator of phytoplankton biomass. Besides, the relationship between this pigment and nutrients is generally used for decision-making regarding water quality management. This relationship has been an ongoing research topic since the 1960s when the first chla – phosphorus (P) models were published (Canfield, 1983; Dillon and Rigler, 1974; Schindler *et al.*, 1977; Vollenweider, 1968). Two alternative positions still debate the role of nutrients and the consequent management efforts necessary to reduce only P (Lewis 2008; Molot *et al.*, 2021; Schindler *et al.*, 2008; Sterner, 2008) or nitrogen (N) and P, (Elser *et al.*, 2007; Lewis *et al.*, 2011; Paerl *et al.*, 2016; Wurtsbaugh *et al.*, 2019) in order to mitigate undesirable phytoplankton blooms.

Nevertheless, the relative importance of P versus N in controlling phytoplankton growth may be related to climate (Lewis, 2000). It is generally accepted that N more often controls phytoplankton growth in warm climates (subtropical and tropical) compared to temperate lakes (Corman *et al.*, 2015; Lewis, 2002; Talling and Lemoalle, 1998). These differences have been attributed to a greater P supply in low-latitude waterbodies, which results from the chemical weathering of rocks, and to a greater internal N loss due to increased denitrification rates as a result of higher temperatures (Lewis, 2000, 2002). Empirical evidence is contradictory though, and while no clear N limitation was found in a comprehensive study including 192 subtropical and tropical lakes (Huszar *et al.*, 2006), other studies have concluded that N or P limitation depends largely on the water body specific characteristics such as its morphometry and watershed (Abell *et al.*, 2012; Elser *et al.*, 2007; Kosten *et al.*, 2009). To improve the ability to predict and manage algal blooms in hot climates ecosystems, further studies analyzing the chla-nutrients relationship (Cunha *et al.*, 2021; De Senerpont Domis, 2013) should be conducted.

Phytoplankton biomass and nutrient levels can significantly vary along the year, thereby modifying the chla-nutrient relationship (Cha *et al.*, 2016; Kolzau *et al.*, 2014; Maberly *et al.*, 2020; Zou *et al.*, 2020). In temperate regions, phytoplankton growth is highly seasonal owing to the pronounced annual changes in temperature and daylight hours. Shallow temperate lakes tend to shift from P limitation in the early spring to N limitation later in the summer (Kolzau *et al.*, 2014, Maberly *et al.*, 2020). Temperature increase throughout the summer results in higher rates of denitrification and P release from superficial sediments, and so in changes in total nutrient concentration and phytoplankton composition and biomass (Jensen and Andersen 1992; Veraart *et* *al.*, 2011). Despite the fact that seasonal thermal effects are less pronounced in subtropical and tropical climates, factors other than temperature may play a key role in controlling nutrient-phytoplankton dynamics. For instance, changes in water depth due to the alternate wet and dry seasons or resuspension of sediments caused by high wind velocities can weaken the chla-nutrient relationship and make phytoplankton biomass less predictable (Corman *et al.*, 2015; Crisci *et al.* 2017; Havens and Hunter, 1999; Hoyer *et al.*, 2005; Lewis, 2000).

Specific lake characteristics may predetermine the response of phytoplankton to nutrient increase (Abell *et al.*, 2012; Kolzau *et al.*, 2014; Phillips *et al.*, 2008; Richardson *et al.*, 2018). Lake morphology is the main variable affecting lake functioning (Scheffer and Van Nes, 2007) and is widely used for lake classification (e.g.: Cheng *et al.*, 2010; Beaulieu *et al.*, 2013; Cha *et al.*, 2016). In temperate lakes, depth, alkalinity, and color have a large influence on the chla-nutrients relationship (Malve and Qian, 2006; Phillips *et al.*, 2012). Nonetheless, all the factors above mentioned have long been overlooked in warm climate lakes.

Regression is the main statistical approach used to determine the relationship between nutrients and chla (Kaiser *et al.*, 1994; Stow and Cha, 2013). Rather than applying tailor-made models, authors frequently extrapolate predictions from regressions that include diverse lake characteristics and that were developed for other climate regions (Cheng *et al.*, 2010). This fact can introduce large variation and prediction errors, leading to unrepresentative results (Qian *et al.*, 2019). While in temperate climates chla and nutrients have often been analyzed using seasonal summer means (Carlson, 1977; Havens and Nurnberg, 2004; Jones and Bachman, 1976; Liang *et al.*, 2020), in warmer climates models are calibrated using annual averages, assuming a constant phytoplankton growth throughout the year (Canfield, 1983; Huszar *et al.*, 2006). In either case, however, averaging masks temporal variance (Delmiro Rocha and Lima Neto, 2021; Walker and Havens, 1995). Bayesian hierarchical modeling represents a good compromise to explicitly account for sources of variability at different levels, such as lake type and climate (Cheng *et al.*, 2010). Using this type of approach, predicted chla concentrations were more accurate than those obtained by a non-hierarchical dummy variable model (Malve and Qian, 2006). Furthermore, Bayesian models can easily be used to support a wide range of decision criteria useful for lake management (Cha *et al.*, 2016; Miao *et al.*, 2009; Obenour *et al.*, 2014; Webb *et al.*, 2010).

In this study, we applied a Bayesian modeling approach to predict the effect of N, P, and seasonal variability on chla in different types of subtropical lakes. The main objectives were to estimate the effects of P and N on phytoplankton chla concentration and to determine how the effects of these nutrients differ between lake types and seasons. Lakes were classified into natural shallow coastal lakes, river-embedded reservoirs, and artificial urban lakes. The annual thermal cycle was divided into warm (high temperature, HT: November-April) and cold (low temperature, LT: May-October) periods. We hypothesized that lake types would present differential responses to P and N, as they vary in depth and trophic status. More specifically, we expected the effect of nutrients to be greater in shallow lakes than in deeper reservoirs due to self-shading in the later. We also tested whether the response of chla concentration to nutrients increase was stronger in HT than in LT.

2. Material and methods

2.1 Study area and data set

The study was carried out in lentic waterbodies of Uruguay (30°–35°S and 53°–58°W) located on the Atlantic Coast of South America, where the climate is humid subtropical (Kottek et al, 2006). Data on chla and nutrients were obtained from previous studies (1992-2014) (compiled by Bonilla et al., 2015) and more recent data (2015-2020) from the National Environmental Observatory (OAN) (DINACEA, 2020). We examined the relationships between chla and nutrients (total P; TP and total N; TN) for 13 water bodies sampled at different times of the year (total n = 394) (Table 1). To examine how the effect of nutrients on chla concentration varied across lake types, we classified the water bodies by morphology (depth and size) and origin (artificial vs. natural) and obtained three types of lakes; natural shallow lakes (NatL), river embedded reservoirs (RRes), and artificial urban lakes (ArtL) (Table 1). To account for seasonal effects on the chla-nutrients relationship we classified our data by thermal period (HT and LT) using the monthly average temperatures: HT; air temperature, by month of sampling, ≥ 17.5 °C (annual mean) and LT; air temperature, by month of sampling, < 17.5 °C (Table 1).

2.2 Bayesian modelling framework

We used a regression model within a full Bayesian framework to relate chla to TN and TP. The framework used take into account variance related to specific among-lake variations without over-fitting the model, being a useful approach in predictive modelling of chla concentrations when data arises from many different lakes (Malve and Qian, 2006; Qian et al., 2019). To meet our goals the three lake types (NatL, RRes and ArtL) were fitted as dummy variables to achieve a type-specific slopes for each nutrient in each lake type.

Our model assumes that the $\log_{10}$(chla) concentration is normal distributed with mean μ and standard error σ:

$\log_{10}(y_{ijk}) \sim \text{Normal}(\mu_{ijk}, \sigma)$

$\mu_{ijk} = \beta_{0,ijk} + \beta_{1,ijk}\log(TP_{ijk}) + \beta_{2,ijk}\log(TN_{ijk})$

$\beta_{0,ijk} = \alpha_0 + \alpha_1\,NatL_{ijk} + \alpha_2\,ArtL_{ijk} + \alpha_3\,HT_{ijk} + \alpha_4\,NatL\;HT_{ijk} + \alpha_5\,ArtL_{ijk}\,HT_{ijk} + \gamma_j + \eta_k + \varepsilon_{t(i)}$

$\beta_{1,ijk} = \varphi_0 + \varphi_1\,NatL_{ijk} + \varphi_2\,ArtL_{ijk}$

$\beta_{2,ijk} = \nu_0 + \nu_1\,NatL_{ijk} + \nu_2\,ArtL_{ijk}$

where y_{ijk} is the i^{th} observed chla value ($i = 1, \ldots, N_{jk}$) from lake j ($j = 1, \ldots, 13$) in year k ($k = 1, \ldots, 29$), $\beta_{0,ijk,}$ are intercepts; $\alpha_{0\text{-}5}$ are parameters for the fixed effects given by the temperature periods (HT vs LT) and waterbody type (NatL and ArtL), $\beta_{1,ijk}$ and $\beta_{2,ijk}$ are slopes for nutrient concentrations, γ_j are spatial random effects associated with individual waterbodies, η_k are temporal random effects associated with years, and ε_t are disturbances at time *t(i)* (ordinal rank corresponding to the day on which value *i* was recorded). Random effects for years were considered independent, but we allowed for temporal dependence within years by assuming that the disturbances arise from an AR(1) process with autocorrelation coefficient ρ.

We used the following diffuse prior probability distributions for the model parameters:

$\alpha_{0\text{-}5} \sim \text{Normal}(0, 10)$

$\varphi_{0\text{-}2} \sim \text{Normal}(0, 10)$

$\nu_{0\text{-}2} \sim \text{Normal}(0, 10)$

$\gamma_j \sim \text{Normal}(0, \sigma_\gamma)$

$\sigma_\gamma \sim \text{HalfCauchy}(0, 5)$

$\eta_k \sim \text{Normal}(0, \sigma_\eta)$

$\sigma_\eta \sim \text{HalfCauchy}(0, 5)$

$\varepsilon_t \sim \text{Normal}(\rho\,\varepsilon_{t-1}, \sigma)$

$\sigma \sim \text{HalfCauchy}(0, 5)$

Posterior predictive checks were conducted to examine model fit (McElreath, 2017). The model was then used to obtain predictions of mean chla values in different scenarios of nutrients for each lake type. First, predictions of chla were conducted with TP varying in the range of our data, while TN was fixed at the mean value. The same procedure was followed, however, changing the fixed nutrient; TN varied, and TP was fixed at the mean. We then used the model to obtain the probability of exceeding two different thresholds levels of chla (5 µg/L and 10 µg/L) as a function of TP concentrations. The threshold levels of chla were selected based on mean values for the lake types (NatL and RRes) and the temperature periods (HT vs LT). The threshold of 10 µg/L is particularly significant for management as it is commonly used as an alert level of risk exposure to toxic cyanobacteria in recreational waters (Chorus, 2012). The exceedance probability was taken as the proportion of Markov chain Monte Carlo (MCMC) samples from the posterior distribution of chla that had values greater than the threshold. For all posterior predictions the random effects and the disturbances were set to zero.

Models were fitted using the MCMC algorithm to sample from the posterior distribution of parameters (Bürkner, 2017). We ran 4 MCMC chains for 10000 iterations and discarded 3000 iterations (warmup) to obtain a total of 28000 samples from the posterior distribution. Posterior distributions of individual parameters were summarized as medians and 95% credible intervals. Convergence of the chains was assessed using visual inspection of trace plots and the Gelman-Rubin convergence diagnostic (R_{hat}) (Gelman et al., 2014). R_{hat} values for all parameters were < 1.002, indicating no apparent departures from convergence. Statistical analyses were done in the R environment (R Core Team, 2020).

3. Results

The values of chla ranged from three orders of magnitude with the highest values obtained in the ArtL lake type (Fig. 1). The RRes and ArtL lake types displayed seasonal trends with higher chla values in HT than in LT, while such trend was less pronounced in NatL (Fig. 1). The summarized lake data displayed large variations in nutrient concentration between temperature periods and ecosystem types (Table 1, Fig. S1). The highest nutrient values were observed in ArtL, which presented eutrophic conditions both in HT and LT (Table 1).

The hierarchical Bayesian model indicated clear effects of the two nutrients on chla concentration in the three studied lake types (Fig. 2). P had the largest positive effect size on NatL and RRes, while N only had a positive effect on eutrophic urban lakes. Pronounced differences were also estimated in all lake types between the two temperature periods. At the same nutrient levels, higher mean values of chla were found in HT compared to LT (Fig. 2). The predictions made based on subsequent distributions were used to visualize the effects of nutrients and the temperature periods under different scenarios, allowing to observe the differences between the three lake types (Fig. 3 and Fig. 4). In all predictive scenarios, higher chla concentrations were reported in HT, in particular regarding RRes (larger separation between HT and LT curves in Fig. 3 and Fig. 4). The positive effect of P on NatL and RRes (Fig. 3, upper panel) and the positive effect of N in ArtL (Fig. 3, lower panel) can also be noticed by analyzing the nutrient range from our data. Fig. 4 illustrates the probability of exceeding the two selected thresholds levels of chla with increasing TP. In NatL and RRes exceedance probabilities increased rapidly as TP did (Fig.

4). On the contrary, in ArtL, no effect of P was estimated; and probabilities were always above the tiers.

4. Discussion

Our results revealed clear differences regarding the effects of nutrients on chla among subtropical lake types and between the two temperature periods. Three broad lake types captured large differences in chla response to nutrients, which may have consequences in terms of management improvement. P was the most important nutrient for chla prediction, particularly in the HT period, contradicting classic paradigms that postulate N as the prevalent nutrient in controlling phytoplankton chlorophyll *a* in warm climate lakes. Moreover, our results underscored the relevance of analyzing chla data by warm/cold periods rather than by the common annual averages which may overlook the effects of nutrients on phytoplankton control.

4.1 Importance of N and P in predicting chla in subtropical lakes

Our results suggest that the strength of N and P in predicting chla is contingent upon lake type and the trophic state, following a general trend encountered in temperate lakes (Canfield 1983; Filstrup and Downing, 2017). N plays a role in controlling phytoplankton biomass during eutrophic conditions in warmer months, when increased denitrification and P release from sediments occur (Liang *et al.*, 2020; Moss *et al.*, 2012; Søndergaard *et al.*, 2013). Light limitation is also common in highly turbid hypereutrophic conditions. This results in phytoplankton producing more pigments and increasing the physiological demand for N (Sterner, 2008). The paradigm over N as more relevant than P in controlling chla in warm climates (Lewis, 2000, 2002; Talling and Lemoalle, 1998) is not supported by our study in line with other empirical evidence (Huszar *et al.*, 2006; Muhid and Burford, 2012; Rowland *et al.*, 2019). Therefore, whether N or P is the main nutrient to predict chla is more related to the lake characteristics and the trophic state than to the differences between climate regions. P seems to be by far the most important controlling nutrient of chla, except in hyper eutrophic artificial lakes where N prevails.

4.2 Seasonal effects on the chla-nutrient relationship in subtropical climates

Our results underscored the relevance of considering seasonality for modelling the nutrient-chla relationship in subtropical lakes. The chla-nutrient relationship exhibited a strong dependence on seasonality, especially in reservoirs. Studies in temperate lakes are usually based on summer average of explanatory and response variables, when light and temperature allow maximum phytoplankton growth. The alternative of using an annual lake average to model chla is a common approach in studies conducted in warm regions assuming that phytoplankton growth is similar along the year (Cunha *et al.*, 2013; Huszar *et al.*, 2006). However, such an approach can mask variance and underestimate the strength of nutrients as drivers of phytoplankton yield due to seasonal patterns (Li *et al.* 2014; Rowland *et al.* 2019). This not only refers to the water temperature cycle, but also to changes in precipitation and wind cycles. For instance, tropical lakes may have seasonal patterns in phytoplankton following dry and wet seasons (Melack 1979; Rangel *et al.*, 2012). Subtropical lakes, in turn, may have seasonal patterns depending on wind dynamics, affecting the chla-nutrient relationship dependent on lake morphology (Havens *et al.* 1999; Hennemann and Petrucio, 2016). We concluded that further studies including seasonal variations in the response of chla to nutrients are needed to improve the prediction and understanding of warm climate lakes.

4.3 Lake type effects on the chla-nutrient relationship

Our study showed that lake type is a key factor for modeling chla response in subtropical lakes, consistent with studies from other climatic regions (Dolman *et al.*, 2016; Malve and Qian, 2006; Phillips *et al.*, 2008; Richardson *et al.*, 2018). Even though lake classification criteria differ between studies (i.e., depth, surface area, color, alkalinity, etc.), they all reveal that chla due to nutrients depends on the lake type. In the particular case of reservoirs, the relationship between chla and nutrients was poor probably due to highly variable flow rates that rely on seasonality, extreme events, and operational management (Aubriot *et al.* 2020; Delmiro Rocha and Lima Neto, 2021; Hou *et al.*, 2017; Rangel *et al.*, 2012). For instance, high flow, frequent in winter, translated into phytoplankton dilution regardless of the nutrients available as previously demonstrated in the reservoirs analyzed in our study (Chalar, 2006; Chalar *et al.*, 2014). Models including other factors like flow patterns, operational measures and turbidity are needed to increase chla prediction capacity in this lake type.

We found a large variance within the same lake type. This could be ascribed to the natural variation occurring between lakes as previously suggested (Reynolds, 1992; Richardson *et al.*, 2018, Phillips *et al.*, 2008). One of the advantages of using a Bayesian framework is prediction improvement by pooling information across lakes and lake type, and thereby increasing the predictive accuracy. This is particularly powerful for prediction outside the range of data available for a specific lake or lake type or when little data are available (Malve and Qian, 2006; Stow *et al.*, 2009). The differences found between climates were less than the effect of local factors (type of lake, land use, and trophic state) when it came to determining the role of nutrients on phytoplankton chla (Coppens *et al.*, 2015; Kosten *et al.*, 2009; Rowland *et al.*, 2019). Furthermore, each type of lake may be associated with a category of risk or susceptibility to develop phytoplankton blooms, which can be useful for environmental management and eutrophication control (Richardson *et al.*, 2018). The classification used in our study is simple, and based on basic lake characteristics. It has demonstrated to be a useful tool to capture the variability of chla response to nutrients. Moreover, it can be easily included in models for environmental monitoring.

4.4 Other factors

Our results demonstrated the importance of considering seasonality and ecosystem morphology in modeling the response of chla to nutrients; however, other ecological factors play a part too. It is generally assumed that in warmer climates the relationship between chla and nutrients is weaker than in temperate ones. This has been mainly attributed to turbidity and trophic interactions (Abell *et al.*, 2012; Canfield, 1983; Cunha *et al.*, 2013; Huszar *et al.*, 2006). The highly turbid ecosystems frequently found in warm climate lakes are more likely to be light-limited (Abell *et al.*, 2012). In addition, in warm climates, fish top-down control on large zooplankton is strong throughout the year and abundant omnivorous fish feeds on phytoplankton (Iglesias *et al.*, 2007; Meerhoff *et al.*, 2007; Van Leeuwen *et al.*, 2007), being the phytoplankton biomass controlled by a diverse pool of potential grazers (Mazumder and Havens, 1998). These factors may explain the larger variance in the chla-nutrients relationship reported in the literature in warm climates. As trophic dynamics is associated to both seasonality and morphology, some of the effects have already been captured by our modelling approach.

4.5 Management implications

The currently accepted paradigm indicating a weaker relationship between nutrients and chla in warm lentic ecosystems needs to be reconsidered, as shown by our study. The apparent low effect of nutrients as control factors of phytoplankton growth/biomass, could mislead to implement less effort in nutrient control (decreasing external loads or preventing inputs) for mitigating the effects of eutrophication in warm climate freshwaters (Cunha *et al.*, 2021). More attention should be paid to nutrient pollution derived from anthropogenic activities in warm climates in view of the active growth of phytoplankton throughout the year including harmful cyanobacteria (Haakonsson *et al.*, 2017; Long *et al.*, 2021; Yang *et al.*, 2016). In addition, with nutrient increase, shallow warm lakes are more likely to be dominated by cyanobacteria than temperate ones (Kosten *et al.*, 2012), with significant implications for ecosystem health and services. Moreover, our results indicated that the risk of exceeding safe chla levels increased dramatically as quite moderate P concentration did. This was more evident in natural lakes regardless of seasonality, and as far as reservoirs are concerned, mainly in warm periods. In spite of the fact that chla presence in artificial eutrophic lakes showed no significant response to P, its relationship with N needs further attention, so as to clarify its role as a limiting factor in eutrophic conditions. Further studies should be undertaken in warm climate freshwaters, both subtropical and tropical, in order to shed some light on the effect of nutrients depending on lake type and trophic state, on total biomass and the dominance of phytoplankton groups. Finally, both lake-type characteristics and seasonal effects should be considered to advance our understanding and strengthen our management capacity of warm freshwater.

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Table 1. Characteristics of lake types of this study, water temperature and predictive variables grouped by temperature period (warm, cold). Medians (min. - max.) values are shown for all variables.

Figure 1. Density distribution of chlorophyll *a* (µg/L; $\log_{10}$) in the three lake types by temperature period (warm vs. cold). NatL= Natural lakes, RRes = River embedded reservoirs, ArtL = Artificial lakes.

Figure 2. Summary of the posterior distribution (medians and 95% credible intervals) of the regression coefficients for the fixed effects (a), and standard deviation of the random effects η and γ, the auto-correlation term ρ and standard deviation σ (b). α_{0-5} are coefficients for the fixed effects given by temperature period (warm vs cold) and waterbody type (NatL and ArtL). φ_0-φ_2 and ν_0-ν_2 are the random slopes for TP and TN respectively. γ are spatial random effects associated with individual waterbodies and η are temporal random effects associated with years.

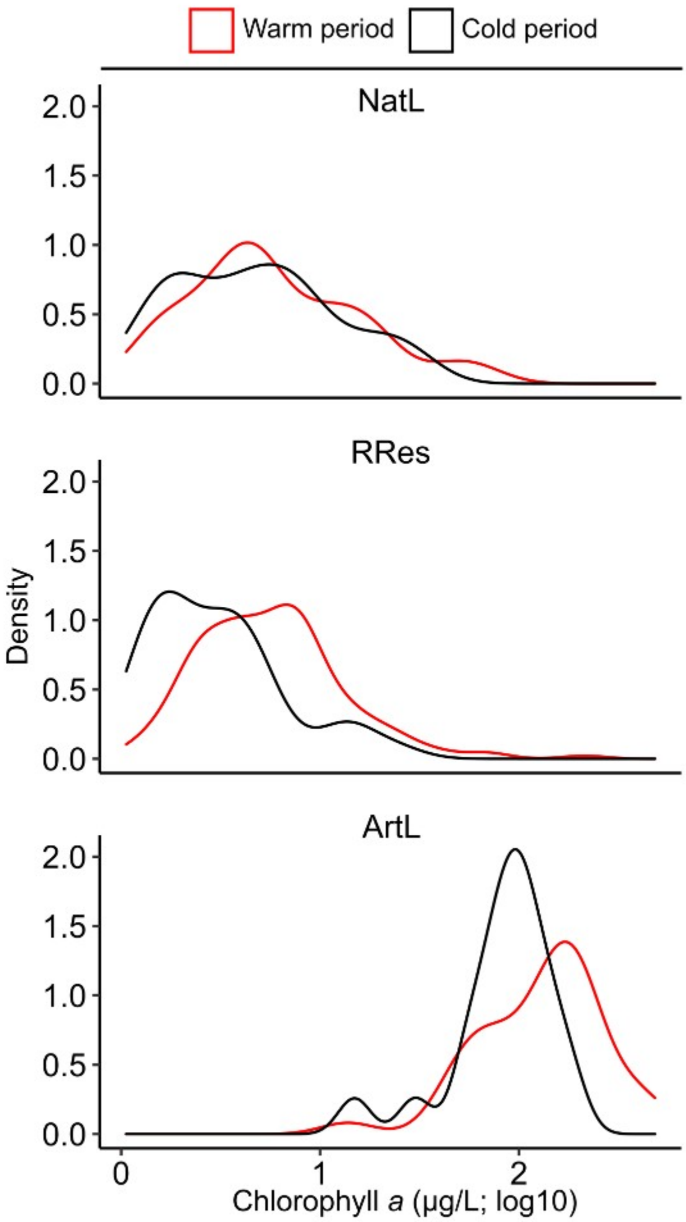
Figure 3. Posterior predictive distribution of chlorophyll *a* ($\log_{10}$) as a function of total phosphorus (TP) (top row) and total nitrogen (TN) (bottom row), by lake type (NatL= Natural lakes, RRes = reservoirs, ArtL = Artificial lakes) and temperature period (warm vs. cold).

Figure 4. Probability of exceeding 5 µg/L (upper row) and 10 µg/L (lower row) threshold concentrations of chlorophyll *a* (chla) as a function of TP (total phosphorous) in the warm (red curves) and cold (black curves) temperature periods. NatL= Natural lakes, RRes = reservoirs and ArtL = Artificial lakes.

Table 1. Characteristics of lake types of this study, water temperature and predictive variables grouped by temperature period (warm, cold). Medians (min. - max.) values are shown for all variables.

Lake type, Num. lakes; *Num. samples*	Depth (m)	Surface Area (km^2)	Water Temperature (ºC)		Total Phosphorus (µg/L)		Total Nitrogen (µg/L)	
			Warm	Cold	Warm	Cold	Warm	Cold
Natural shallow lakes (NatL)	1.9	30	23	17	62	60	670	450
6; *149*	(1.3-4.1)	(0.53-79)	(15-29)	(9-25)	(16-271)	(5-269)	(46-3850)	(50-1650)
River embedded reservoir (RRes)	26	551	25	15	75	84	610	735
4; *151*	(15-35)	(100-1070)	(19-36)	(10-22)	(5-265)	(15-176)	(50-2380)	(260-6570)
Artificial urban lakes (ArtL)	4.7	0.15	24	14	189	194	2460	2570
3; *58*	(2.2-9.8)	(0.01-0.24)	(18-25)	(12-15)	(44-864)	(46-1076)	(790-7260)	(1080-11480)

Figure 1.



Warm period
Cold period
NatL
RRes
ArtL
Density
2.0
1.5
1.0
0.5
0.0
0
1
2
Chlorophyll *a* (µg/L; log10)

Figure 2

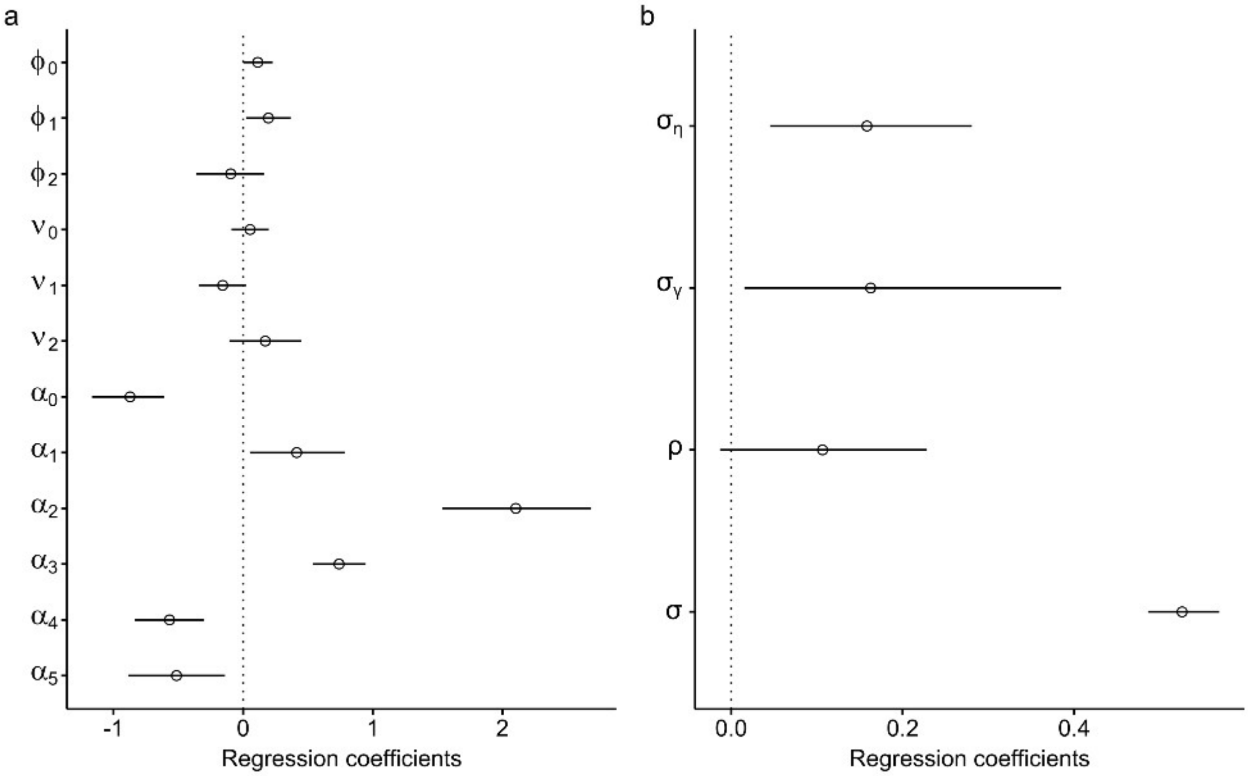

a
ϕ_0
ϕ_1
ϕ_2
ν_0
ν_1
ν_2
α_0
α_1
α_2
α_3
α_4
α_5
-1
0
1
2
Regression coefficients
b
σ_η
σ_γ
ρ
σ
0.0
0.2
0.4
Regression coefficients

Figure 3

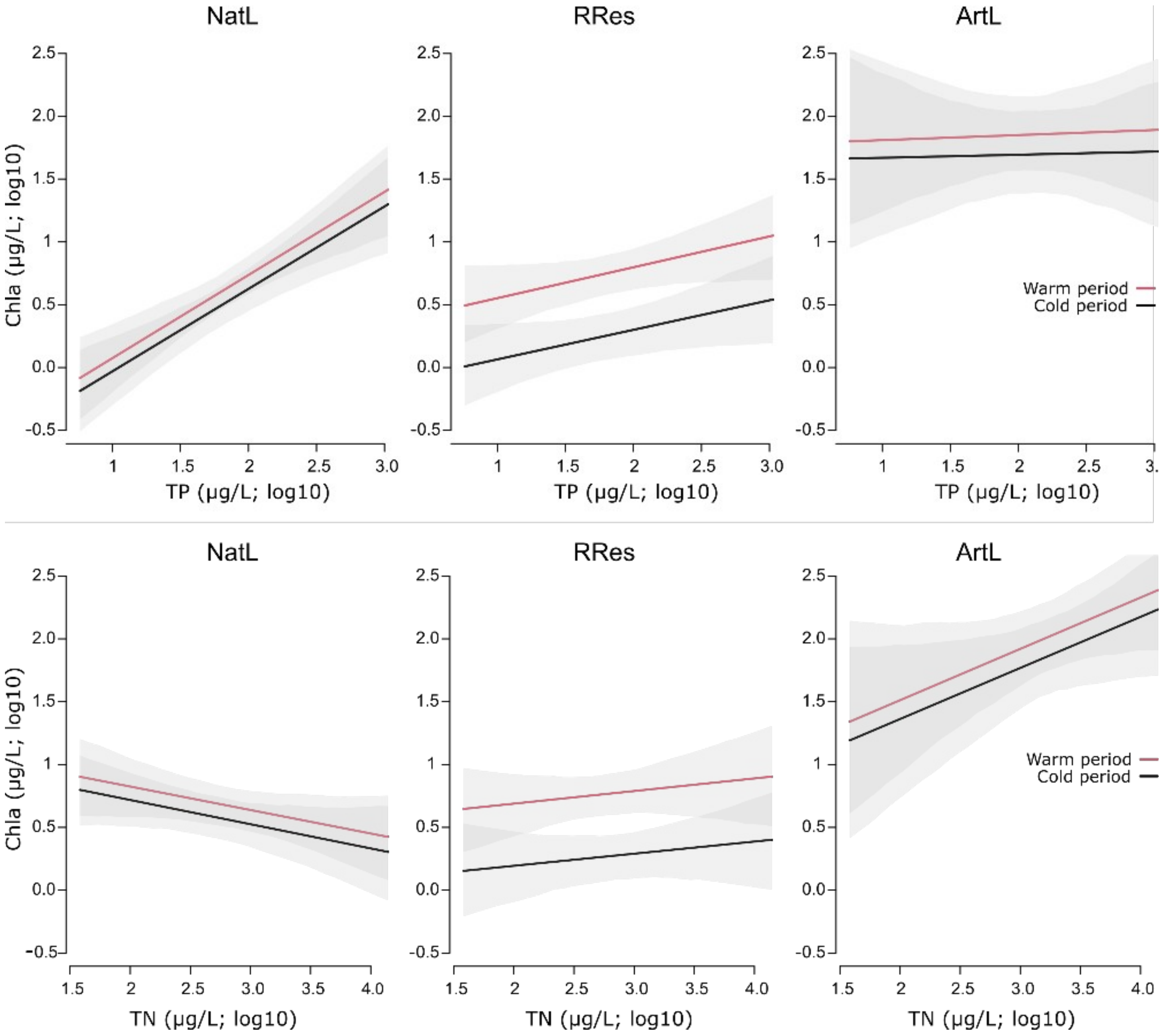
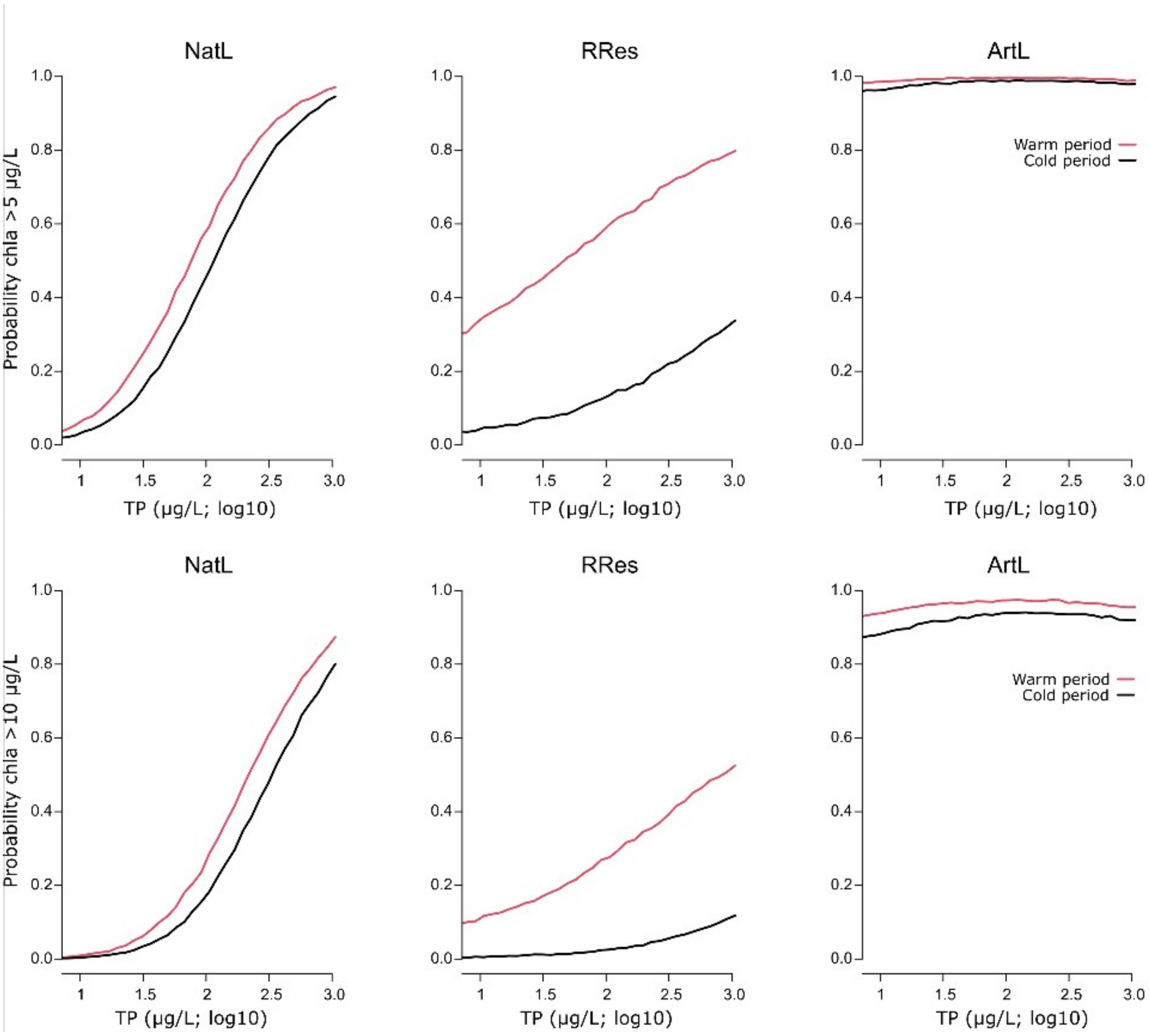
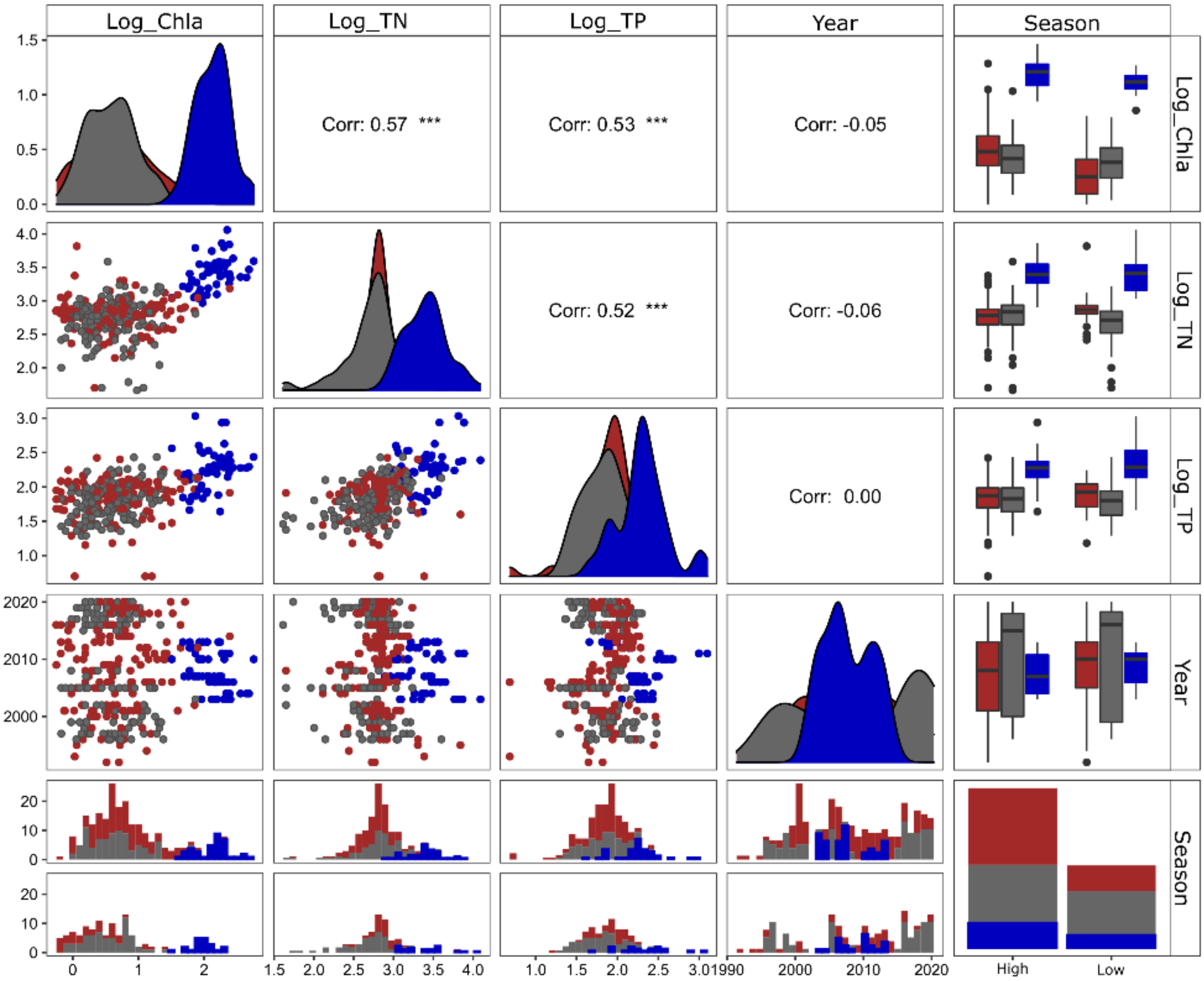

NatL
RRes
ArtL
Chla (µg/L; log10)
2.5
2.0
1.5
1
0.5
0.0
-0.5
1
1.5
2
2.5
3.0
TP (µg/L; log10)
Warm period
Cold period
NatL
RRes
ArtL
Chla (µg/L; log10)
1.5
2
2.5
3.0
3.5
4.0
TN (µg/L; log10)
Warm period
Cold period

Figure 4


NatL
RRes
ArtL
Probability chla >5 µg/L
Probability chla >10 µg/L
1.0
0.8
0.6
0.4
0.2
0.0
1
1.5
2
2.5
3.0
TP (µg/L; log10)
Warm period
Cold period

Supplementary Material

Figure S1. Correlation matrix of the fixed and random variables included in the Bayesian regression model. Left panels report scatter plots, right panel shows linear correlation coefficients and the diagonal panel shows distribution of the variables: Chla, log TN, log TP, year and season. Each lake type is indicated by a different color; Grey = natural lakes, red = reservoirs and blue = artificial lakes.



III. Temperature and precipitation shape the distribution of harmful cyanobacteria in subtropical lotic and lentic ecosystems

Hasta ahora hemos visto como la biomasa del fitoplancton depende de las altas concentraciones de nutrientes en la región subtropical estudiada. En este capítulo nos enfocamos en analizar como los forzantes climáticos (temperatura y precipitaciones) influyen sobre la distribución y la biomasa de cianobacterias planctónicas en ecosistemas eutrofizados. Cuando los ecosistemas alcanzan niveles altos de nutrientes estos variables podrían tener gran influencia sobre las biomasa y distribución de cianobacterias. Pretendemos aportar evidencias sobre la distribución de las cianobacterias en climas subtropicales, en particular en condiciones eutróficas, y evaluar los efectos de forzantes climáticos sobre la misma.

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Temperature and precipitation shape the distribution of harmful cyanobacteria in subtropical lotic and lentic ecosystems

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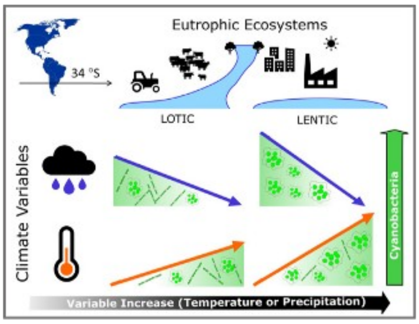
HIGHLIGHTS

- Limited knowledge of cyanobacteria dynamics in subtropical freshwaters, particularly in lotic ecosystems affects management.
- Cyanobacteria biovolume were modeled for 36 subtropical ecosystems in relation to water temperature and cumulative rainfall.
- Rainfall is a significant variable for predicting cyanobacteria biovolume in eutrophic lotic ecosystems.
- The main differences between ecosystems were found at the cyanobacteria genus level.

GRAPHICAL ABSTRACT



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ABSTRACT

Cyanobacterial blooms are expected to become more frequent in freshwaters globally due to eutrophication and climate change effects. However, our knowledge about cyanobacterial biogeography in the subtropics, particularly in lotic ecosystems, is still very limited and the relationship of blooms to temperature and precipitation remains unclear. We took advantage of a comprehensive database of field data compiled over several years (1997 to 2015) to compare cyanobacteria biomass and distribution between lentic and lotic subtropical freshwaters (36 ecosystems, 30°–35°S) and to investigate the role of water temperature and precipitation as significant predictors in eutrophic ecosystems. A filamentous Nostocales, *Dolichospermum* (*Anabaena*), was the most widely distributed and frequent genus in the region of the study, followed by the colonial *Microcystis*, supporting observations of a global latitudinal pattern. Similar total cyanobacteria biovolumes (TCB) were found in lentic and lotic ecosystems, but the proportion of *Dolichospermum* was higher in lotic ecosystems. Using generalized linear models (GLMs), we found that temperature and rainfall explained 27% of the variation in TCB in lotic ecosystems, while temperature explained 19 and 28% of *Dolichospermum* and *Microcystis* biovolume, respectively. In lentic ecosystems, accumulated rainfall explained 34% of the variation of *Microcystis* biovolume while temperature explained 64%. Our results imply that the increase in extreme meteorological events and temperature predicted by climate models will promote increasingly severe cyanobacterial blooms in eutrophic subtropical freshwaters. Our analysis provides new information about the occurrence of bloom-forming cyanobacteria for southeastern South America and thus fills an important knowledge gap for subtropical freshwaters.

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1. Introduction

Harmful Cyanobacterial blooms (CyanoHABs) threaten and imperil water use worldwide, due to their capacity to produce potent toxins (Chorus and Bartram, 1999). Cultural eutrophication is among the primary causes of blooms, and the nutrients nitrogen and phosphorus in particular have long been identified as the main drivers of this phenomenon (Downing et al., 2001; Gobler et al., 2016; Smith, 1986; Smith and Schindler, 2009). Recent studies have shown that water temperature and rainfall regimes, may play a key role in the proliferation of cyanobacteria, especially in eutrophic ecosystems (Bormans et al., 2005; O'Neil et al., 2012; Paerl and Huisman, 2009; Reichwaldt and Ghadouani, 2012). Field observations (Beaulieu et al., 2013), time series/large data set comparisons (Elliott, 2012; Wagner and Adrian, 2009) and laboratory studies (Coles and Jones, 2000; Davis et al., 2009; Mehnert et al., 2010) have shown a positive relationship between temperature increases and cyanobacteria growth and/or dominance in freshwaters (but also see Lürling et al., 2013). The increase in temperature can favor the persistence of cyanobacteria blooms for longer periods during summer in eutrophic freshwaters (Deng et al., 2014; Paerl and Huisman, 2009; Wagner and Adrian, 2009). Alterations in precipitation impact the nutrient loading dynamics and may therefore also favor cyanobacterial blooms (Jeppesen et al., 2011; Reichwaldt and Ghadouani, 2012). For instance, this may occur when extreme rainfall is followed by periods of droughts (Paerl and Huisman, 2009). Rainfall may also have the opposite effect by causing a washout effect of cyanobacterial blooms, as found over a 10-year period in an eutrophic river in Florida (USA), where high rainfall resulted in cyanobacteria decrease (Phlips et al., 2007), although rainfall patterns effects on the distribution on bloom-forming genera seem to have been ignored in limnological studies, probably due to its complexity (Reichwaldt and Ghadouani, 2012). A better understanding of the effects of rainfall on cyanobacterial blooms dynamics is therefore needed.

Almost all bloom-forming species have common biological characteristics (gas vesicles, mucilage and large individual size) that contribute to the recruitment of resources in the water column and avoidance of sedimentation and predation (Bonilla and Pick, under review; Reynolds, 2006). However, differences between genera or even species can result in divergent responses to environmental conditions (Carey et al., 2012; Dolman et al., 2012; Komárek, 2016; Rigosi et al., 2015). How taxa may respond to climate change effects is still not clear (O'Neil et al., 2012), though it has been suggested that some taxa are more sensitive to changes in temperature, (Rigosi et al., 2014) or rainfall patterns (Reichwaldt and Ghadouani, 2012). Further ecological studies at the genus levels are needed to better understand the environmental conditions that favor cyanobacterial blooms to improve management plans.

Current predictions of future cyanobacterial trends are mostly based on studies of temperate lakes (Elliott, 2012), limiting our frame of understanding in warmer ecosystems (De Senerpont Domis et al., 2013a). Moreover, cyanobacteria distribution and dynamics in lotic ecosystems are still less studied (Soares et al., 2007). Even in South America, which is the continent of rivers (Carril et al., 2016; Neiff, 1996), the distribution of its harmful cyanobacteria is mostly limited to lentic ecosystems (Soares et al., 2007), and only few studies have attempted to analyze field data spanning wide geographic areas (Kosten et al., 2012; Soares et al., 2013). Although for lentic ecosystems at intermediate subtropical latitudes the role of the hydrology and climatology on overall phytoplankton dynamics is clear (De Senerpont Domis et al., 2013b), evidence for lotic ecosystems has so far been scarce and further studies are clearly required (De Senerpont Domis et al., 2013a). Climate change scenarios for South America predict increases in the frequency of extreme rainfall and drought events (Marengo et al., 2010). Changes in climate variables effects on phytoplankton, vary in different regions and latitudes (De Senerpont Domis et al., 2013a; Phlips et al., 2007), therefore it is important to gain in our knowledge about the role of temperature and precipitation as predictor factors of cyanobacteria biovolume in this region as well.

In this study, we conducted an overview of bloom-forming cyanobacteria comparing lentic and lotic freshwaters in a subtropical region of South America, using field data from a broad range of ecosystems collected between 1997 and 2015. Our goals were double: (1) to identify main cyanobacteria genera and their distribution and (2) to assess the relationship of total cyanobacteria and most frequent genera biovolume to water temperature and rainfall, comparing lentic and lotic eutrophic ecosystems. Our analysis was based on the hypothesis that in the subtropics, temperature and precipitation are significant predictors of cyanobacteria biovolume in lotic nutrient rich ecosystems, as well as in lentic ecosystems. We also hypothesized that cyanobacteria genera differed in their response to temperature and rainfall.

2. Material and methods

2.1. Study area general characteristics

The study was performed in sites across Uruguay (30°–35°S and 53°–58°W), a country of 176.000 km^2 located at the southern limit of the subtropical climate zone on the Atlantic Coast of South America. It has an extended hydrographic network of lotic ecosystems, natural shallow lakes, artificial reservoirs and coastal lagoons. For the period 2001 to 2015 the mean annual air temperature and mean annual precipitation were 18.2 °C and 1370 mm, respectively. Mean number of days with extreme precipitation (>50 mm) was 71 (period: 2001 to 2010) (source: National Meteorological Institute, InuMet, http://www.meteorologia.com.uy/). Though natural grasslands constitute the dominant terrestrial ecosystem of Uruguay (covering 64.3% of the country's surface area), expansion and intensification of livestock and agricultural activities over the last two decades (MGAP-DIEA, 2014, 2013) have led to widespread freshwater eutrophication in the main watersheds (Bonilla et al., 2015).

2.2. Dataset

Our study is based on a dataset assembled from sampling by several national institutions: The University of the Republic (UdelaR), the Ministry of the Environment (DINAMA), the National Water Company (OSE), the Technological Laboratory of Uruguay (LATU) and the City of Montevideo (IM) (compiled by Bonilla et al., 2015). For this study, we used a subset of this data matrix, containing cyanobacteria species biovolume information from 36 water bodies (artificial lakes and reservoirs, natural shallow lakes and coastal brackish lagoons, medium-sized rivers of order ≤5, and large rivers of order > 5, totalizing 66 sampling points, sampled between 1997 and 2015 (Fig. 2; Table A.1). Because the sampling frequency, and thus the number of data points, differed greatly between ecosystems, a maximum of one input per sampling site per season (summer, autumn, spring and winter) were selected for our analysis ($n = 234$). Most ecosystems were previously classified as eutrophic to hypereutrophic, per total phosphorous concentration (Table A.1).

Since most of the ecosystems were shallow and polymictic, water samples for cyanobacteria identification and counting were taken from the subsurface (ca. 20 cm depth) and preserved in Lugol's solution. Quantification was performed following the standard sedimentation method (Utermöhl, 1958) and species biovolume was calculated with simple geometric shapes (Hillebrand et al., 1999) using cell measurements. When data were available in cells L^{-1}, the biovolume of each taxon was estimated from cell linear measurements from our database. Since the cyanobacteria dataset includes samples counted by different taxonomists in several institutions, and because diacritical attributes to confirm species (e.g. in akinetes) were not always present, to ensure taxonomic consistency we evaluated species biovolume at the genus level.

When water temperature was not available for lotic ecosystems (22% of the cases), it was estimated using a linear regression model between surface water temperature and mean daily air temperature for the 7 days before the sampling date ($r^2 = 0.89$, $F = 1311$, $DF = 160$, $p < 0.01$). To verify the predictive accuracy of the model, a cross-validation was performed (Residuals = 160, SS = 469, MS = 3). Similar methods have been used to estimate surface water temperature from air temperature for rivers (Rivers-Moore and Lorentz, 2004) and streams (Benyahya et al., 2007; Lewis et al., 2000). Daily precipitation data and the mean daily air temperature was obtained from INIA (Source: National Institute of agricultural investigation, http://www.inia.uy/gras/Clima/Banco-datos-agroclimatico) selecting the closest climate station to each sampling site.

All lentic ecosystems are polymictic, except one lake (Ton Ton Lake), and most of them are shallow (<5 m) except the reservoirs (mean depth = 17 m, $n = 5$) and two lakes (Ton Ton Lake and Javier Lake). They also vary widely in size between small artificial lakes (1.3 to 23.5 ha, $n = 5$), coastal lagoons (from <60 to >350.000 ha, $n = 8$) and reservoirs (1.5 to 7 ha and >10.000 ha, $n = 9$). Lotic ecosystems orders were determined using a hydrographic map digitalized at scale 1:100.000 (Source: Ministry of Transport and Public Works). Lotic ecosystems are "flashy" (rapid and frequent changes in flow in short periods of time), due to the short-duration-high-magnitude rainfall events occurring in the region (Goyenola et al., 2015). Limited data about water flow of these lotic ecosystems is available, although there are notable differences between large (order > 5) and medium-sized rivers (order < 5) (1643 $m^3 s^{-1}$, $n = 4$ and 7.8 $m^3 s^{-1}$, $n = 4$ for large and medium-sized rivers, respectively) (unpublished data).

2.3. Data analysis

Cyanobacteria scum's (defined as cyanobacterial biovolume > 100 $mm^3 L^{-1}$) and samples with total cyanobacterial biovolume below 0.001 $mm^3 L^{-1}$ were excluded ($n = 49$) from the statistical analyses. As we wanted to assess surface water temperature (WT) and precipitation (accumulated precipitations 7 days before sampling, CP7) as predictors of cyanobacteria biovolume in nutrient-rich ecosystems we only used the ecosystems classified as eutrophic (Table A.1, 15 ecosystems, marked in bold, $n = 140$). We sought to clarify the independency of WT and CP7 from trophic indicators (total phosphorus and nitrogen). Because our database did not contain simultaneous measurements of cyanobacterial biovolume and nutrient concentration in water in all cases, we assessed the hypothesis of autocorrelation between WT, CP7 and nutrients (total phosphorus and total nitrogen), based on an earlier, unpublished database, and found that no significant correlation existed between these variables in lentic and lotic ecosystems (Pearson Test, $p > 0.05$), with the exception of total nitrogen and CP7 in lotic ecosystems ($p < 0.05$, rho = −0.33). Generalized linear models (GLMs) were conducted to quantify the strength of the explanatory variables (WT, CP7) of total cyanobacterial biovolume (TCB) and of the most frequent genera biovolume, in lentic and lotic ecosystems. To access the influence of ecosystem type on the TCB, ecosystem type was first used as co-variable (lentic vs. lotic). For the prediction of main genera biovolume presence (biovolume of genera > 0) was used. To meet the conditions of normality and homogeneity of variance of the residuals, the response variable (biovolume) was ln-transformed and all models were subjected to a residual analysis to ensure that they met GLM assumptions (Birks, 2012). The identity function was used as the connecting function. Steps were run by sequentially deleting the least significant term and comparing successive steps in model simplification with Akaike's Information Criterion (AIC). When more than one variable was included in the final model, we also examined the proportional contribution of each predictor to the overall R^2 (Johnson and Lebreton, 2004). Statistics were performed and plotted using the software R (R Core Team, 2015) and R packages ggplot, doBY and DAAG (Højsgaard et al., 2014; Maindonald and Braun, 2014; Wickman, 2009). The georeferenced map with the distribution of the main cyanobacteria genera was elaborated using the GIS program ArcMap10.

3. Results

3.1. Frequency and distribution of cyanobacteria.

Twenty-four cyanobacteria genera were identified distributed among Chroococcales (8), Nostocales (7) and Oscillatoriales (9) (data not shown) of these, 13 genera, mostly filamentous, reached >3% of total occurrence (Fig. 1). *Dolichospermum* was the most frequently encountered genus and it had the widest geographical distribution

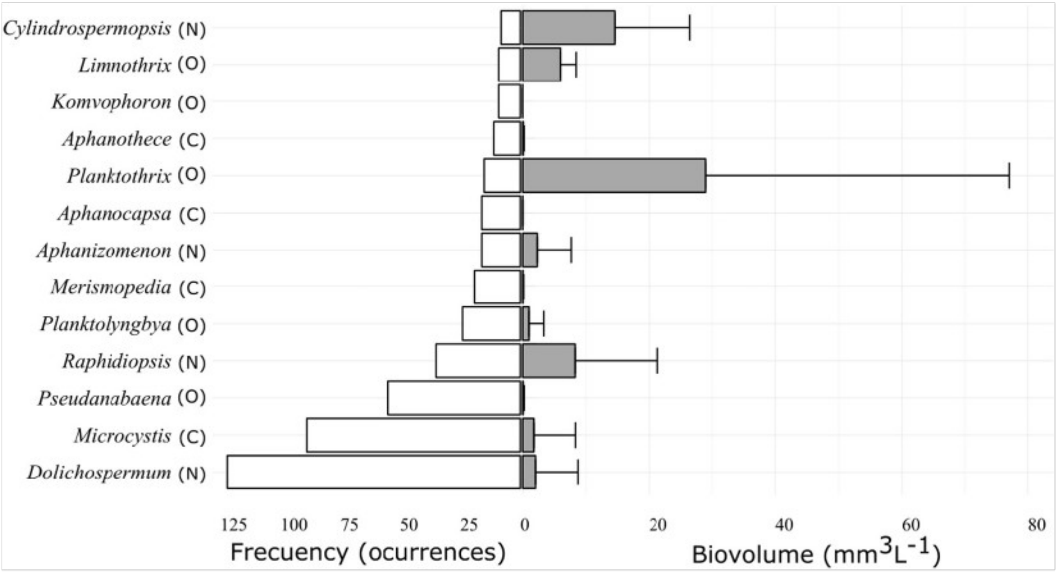

Fig. 1. Most frequent genera in the dataset: frequency (left, white) and average biovolume (data between >0.001 and <100 $mm^3 L^{-1}$) with STD (right, grey). C = Chroococcales, N = Nostocales and O = Oscillatoriales.

(present in 38 of 66 sites) including lentic and lotic freshwaters (Fig. 2). *Microcystis* was the second most frequent and second most widely distributed genus (in 34 of 66 sites, both lentic and lotic) (Figs. 1 and 2). These two genera co-occurred at least once in 19 sites, in both lentic and lotic ecosystems across the whole country, though high biovolumes (>2 mm^3 L^{-1}) occurred only in Uruguay and Rosario rivers (1 occurrence) and one artificial reservoir of Negro River (Fig. 2; ecosystem numbers 23 and 33, Table A.1). *Pseudanabaena* was the third most frequent taxon (56 occurrences), while *Cylindrospermopsis* was present in 8 samples (Fig. 1). No significant differences were found in total cyanobacteria biovolume (TCB) between eutrophic lentic (median: 0.073 mm^3 L^{-1}, first and third quantiles: 0.009–1.050 mm^3 L^{-1}) and eutrophic lotic ecosystem (median: 0.094 mm^3 L^{-1}, first and third quantiles: 0.011–0.427 mm^3 L^{-1}) (Kruskal-Wallis chi-squared = 0.18, df = 1, *p*-value = 0.69). In lentic ecosystems *Microcystis* represented a higher biovolume than *Dolichospermum* (median: 3.348 mm^3 L^{-1} and 0.342 mm^3 L^{-1}, respectively), while in running waters the opposite trend was found (median: 1.867 mm^3 L^{-1} and 1.381 mm^3 L^{-1}, for *Dolichospermum* and *Microcystis*, respectively). However, in lentic waterbodies the biovolume of the two genera represented a similar mean proportion of the TCB (*Microcystis*: 17% against *Dolichospermum* 26%), while for lotic waterbodies *Dolichospermum* presented 58% of the TCB, against 29% for *Microcystis*.

3.2. Prediction of cyanobacteria in eutrophic ecosystems using water temperature and precipitation

TCB showed a general inverse trend with rainfall and a positive one with water temperature. High TCB (>10 mm^3 L^{-1}) was rarely found when CP7 was above 50 mm and WT below 20 °C (Fig. 3) (except for five cases in artificial lakes). Water temperature and ecosystem type (lentic or lotic) explained 10% of the variance of the TCB and the response to temperature was the same in both ecosystem types (Table 1, model 1), as the interaction term was not significant. The overall R^2 was decomposed and normalized, to determine that temperature explained most of the total variance ($R^2 = 0.83$) rather than ecosystem type ($R^2 = 0.17$). No general significant model was found for TCB using cumulative precipitation as predictor for all ecosystems combined. However, when lotic ecosystems were analyzed separately, WT and CP7 explained 27% of the TCB variance (Table 1), where WT explained most of this variance ($R^2 = 0.67$) and CP7 ($R^2 = 0.33$).

The two most frequent and most distributed genera were also related to the predictive variables. *Microcystis* biovolume increased with WT in both type of ecosystems, with WT explaining 28 and 64% of its variation, for lotic and lentic water bodies, respectively (Table 1, Fig. 4). *Dolichospermum* biovolume was correlated with WT in lotic ecosystems only (Table 1 and Fig. 4A–B). *Microcystis* biovolume was inversely

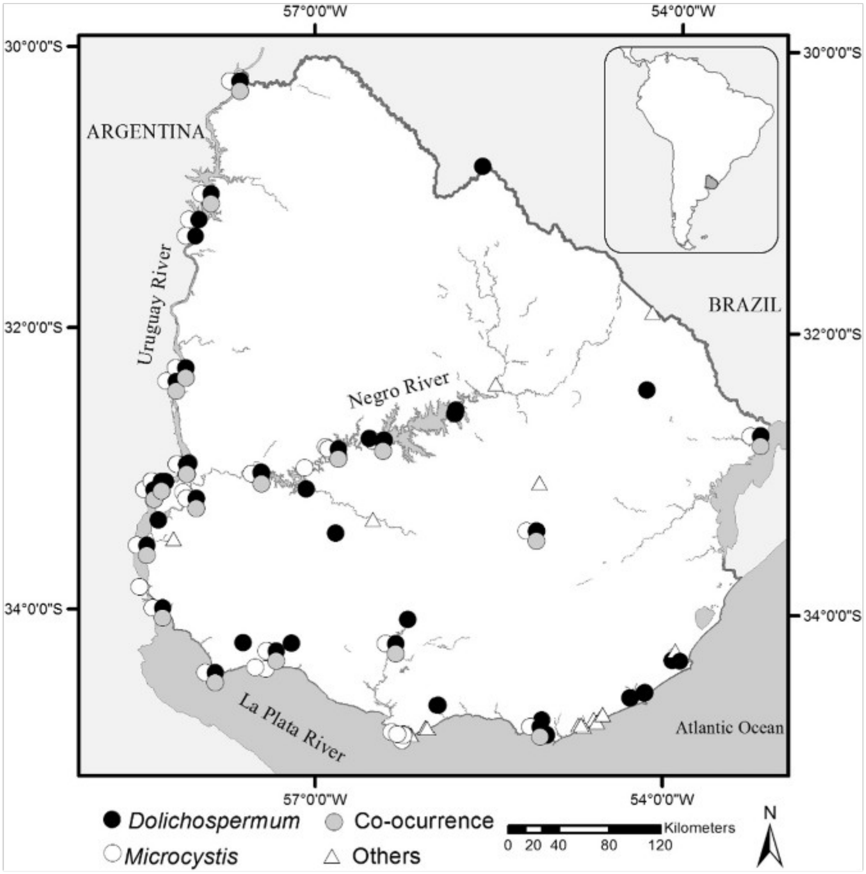

Fig. 2. Distribution of *Dolichospermum* (black circles), *Microcystis* (white circles) and co-occurrence of both (grey circles) across Uruguay. "Others" (white triangles) represent other cyanobacterial genera, shown only when none of the two most frequent genera has been recorded.

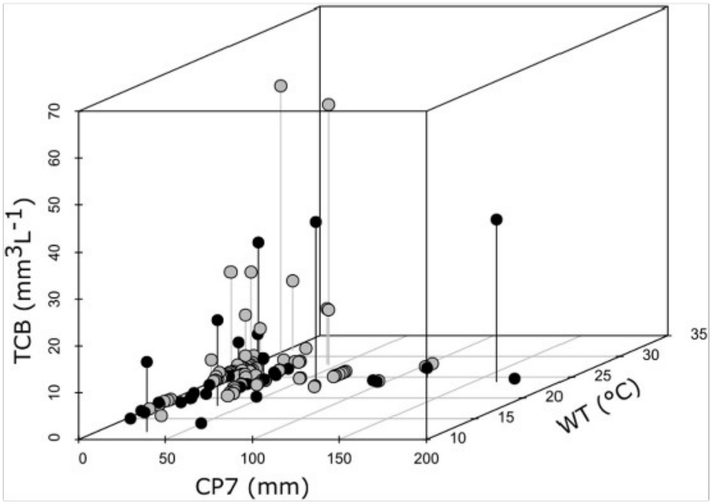

Fig. 3. Total cyanobacterial biovolume (TCB, from >0.001 to <100 mm^3 L^{-1}) in lentic (black) and lotic (grey) eutrophic ecosystems ($n = 140$) against 7-day cumulative precipitation (CP7) (mm) and surface water temperature (WT, °C).

related to CP7 in lentic ecosystems, while *Dolichospermum* was it in lotic ecosystems (although explained variance was low) (Table 1, Fig. 4D). A very high biovolume event occurred (58 mm^3 L^{-1}, Uruguay River, Bella Unión, February 2008) at low CP7 (<16 mm) (Fig. 3), in agreement with the tendency revealed by the model.

4. Discussion

We took advantage of a comprehensive database for subtropical eastern South American freshwaters, compiled over several years, to clarify the distribution of main bloom-forming cyanobacteria in lotic and lentic subtropical ecosystems and to investigate the role of water temperature and precipitation as significant predictors in eutrophic ecosystems. Our data provide evidence that these two factors influence most frequent genera of bloom-forming cyanobacteria and total cyanobacteria biovolume in nutrient-rich lotic freshwaters, as well as in lentic ecosystems.

4.1. Temperature and precipitation as predictive variables in eutrophic freshwaters

Despite the differences between the stagnant and running water environments, total cyanobacteria biovolume was similar between the studied eutrophic lotic and lentic ecosystems, indicating that bulk cyanoHABs primarily responded to the trophic status (eutrophic) of the ecosystems. Contrary to our hypothesis, we found no interaction between temperature and ecosystem type in explaining TCB. This implies that despite the divergence in the general hydrological characteristics of lentic and lotic ecosystems, temperature had a similar effect on bulk cyanobacteria biovolume. On the other hand, the variance explained by the temperature was low (10% of TCB), probably because cyanobacteria are a heterogeneous group of organisms and the analysis at TCB level masks ecophysiological differences at lower taxonomic levels, giving information of a diverse group of organisms. The higher proportion of *Dolichospermum* in lotic ecosystems implies that while temperature is important, the cyanobacterial genera are determined at least in part by the ecosystem type, in agreement with our hypothesis. *Microcystis* biovolume high correlation with temperature in our lentic ecosystems, is in line with observations elsewhere (Almanza et al., 2016; Deng et al., 2014; Mowe et al., 2015), likely due to the influence of annual temperature cycles on *Microcystis* growth (Davis et al., 2009; Deng et al., 2014). By contrast, *Dolichospermum* biovolume were not significantly related to temperature in lentic ecosystems, suggesting that this genus is less influenced by changes in water temperature than *Microcystis*, which is consistent with a general trend found in North American lakes (Rigosi et al., 2014). However, in lotic ecosystems both genera showed a positive relationship with temperature, increasing their biovolume toward higher temperatures. This reveal that also eutrophic lotic ecosystems are vulnerable to blooms by the main CyanoHAB genera in the subtropics, when temperature increases.

In lentic ecosystems, no correlation was found for *Dolichospermum* biovolume and TCB with precipitation. At the same time only a single dense bloom was observed in lakes after heavy rain (Fig. 3). These results indicate that cyanobacteria as a group are not influenced by rainfall effects, at least after short periods of time (7 days). Neither a positive effect on bloom formation caused by rainfall (by nutrients input) nor wash-out effect caused by rainfall was detected. However, *Microcystis* did decrease in biovolume due to precipitation increase, highlighting it as more sensitive to wash-out effect than the filamentous cyanobacteria. *Microcystis* usually bloom in eutrophic stagnant freshwaters exposed to high solar irradiance and stratification (Hunter et al., 2008; Reynolds, 2006), accumulating on the surface (Bonilla and Pick, 2017) and are therefore sensitive to mixing or wash-out effects. For example, rainfall regime explained the *Microcystis* high biovolume under water column stability in dry periods (low rainfall) in a Brazilian reservoir (de Castro Medeiros et al., 2015).

We also found that rivers were more sensitive than lentic ecosystems to rainfall, observed in the inverse pattern between total cyanobacteria biovolume and accumulated rainfall. This is in agreement with what could be expected, as blooms in rivers usually occur during low discharge periods following low rainfall and droughts (Davis and Koop, 2006; Ha et al., 1999; Maier et al., 2001; Marshall and Burchardt, 1998). For instance, this is the case of the large (1000 km) subtropical bloom of *Dolichospermum* reported in the Darling River, Australia (Davis and Koop, 2006) and probably also the dense bloom of the same genus in the Uruguay river (February 2008) from our study, as it occurred during a severe drought (Ferrari et al., 2011; Scarpati et al., 2014). These results are important because little data about river flow is available for the studied region, and it is a difficult variable to measure in simple monitoring programs. Using more widely

Table 1
Significant models for biovolume ($mm^3 L^{-1}$) of total cyanobacteria in eutrophic ecosystems (Models 1–2), *Microcystis* (Mic) (Models 3–5) and for *Dolichospermum* (Dol) (Model 6–7). Predictors include water temperature (WT), 7-day cumulative precipitation (CP7) and Type of ecosystem (2 levels; Lentic, LE or Lotic, LO). "*" = significant parameter ($p < 0.05$).

Model	Type	Predictor	Generalized linear model	Deviation (%)	df	AIC
1	All	WT, Type	$\mathrm{Ln\ BV} = -8.1^{*} + 0.3^{*}\mathrm{WT} - 1.2^{*}\mathrm{TypeLO}$	10	139	673
2	Lotic	WT, CP7	$\mathrm{Ln\ BV} = -11.56^{*} + 0.39^{*}\mathrm{WT} - 0.03^{*}\mathrm{CP7}$	27	101	456
Main genera						
3	Lentic	CP7	$\mathrm{Ln\ BV\ Mic} = -0.58 - 0.04^{*}\mathrm{CP7}$	34	19	101
4	Lentic	WT	$\mathrm{Ln\ BV\ Mic} = -36.7^{*} + 1.4^{*}\mathrm{WT}$	64	10	51
5	Lotic	WT	$\mathrm{Ln\ BV\ Mic} = -17.1^{*} + 0.5^{*}\mathrm{WT}$	28	54	259
6	Lotic	WT	$\mathrm{Ln\ BV\ Dol} = -12.3^{*} + 0.4^{*}\mathrm{WT}$	19	78	356
7	Lotic	CP7	$\mathrm{Ln\ BV\ Dol} = -2.02^{*} + -0.02^{*}\mathrm{CP7}$	7	78	367

available meteorological data, the application of cumulative precipitation can provide indirect but valuable information about hydrological conditions that may favor CyanoHABs and thus aid in the monitoring and prediction of blooms.

4.2. Distribution of cyanobacteria taxa in subtropical freshwaters

Among the most frequent taxa of our analysis, *Microcystis* is probably the widest distributed and truly cosmopolitan cyanobacteria genus in the world (Cook et al., 2004; Hodoki et al., 2012; Izydorczyk et al., 2008; Willame et al., 2005). However, *Dolichospermum* distribution seems to have a latitudinal pattern resulting in lower biovolume in warm climates (Ndlela et al., 2016; Willame et al., 2005). Also in South America, a similar pattern has been observed. In Argentina blooms occur from latitudes 25° S to 54° S, with Nostocales, such as *Dolichospermum*, showing a wider distribution than *Microcystis* in colder regions of the country (Aguilera et al., 2017), and in Brazil toxic *Dolichospermum* blooms were restricted to colder, subtropical lakes while *Microcystis* blooms occurred throughout the country (Sant'Anna et al., 2008). Our data fall in a geographical region between temperate and tropical latitudes, thus looking at this global pattern reviewed, we could expect either of the two genera to be the most prevalent genus. We conducted our analysis in both lotic and lentic ecosystems and found *Dolichospermum* to be the most frequent genera. Most of the increasing numbers of publications about cyanobacterial biogeography (e.g. Sukenik et al., 2012) are from lentic ecosystems, further studies at the species or genera level comparing running and stagnant water bodies are needed to refine our knowledge of cyanobacterial biogeography.

4.3. Climate change and cyanobacteria in subtropical freshwaters

For this region, increases in temperature and precipitation (annual and seasonal means), but also in extreme climate events (droughts and extreme rainfalls) are expected (IPCC, 2007). Heavy rainfall increases (Barros et al., 2015) and higher frequency and severity of droughts will affect hydrological and thermal freshwater regimes, particularly those of lotic environments (Barros et al., 2015; Penalba and Rivera, 2013; Van Vliet et al., 2013). Although more evidence is needed to confirm expansion of *Dolichospermum*, our results support the hypothesis of its growing global distribution, augmented to be due to climate change (Li et al., 2016). For instance, the dense *Dolichospermum*

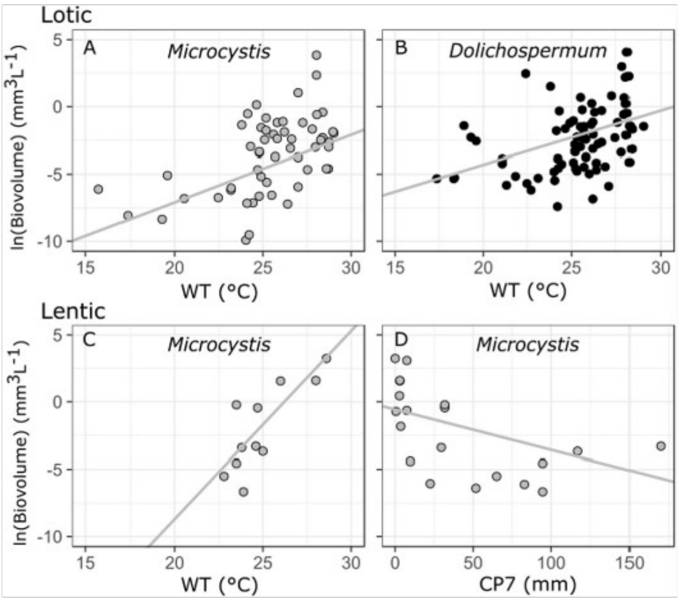

Fig. 4. Cyanobacterial biovolume in relation to surface water temperature (WT) (A–C) and 7-day cumulative precipitation (7CP) (D) in eutrophic ecosystems, significant models with deviation higher than 15% shown. Lotic ecosystems above: *Microcystis* (A) and *Dolichospermum* (B). Lentic ecosystems below: *Microcystis* (C y D). Lines are the fitted generalized linear model (Models 3–6, Table 1).

bloom in the Uruguay river (February 2008) occurred during a severe drought (Ferrari et al., 2011; Scarpati et al., 2014). Other Nostocales, like *Cylindrospermopsis*, are also expanding their distribution as competitive genera among bloom forming cyanobacteria in freshwaters (Bonilla et al., 2016, 2012; Mehnert et al., 2010), which will be also trigged by global warming effects in the future (Sukenik et al., 2012). *Cylindrospermopsis*, which we found in lentic artificial lakes, is one of the most frequent cyanobacteria in southern South America (Dörr et al., 2010; Sant'Anna et al., 2008; Soares et al., 2010; Vidal and Kruk, 2008). Overall, we could therefore hypothesize an increase in Nostocales biomass for lentic and lotic ecosystems of the studied region in the context of climate change.

5. Final remarks

To our knowledge this is the first study that shows the relevance of temperature and precipitation on the distribution of cyanobacteria comparing lentic and lotic freshwaters in a subtropical region. The filamentous *Dolichospermum* (Nostocales) was the most distributed and the most frequent genus in the studied region. Our study showed the relevance of water temperature and cumulative precipitation in predicting biovolume of main cyanobacteria taxa in nutrient rich lentic but also lotic ecosystems. These findings have implications for environmental management, as different human activities can affect both water temperature and discharge in lotic ecosystems, favoring cyanobacterial growth. Since lotic ecosystems are a major water landscape in South America, our findings pointed out the need of more studies on lotic ecosystems in the continent to evaluate the distribution and the impact of CyanoHABs. Further, our results highlight the value of studying cyanobacteria responses to environmental factors at low taxonomic level to improve our understanding of these organisms and their environment and facilitate management decisions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2017.07.067.

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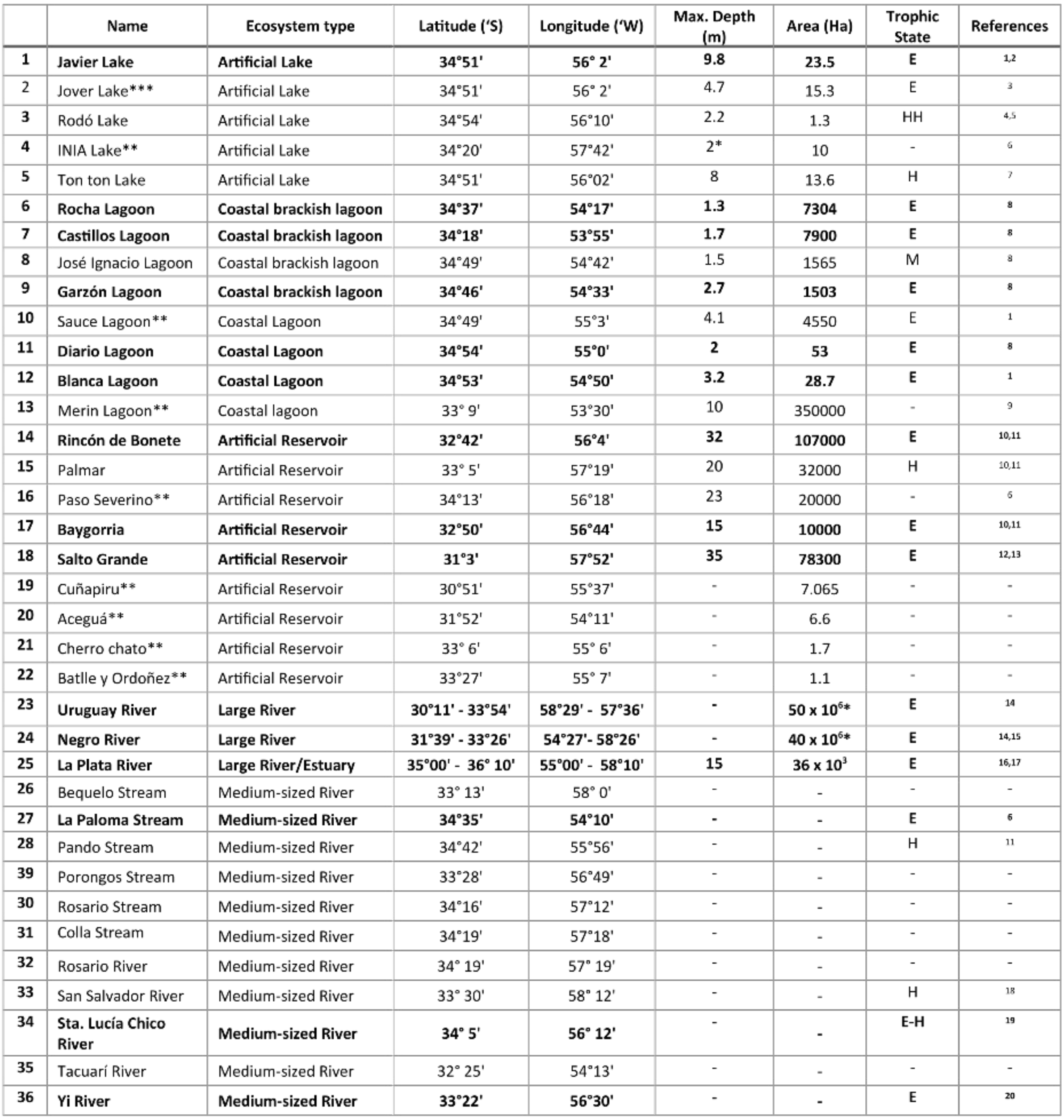
Appendix A

Table A.1: List of the studied freshwater ecosystems. Latitude and longitude, maximum depth (*: mean depth), area and trophic state based on total phosphorus (H: hypereutrophic, E: eutrophic, M: mesotrophic) are shown. Ecosystems marked in **bold** are the ones included in statistic (Classifies as eutrophic and water temperature data available).



	Name	Ecosystem type	Latitude (‘S)	Longitude (‘W)	Max. Depth (m)	Area (Ha)	Trophic State	References
1	**Javier Lake**	**Artificial Lake**	**34°51'**	**56° 2'**	**9.8**	**23.5**	**E**	**1,2**
2	Jover Lake***	Artificial Lake	34°51'	56° 2'	4.7	15.3	E	3
3	Rodó Lake	Artificial Lake	34°54'	56°10'	2.2	1.3	HH	4,5
4	INIA Lake**	Artificial Lake	34°20'	57°42'	2*	10	-	6
5	Ton ton Lake	Artificial Lake	34°51'	56°02'	8	13.6	H	7
6	**Rocha Lagoon**	**Coastal brackish lagoon**	**34°37'**	**54°17'**	**1.3**	**7304**	**E**	**8**
7	**Castillos Lagoon**	**Coastal brackish lagoon**	**34°18'**	**53°55'**	**1.7**	**7900**	**E**	**8**
8	José Ignacio Lagoon	Coastal brackish lagoon	34°49'	54°42'	1.5	1565	M	8
9	**Garzón Lagoon**	**Coastal brackish lagoon**	**34°46'**	**54°33'**	**2.7**	**1503**	**E**	**8**
10	Sauce Lagoon**	Coastal Lagoon	34°49'	55°3'	4.1	4550	E	1
11	**Diario Lagoon**	**Coastal Lagoon**	**34°54'**	**55°0'**	**2**	**53**	**E**	**8**
12	**Blanca Lagoon**	**Coastal Lagoon**	**34°53'**	**54°50'**	**3.2**	**28.7**	**E**	**1**
13	Merin Lagoon**	Coastal lagoon	33° 9'	53°30'	10	350000	-	9
14	**Rincón de Bonete**	**Artificial Reservoir**	**32°42'**	**56°4'**	**32**	**107000**	**E**	**10,11**
15	Palmar	Artificial Reservoir	33° 5'	57°19'	20	32000	H	10,11
16	Paso Severino**	Artificial Reservoir	34°13'	56°18'	23	20000	-	6
17	**Baygorria**	**Artificial Reservoir**	**32°50'**	**56°44'**	**15**	**10000**	**E**	**10,11**
18	**Salto Grande**	**Artificial Reservoir**	**31°3'**	**57°52'**	**35**	**78300**	**E**	**12,13**
19	Cuñapiru**	Artificial Reservoir	30°51'	55°37'	-	7.065	-	-
20	Aceguá**	Artificial Reservoir	31°52'	54°11'	-	6.6	-	-
21	Cherro chato**	Artificial Reservoir	33° 6'	55° 6'	-	1.7	-	-
22	Batlle y Ordoñez**	Artificial Reservoir	33°27'	55° 7'	-	1.1	-	-
23	**Uruguay River**	**Large River**	**30°11' - 33°54'**	**58°29' - 57°36'**	**-**	**50×10^6***	**E**	**14**
24	**Negro River**	**Large River**	**31°39' - 33°26'**	**54°27'- 58°26'**	**-**	**40×10^6***	**E**	**14,15**
25	**La Plata River**	**Large River/Estuary**	**35°00' - 36° 10'**	**55°00' - 58°10'**	**15**	**36×10^3**	**E**	**16,17**
26	Bequelo Stream	Medium-sized River	33° 13'	58° 0'	-	-	-	-
27	**La Paloma Stream**	**Medium-sized River**	**34°35'**	**54°10'**	**-**	**-**	**E**	**6**
28	Pando Stream	Medium-sized River	34°42'	55°56'	-	-	H	11
39	Porongos Stream	Medium-sized River	33°28'	56°49'	-	-	-	-
30	Rosario Stream	Medium-sized River	34°16'	57°12'	-	-	-	-
31	Colla Stream	Medium-sized River	34°19'	57°18'	-	-	-	-
32	Rosario River	Medium-sized River	34° 19'	57° 19'	-	-	-	-
33	San Salvador River	Medium-sized River	33° 30'	58° 12'	-	-	H	18
34	**Sta. Lucía Chico River**	**Medium-sized River**	**34° 5'**	**56° 12'**	**-**	**-**	**E-H**	**19**
35	Tacuarí River	Medium-sized River	32° 25'	54°13'	-	-	-	-
36	**Yi River**	**Medium-sized River**	**33°22'**	**56°30'**	**-**	**-**	**E**	**20**

* Area of draining basins. **No water temperature data ***Not included in statistics as only “scum data” available (BV > 100 mm^{3}L^{-1})

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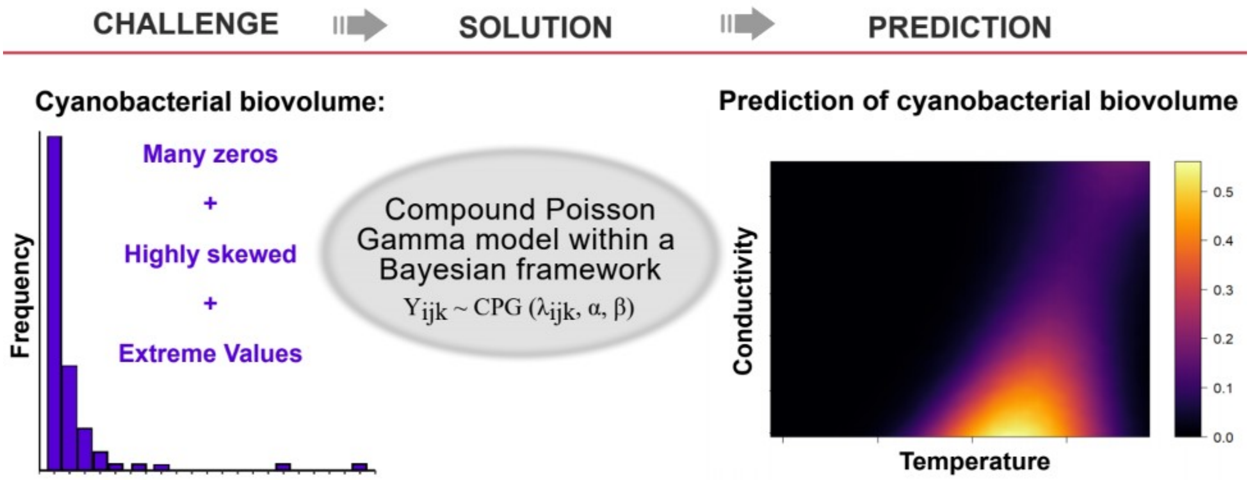
IV: Predicting cyanobacterial biovolume from water temperature and conductivity using a Bayesian compound Poisson-Gamma model

Hasta ahora hemos visto como la eutrofización es una gran problemática a nivel del país y como las floraciones de cianobacterias ocurren en todo el territorio y en todos los tipos de ecosistemas. En este último capítulo seguimos avanzando en evaluar los efectos de las variables climáticas en ecosistemas eutróficos pero buscando además avanzar en la capacidad de modelación y de predicción de estos organismos. Se seleccionó el Rio de la Plata, como sitio de estudio para el desarrollo del modelo, dado su gran importancia económica y social para la región. Este sistema presenta síntomas de eutrofización hace décadas y las floraciones de cianobacterias en el mismo son cada vez más recurrentes. Se desarrolló un nuevo modelo Bayesiano para determinar el efecto de las variables (temperatura del agua y conductividad; proxy de la salinidad) sobre la ocurrencia de cianobacterias y predecir su biomasa (biovolumen).



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Predicting cyanobacterial biovolume from water temperature and conductivity using a Bayesian compound Poisson-Gamma model

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A B S T R A C T

Eutrophication and climate change scenarios engender the need to develop good predictive models for harmful cyanobacterial blooms (CyanoHABs). Nevertheless, modeling cyanobacterial biomass is a challenging task due to strongly skewed distributions that include many absences as well as extreme values (dense blooms). Most modeling approaches alter the natural distribution of the data by splitting them into zeros (absences) and positive values, assuming that different processes underlie these two components. Our objectives were (1) to develop a probabilistic model relating cyanobacterial biovolume to environmental variables in the Río de la Plata Estuary (35°S, 56°W, n = 205 observations) considering all biovolume values (zeros and positive biomass) as part of the same process; and (2) to use the model to predict cyanobacterial biovolume under different risk level scenarios using water temperature and conductivity as explanatory variables. We developed a compound Poisson-Gamma (CPG) regression model, an approach that has not previously been used for modeling phytoplankton biovolume, within a Bayesian hierarchical framework. Posterior predictive checks showed that the fitted model had a good overall fit to the observed cyanobacterial biovolume and to more specific features of the data, such as the proportion of samples crossing three threshold risk levels (0.2, 1 and 2 $\mathrm{mm}^3\ \mathrm{L}^{-1}$) at different water temperatures and conductivities. The CPG model highlights the strong control of cyanobacterial biovolume by nonlinear and interactive effects of water temperature and conductivity. The highest probability of crossing the three biovolume levels occurred at 22.2 °C and at the lowest observed conductivity (~0.1 mS cm^{-1}). Cross-validation of the fitted model using out-of-sample observations (n = 72) showed the model's potential to be used *in situ*, as it enabled prediction of cyanobacterial biomass based on two readily measured variables (temperature and conductivity), making it an interesting tool for early alert systems and management strategies. Furthermore, this novel application demonstrates the potential of the Bayesian CPG approach for predicting cyanobacterial dynamics in response to environmental change.

1. Introduction

Harmful cyanobacterial blooms (CyanoHABs) have been registered with increasing frequency in many aquatic habitats worldwide during recent decades (Carey et al., 2012; Huisman et al., 2018). Eutrophication and climate change are the major factors underlying the escalation of the extent and duration of CyanoHABs (Bonilla and Pick, 2017; O'Neil et al., 2012). The toxins that may be contained in these blooms threaten supplies of drinking water, endanger human activities and have negative effects on fish populations that can imperil fisheries (Dodds et al., 2009; Steffensen, 2008). Consequently, the prediction of cyanobacterial occurrence and biomass has become critical both to developing strategies preventing CyanoHAB formation and to reducing the impact of blooms already underway (Glibert et al., 2010). However, modeling cyanobacteria is a challenging task due to the dynamic nature of their biomass, which changes rapidly in space and time (Oliver

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et al., 2012).

The dominance of cyanobacteria in the phytoplankton of freshwater and brackish ecosystems is related to climate, hydrology and eutrophication. Favorable conditions that may trigger blooms include high water temperature (Beaulieu et al., 2013; Elliott, 2010; Haakonsson et al., 2017; Paerl and Huisman, 2008), low salinity (Engström-Öst et al., 2011), high nutrient concentrations (Downing et al., 2001; Gobler et al., 2016; Smith, 1986; Smith and Schindler, 2009), high light penetration (Davis and Koop, 2006) and water column stability (Carey et al., 2012; Wagner and Adrian, 2009). However, the variables that best explain occurrence are not always those that best predict it (Shmueli, 2010). In eutrophic ecosystems, nutrients (phosphorus, P, and nitrogen, N) are major determinants of CyanoHABs (Lancelot and Muylaert, 2011; Lehman et al., 2010), but other variables, such as water temperature, salinity and hydrological features, can be more effective as predictors of bloom dynamics (Olli et al., 2015; Robson and Hamilton, 2004; Taş et al., 2006). Measuring nutrient concentrations is time-consuming, which limits their utility as predictors for early warning systems. Ideally, such systems would include environmental features that can be measured rapidly.

Prediction of planktonic cyanobacterial biomass and abundance has traditionally relied on a variety of quantitative methods, such as linear and nonlinear regression (Downing et al., 2001; Kosten et al., 2012; Persaud et al., 2015), additive models (Beaulieu et al., 2013; Taranu et al., 2012), regression trees (Ghaffar and Stevenson, 2016), simulation models (Elliott, 2010) and artificial neural networks (Ahn et al., 2011; Yang et al., 2016). More recent approaches include fully probabilistic models such as Bayesian networks (Johnson et al., 2010; Rigosi et al., 2015) and Bayesian regression analysis (Cha et al., 2014; Hamilton et al., 2009; Obenour et al., 2014). Bayesian approaches have high predictive power and allow for realistic quantification of uncertainty and separation of measurement and process errors (Franks, 2018; Hamilton et al., 2009), which are key features for prediction. A Bayesian probabilistic approach is useful for risk management applications such as, for example, predicting cyanobacterial biovolume exceedance of different risk exposure levels (Cha et al., 2014).

Cell abundance is the most used response variable in predictive CyanoHAB models (e.g., Cha et al., 2017; Ghaffar and Stevenson, 2016) whereas biovolume, a more accurate indicator of biomass, has been less frequently used (Dolman et al., 2012; Kosten et al., 2012). The reasons behind this trend likely include the lesser availability of biovolume data (as a result of the great effort involved in measuring the volume of each taxon). Additionally, biovolume is a continuous variable with a skewed distribution that includes many zeros as well as extreme values, all of which pose challenges for modeling. Species data often contain a large proportion of zeros (Fletcher et al., 2005). To deal with this problem there are two common approaches: adding a small arbitrary value to eliminate the zeros (e.g.: $x + 0.1$), or using two-part "hurdle" models (one for the zeros, the other for the positive values); the latter approach requires an artificial split in the distribution of the data. Hurdle models have been used to predict microcystin concentrations in lakes and reservoirs (Taranu et al., 2017). An alternative approach, based on the compound Poisson-Gamma (CPG) distribution, allows for joint modeling of zeros and strictly positive values of a continuous variable, and for extreme values, such as those arising from blooms (Lecomte et al., 2013a; Pennington, 1996). The CPG distribution has been used by ecologists to model biomass of fishery catches (Foster and Bravington, 2013; Lecomte et al., 2013a) and benthic macroinvertebrates (Lecomte et al., 2013b). Despite its suitability for dealing with ecological data, to our knowledge, the CPG approach has not yet been used to model phytoplankton biovolume.

The selection of a suitable indicator is critical to a successful risk prediction. Most regulatory and advisory guidelines for drinking and recreational waters define levels or risk exposure to cyanobacteria based on some kind of concentration indicator (Chorus and Bartram, 1999). The most commonly used indicators are chlorophyll *a* concentration and cyanobacterial cell abundance or biovolume (Chorus and Bartram, 1999). Among these three variables, biovolume is the most accurate for estimating population biomass, since cell size can vary more than one order of magnitude within species and more than two between species (Chorus and Cavalieri, 2000), and toxin concentration is better correlated with biomass than with cell counts (Ibelings et al., 2015). For example, the World Health Organization proposed two biovolume alert levels for drinking water (0.2 and 10 $mm^3\ L^{-1}$) (Chorus and Bartram, 1999), while many countries have implemented two or three guide levels (varying from <0.5 to >15 $mm^3\ L^{-1}$) for recreational waters, with associated consequent actions (Ibelings et al., 2015).

The Río de la Plata Estuary, one of the largest in the world (35000 km^2), is located in the subtropical region of southern South America (Fig. 1). The estuary provides multiple ecosystem services such as transportation, fisheries and tourism, and is the main drinking water supply for Buenos Aires (20 million inhabitants) (Giannuzzi et al., 2012; Nagy et al., 2002). The estuary has shown symptoms of eutrophication for decades (Nagy et al., 2002) and blooms of toxic cyanobacteria have been reported since 1999 (De León and Yunes, 2001). The blooms occur with high frequency especially in summer along both the south (Aguilera et al., 2017; Giannuzzi et al., 2009; Gómez, 2014; Sathicq et al., 2014) and the north shores (Bonilla et al., 2015; Brena et al., 2006; De León and Yunes, 2001; Kruk et al., 2015), including recently (2019) observed massive blooms (Kruk et al., 2019). Changes in physical variables such as temperature and salinity appear to be directly related to these blooms, and thus the development of predictive models based on these variables should lead to improved water monitoring programs. Our objectives were to develop a compound Poisson-Gamma regression model relating cyanobacterial biovolume to readily measured environmental variables, and to use the model within a full Bayesian framework to predict the probabilities of reaching three biovolume thresholds: 0.2 $mm^3\ L^{-1}$, 1 $mm^3\ L^{-1}$, and 2 $mm^3\ L^{-1}$. Because there is no current regulatory framework for recreational waters in Uruguay, we selected these thresholds based on globally accepted risk exposure levels (Chorus and Bartram, 1999; Ibelings et al., 2015) and observed cyanobacterial dynamics in the study region (Bonilla et al., 2015; Haakonsson et al., 2017). We examined cyanobacterial abundances over a five-year period at three sampling points ($n = 277$ observations) located on the shore and 500 m offshore in the Río del Plata Estuary.

2. Material and methods

2.1. Data acquisition

Phytoplankton and environmental variables were sampled at Punta del Tigre in the Río de la Plata Estuary, Uruguay (35°45′56.0″S, 56°33′27.7″W), on a bimonthly (spring and summer) and trimonthly (autumn and winter) basis, between October 2014 and July 2019 (2014–2018, $n = 205$ observations used to calibrate the model; 2018–2019, $n = 72$ observations used for cross-validation). The study area is shallow (<4 m depth), oligohaline and meso-eutrophic (total phosphorus: 118 $\mu g\ L^{-1}$ and 81–144 $\mu g\ L^{-1}$; chlorophyll *a*: 5 $\mu g\ L^{-1}$ and 2–10 $\mu g\ L^{-1}$, medians and 25%–75% quartiles, respectively, $n = 24$; Rafael Arocena, unpublished data). Samples were collected from three sites, one at the shore (sand beach, mean depth = 0.4 m, site 1) and two located

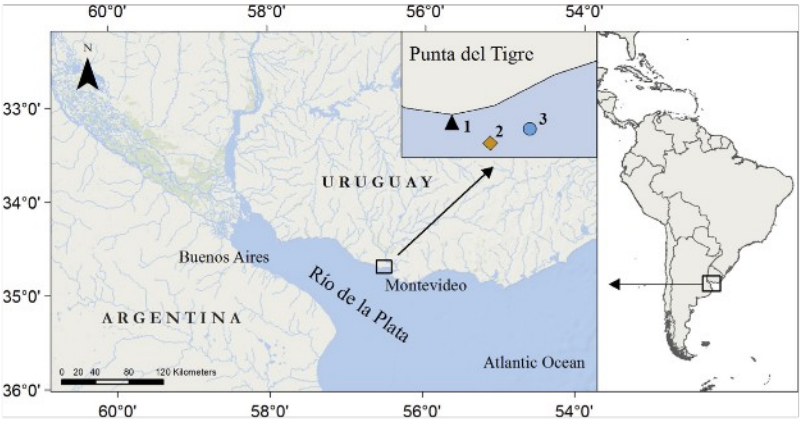

Fig. 1. Location of the three sampling sites (1–3) at Punta del Tigre on the north coast of the Río de la Plata Estuary, Uruguay.

500 m offshore (mean depth − 3.5 m and 3.8 m, sites 2 and 3, respectively) (Fig. 1). Depth, water temperature, conductivity (a proxy for salinity), dissolved oxygen, pH and light penetration were measured at each sampling site.

Phytoplankton samples were taken (in triplicate at most sites and dates; mean number of replicates = 2.71) from the subsurface at each site in 0.5 L bottles and fixed in Lugol's solution. Algae and cyanobacteria taxa were identified to the lowest possible taxonomical level and counted (cells mL^{-1}) in sedimentation chambers using an inverted microscope (Olympus CKX41) and a standard quantification method (Sournia, 1978; Utermöhl, 1958). Taxa volumes (μm^3) were calculated from geometric shape approximations (Hillebrand et al., 1999) using cell measurements (at least 10 cells per taxon, per sample) to obtain the biovolume of each taxon ($mm^3\ L^{-1}$).

2.2. Model development

The Compound Poisson-Gamma (CPG) variables are sums of random variables arising from a common Gamma distribution, in which the number of terms entering the sums has a Poisson distribution. In our application, the total cyanobacterial biovolume in a sample (Y) is viewed as a collection of M cyanobacterial aggregations (groups of organisms viewed as statistical "events", the number of which is sampled from a Poisson distribution), having biovolumes R which follow a Gamma distribution (Lecomte et al., 2013a). More formally, $Y = R_1 + R_2 + R_3 + \ldots + R_M$, where M has a Poisson distribution with mean λ, and the R are identically distributed random variables sampled from a Gamma distribution with shape α and rate β (Withers and Nadarajah, 2011). This implies that there may be samples with no cyanobacteria ($M = 0$). Regression models can be cast in this framework by modeling the Poisson mean as a function of covariates (Lecomte et al., 2013a; Smyth, 1996). In these models, the information in both the zero and positive observations can contribute to the estimation of all parts of the model (Smyth, 1996).

We developed a CPG regression model within a full Bayesian framework using cyanobacterial biovolume as the response variable. The model includes two environmental variables that strongly influence cyanobacterial biomass in coastal ecosystems: surface water temperature and conductivity, a proxy for salinity. Previous studies in coastal ecosystems worldwide (Olli et al., 2015; Robson and Hamilton, 2004; Taş et al., 2006) and in the Río de la Plata Estuary (Kruk et al., 2019; Martínez de la Escalera et al., 2017) have revealed the importance of these two variables for bloom prediction. Preliminary tests with models including pH, flow and depth as possible predictors indicated that these variables had no discernible effect on cyanobacterial biovolume prediction; these variables were thus omitted from further analyses.

Our model assumes that the biovolume observations Y arise from a CPG distribution characterized by three parameters: the Poisson mean (λ), and the Gamma shape (α) and rate (β):

$$Y_{ijk} \sim CPG(\lambda_{ijk}, \alpha, \beta),$$

where the indices correspond to replicate i ($i = 1, \ldots, N_{jk}$), at site j ($j = 1, 2, 3$) and time k ($k = 1, \ldots, 26$). The number of replicates N_{jk} is indexed by site and date because samples were not collected in triplicate at all sites and dates (see 2.1 *Data acquisition*).

The Poisson mean, λ_{ijk}, was modeled on the log scale as:

$$\log(\lambda_{ijk}) = \phi_0 + \phi_1 X_{1ijk} + \phi_2 X_{2ijk} + \ldots + \phi_p X_{pijk} + \eta_{ij} + \nu_{ik} + \varepsilon_{ijk}$$

where ϕ_0 is an intercept and $\phi_1, \ldots, \phi_p$ are slope parameters for p covariates $X_{1ijk}, \ldots, X_{pijk}$; η_{ij} are spatial random effects associated with differences among sites; ν_{ik} are temporal random effects associated with differences among dates; and ε_{ijk} are observation-level errors. Our model included four covariate terms that captured additive and multiplicative effects of the explanatory variables temperature and conductivity: linear and quadratic terms for water temperature, a linear term for conductivity, and a term for the interaction between temperature and conductivity. Inclusion of a quadratic term for temperature allows for dome-shaped relationships between biovolume and temperature, including a thermal optimum at intermediate temperatures, whereas the temperature-conductivity interaction allows the effect of either variable to be affected by the level of the other. Temperature and conductivity were standardized to zero mean and unit variance to facilitate comparisons of effects and improve computational stability.

We used the following diffuse prior distributions for the model parameters:

Regression coefficients:

$$\phi_i \sim \text{Normal}(0, 100)$$

Gamma shape and rate parameters:

$\alpha \sim \text{Gamma}(0.01, 0.01)$

$\beta \sim \text{Gamma}(0.01, 0.01)$

Random effects:

$\eta_{ij} \sim \text{Normal}(0, \sigma^2_{\eta})$

$\nu_{ik} \sim \text{Normal}(0, \sigma^2_{\nu})$

$\sigma^2_{\eta} \sim \text{Normal}_{+}(0, 10)$

$\sigma^2_{\nu} \sim \text{Normal}_{+}(0, 10)$

Observation error:

$\varepsilon_{ijk} \sim \text{Normal}\ (0, \sigma^2_{\varepsilon})$

$\sigma^2_{\varepsilon} \sim \text{Normal}_{+}(0, 10)$

We used prior-posterior comparisons to gauge the information gained from the data relative to the vague priors. We used posterior predictive checks, which compare the observed data to the posterior predictive distribution (Gelman et al., 1996, 2014), to assess both the overall goodness-of-fit of the model and its ability to predict specific aspects of the data which are of particular interest for management.

To conduct these tests, we devised three data-dependent test quantities, calculated as the proportion of samples that exceeded each of three selected cyanobacterial biovolume thresholds (0.2 $mm^3\ L^{-1}$, 1 $mm^3\ L^{-1}$, and 2 $mm^3\ L^{-1}$). The first threshold corresponds to the "Alert Level 1" for drinking waters and the last to the "Guidance Level 1" for recreational waters of the WHO alert level framework (Chorus and Bartram, 1999). The intermediate threshold value (1 $mm^3\ L^{-1}$), used in different countries for recreational waters (Ibelings et al., 2015), corresponds to a biomass typically found prior to visible accumulations (i.e., 2 $mm^3\ L^{-1}$ and beyond) and is therefore useful for developing early warning systems. The three test quantities calculated from the observed data were compared to those generated by simulations from the posterior predictive distribution. We calculated variance components for the random terms in the model to quantify the relative contribution of spatial and temporal variation to fluctuations in biovolume. The fitted model was also used to obtain the probability of exceeding each of the selected biovolume thresholds at different combinations of temperature and conductivity, taken as the proportion of MCMC samples from the posterior distribution of biovolume that had values greater than the threshold.

All analyses were carried out in the R environment (R Core Team, 2018) using the rjags interface (Plummer, 2014) to JAGS (Plummer, 2003), which uses a MCMC algorithm to sample from the posterior distribution of the parameters. An initial adaptive phase was run for 1,000 MCMC iterations to optimize sampler efficiency by tuning the proposal distribution. We ran 5 chains for 2,000,000 iterations, discarded the first half (burn-in), and retained 1 in 1,000 samples (thinning) of the second half to obtain a total of 5,000 MCMC samples. Posterior distributions of individual parameters were summarized as medians and 95% credible intervals. Convergence of the chains was assessed using visual inspection of trace plots and the univariate and multivariate Gelman–Rubin diagnostics (potential scale reduction factors, PSRF) in the CODA package (Plummer et al., 2006).

In addition to the posterior predictive checks, we cross-validated the fitted model against out-of-sample observations (2018–2019; $n = 72$) which were not used to fit the model. The model fitted to the first set of observations (2014–2018) was used to predict cyanobacterial biovolume from temperature and conductivity in the second set of observations (2018–2019). Predictions for new observations were obtained after setting all random effects to zero (these are conditional responses for observations in a hypothetical sampling group; Skrondal, 2009).

3. Results

3.1. Dynamics of cyanobacteria and main predictive variables

The three sampling sites were similar in their limnological characteristics during the study period (Table 1, Fig. 2). Temperature ranged from 9.5 to 29.2 °C, showing a clear seasonal trend, whereas conductivity ranged from 0.1 to 8.7 $mS\ cm^{-1}$ and showed no clear temporal trend (Fig. 2). Cyanobacterial biovolume ranged from 0 $mm^3\ L^{-1}$ (101 of 205 samples) to >60 $mm^3\ L^{-1}$ (Fig. 3). At low biovolume (<0.2 $mm^3\ L^{-1}$), the phytoplankton assemblage was mainly dominated by diatoms (such as *Aulacoseira granulata* and *Actinocyclus normanii*) followed by dinoflagellates, cryptophytes and chlorophytes. During the warm season, when the total biovolume was moderate to high (>1 $mm^3\ L^{-1}$), the assemblage was characterized by cyanobacteria (>60% of total phytoplankton biovolume). The most dominant species were the colonial *Microcystis aeruginosa* and *M. protocystis* and the filamentous *Dolichospermum uruguayensis* and *D. circinale*. A complete list of cyanobacterial taxa is presented in the Supplementary Material (Table S1).

3.2. Fit and parameter estimates of the CPG model

Neither the multivariate (1.07) nor the univariate Gelman-Rubin diagnostics (<1.04 for all parameters) indicated potential problems with convergence, i.e., chains seemed to mix adequately, as the Gelman-Rubin diagnostic was <1.1 (Gelman et al., 2014). The posterior predictive distribution of cyanobacterial biovolumes showed a good overall fit to the observed data (Fig. 4a, Fig. S1 Supplementary Material). Posterior predictive checks showed that model predictions were within a few percentage points of the observed values for the three alert level thresholds, although the model may be slightly underestimating the proportion of samples exceeding the lowest threshold (0.2 $mm^3\ L^{-1}$; Fig. 4b). Comparison of prior and posterior distributions (Fig. 5) showed that the data provided substantial information on the parameters of interest and that parameter estimates were not determined primarily by the prior distribution.

The parameter estimates associated with the covariates in our model, surface temperature (ϕ_1), surface temperature^2 (ϕ_2), conductivity (ϕ_3), and the interaction between surface temperature and conductivity (ϕ_4), showed a clear effect of all covariates on cyanobacterial biovolume (Fig. 5), and point to the presence of nonlinear responses to temperature and conductivity. The components of variance yielded by the model for biovolume indicated that temporal variation was substantially stronger than spatial variation (Supplementary Material, Table S2), matching the patterns observed earlier for the environmental predictors (Fig. 2).

The cross-validation showed that the model captured the main seasonal trends at the three study sites, although the wide credible intervals point to substantial variability in the predicted values (Fig. 6). With the exception of the mid-summer (Nov.–Dec.) samples, there appears to be no systematic over- or under-estimation of mean biovolume across sites. The coefficients of determination for observed and predicted values at the three sites were: $r^2 = 0.37$, for site 1, $r^2 = 0.34$ for site 2 and $r^2 = 0.92$ for site 3 ($n = 8$ observations

Table 1
Environmental characteristics (medians; 25%–75% quartiles) at the three sampling sites (sample sizes in parentheses).

Site	Depth (m)	pH	Dissolved oxygen (mg/L)	Turbidity (NTU)
1	0.4; 0.3–0.6 (26)	8.3; 8.0–8.5 (26)	9.2; 7.3–11.3 (26)	–
2	3.4; 3.2–3.7 (25)	7.9; 7.9–8.2 (25)	9.5; 8.7–10.2 (25)	27; 20.6–42 (25)
3	3.8; 3.6–4.1 (25)	7.9; 7.7–8.2 (25)	9.4; 8.5–9.7 (25)	25; 20.2–42 (25)

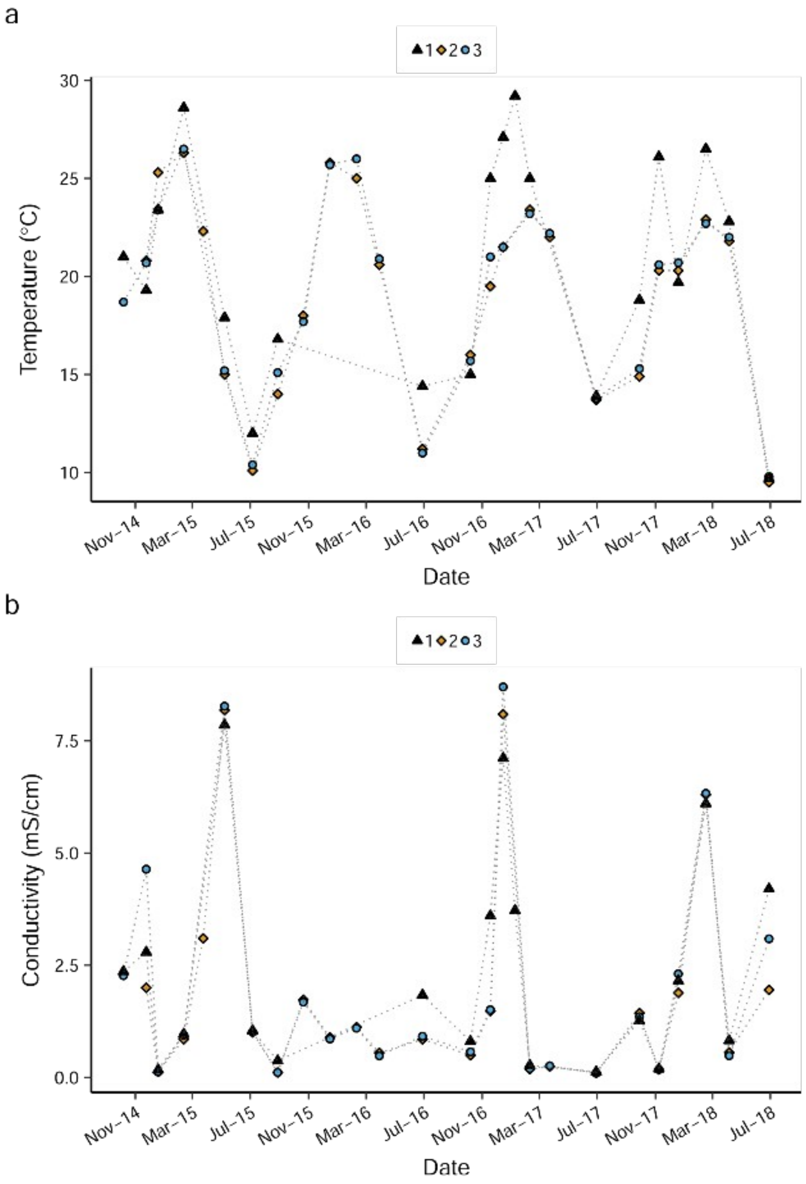

Fig. 2. Temporal and spatial variation in temperature (a) and conductivity (b) at the three sampling sites (site numbering as in Fig. 1).

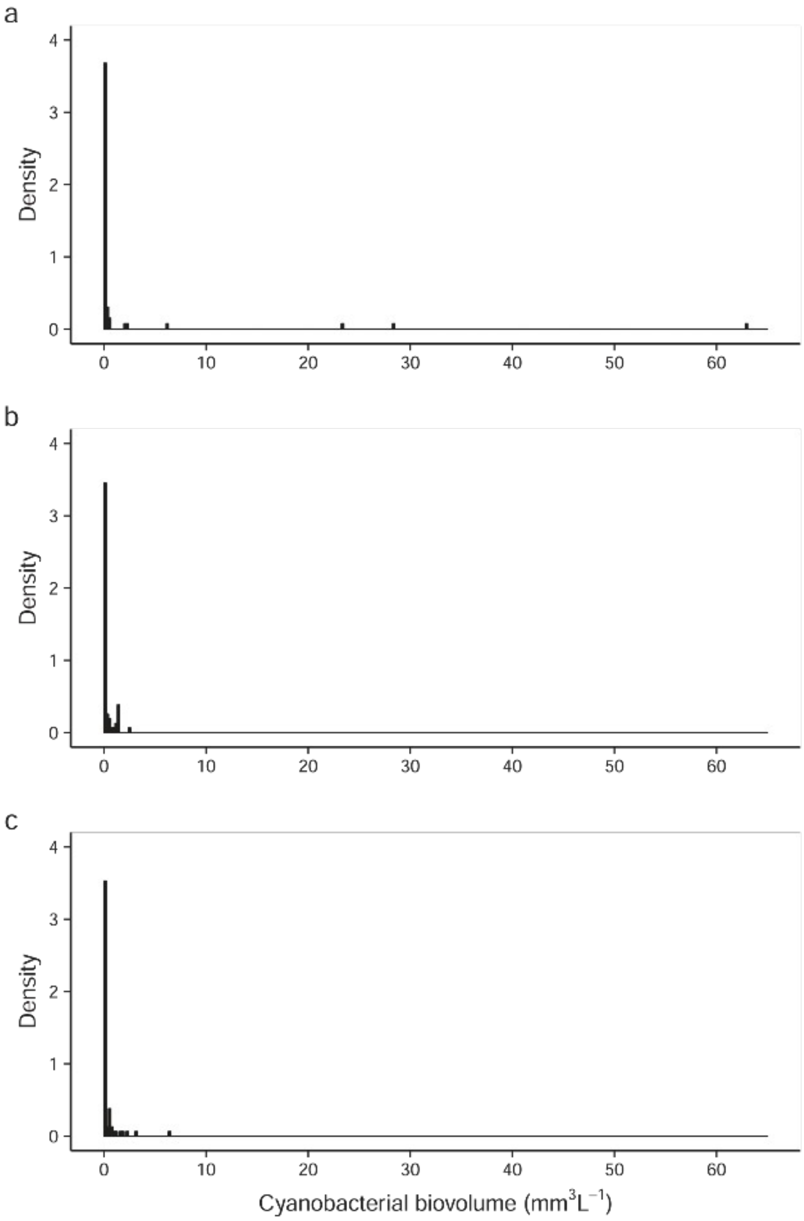

Fig. 3. Distribution of cyanobacterial biovolume at sampling sites 1 (a), 2 (b) and 3 (c) (site numbering as in Fig. 1).

at each site). For all sites combined (site means; n = 8 observations), it was $r^2 = 0.87$.

3.3. *Predicting cyanobacterial exceedance probabilities and biovolume*

The joint structuring effects of water temperature and conductivity on cyanobacteria were visualized by constructing contour plots of the probability of exceeding the three biovolume threshold levels (Fig. 7). As expected, the exceedance probability declined as threshold levels increased (Fig. 7). For the three tiers, the model predicted the highest probability at a temperature of 22.2 °C and at the lowest observed values for conductivity (~0.1 mS cm^{-1}) (Fig. 7). Overall, exceedance probabilities decreased

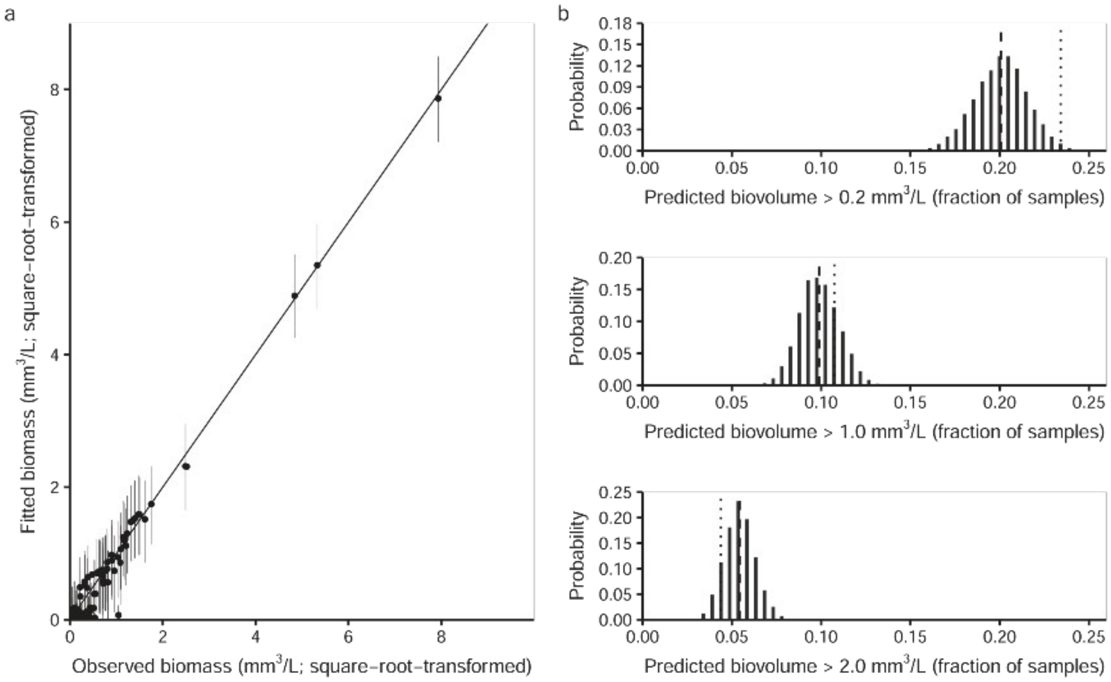

Fig. 4. (a) Observed versus fitted biomass (posterior distribution medians and 95% credible intervals), (b) Posterior predictive checks for the three risk thresholds (from top to bottom: > 0.2, >1.0 and >2.0 mm^3 L^{-1}), showing the distribution of the predicted proportion of samples exceeding each tier. Dashed vertical line: the mean of the predicted distribution, dotted vertical line: the observed proportion of samples exceeding the threshold.

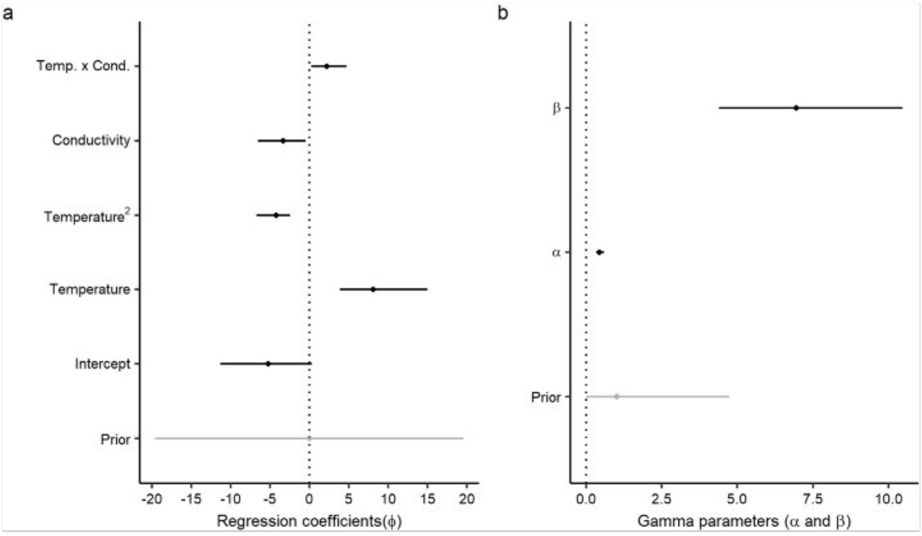

Fig. 5. CPG model parameters. Summary of the posterior distribution (medians and 95% credible intervals) of the regression coefficients (ϕ) and Gamma distribution shape and rate parameters (α and β).

with rising conductivity, and at the highest conductivity the temperature at which the maximum probability occurred was shifted upwards, to ~27 °C (Fig. 7). The nonlinearity in cyanobacterial responses to temperature and conductivity yielded a sharp increase

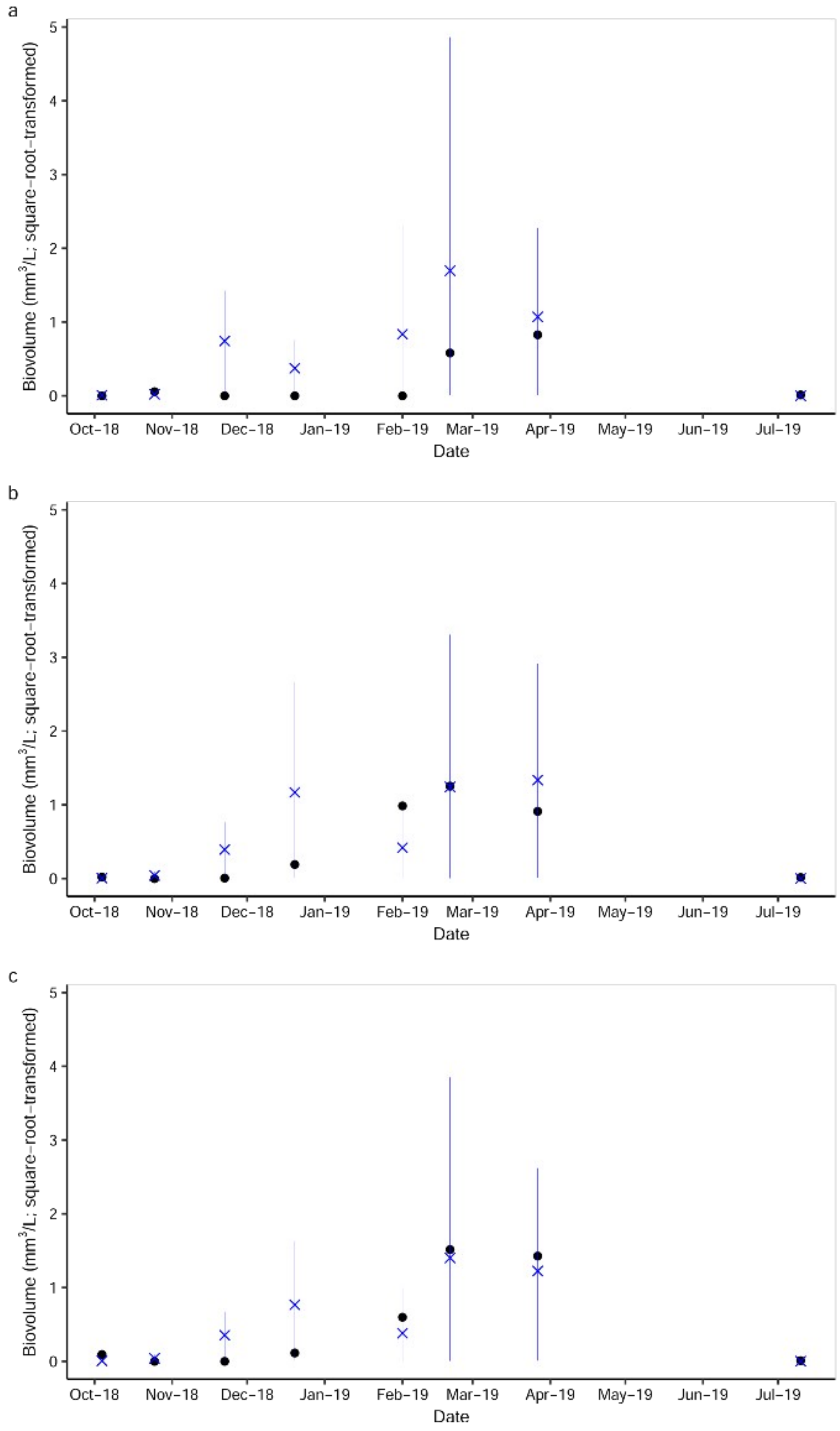

Fig. 6. Comparison of out-of-sample predicted values (mean and 95% credible interval; blue) and observed values (mean; black dots) for cyanobacterial biovolume at sampling sites 1 (a), 2 (b) and 3 (c) (site numbering as in Fig. 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

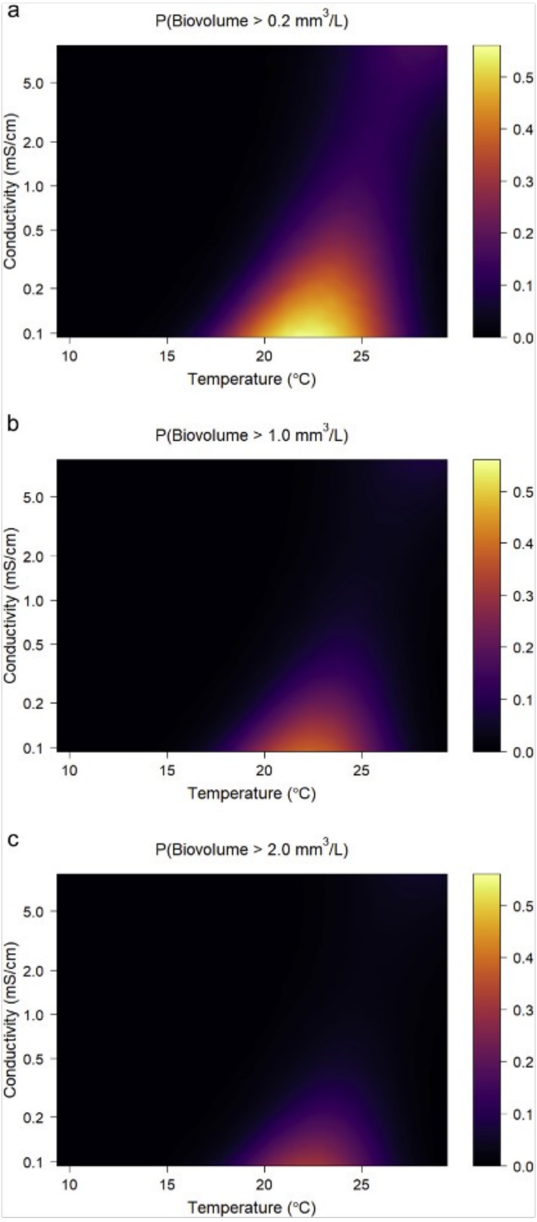

Fig. 7. Probability of exceeding three risk levels of exposure to cyanobacteria as a function of water temperature (°C) and conductivity (mS cm-1). (a) > 0.2 mm^3 L^{-1}; (b) > 1 mm^3 L^{-1}; (c) > 2 mm^3 L^{-1}.

in exceedance probabilities when conductivity falls below ~0.5 mS cm^{-1}. Temperature effects, such an increase from 20 to 25 °C, were most pronounced for the lowest threshold (Fig. 8). At 20 °C, cyanobacterial biovolume will most likely not reach any threshold when conductivity is greater than ~2 mS cm^{-1}, whereas at 25 °C even the highest tier has a substantial chance to be surpassed, even at high conductivity (Fig. 9).

4. Discussion

We presented a novel CPG approach to modeling cyanobacterial biovolume within a Bayesian probabilistic framework. This approach provides a full accounting of uncertainty in predictions, as it incorporates variation which originates from both sampling error and uncertainty in parameter values. Using two environmental variables, which are readily measured *in situ*, we were able to predict the probability of cyanobacterial biovolume exceeding three threshold values relevant to management. The risk of exposure expressed in probabilities can be a useful tool for early warning systems, particularly for coastal eutrophic environments that are susceptible to develop CyanoHABs.

CyanoHABs can occur within a very short period of time, shifting rapidly from undetected levels to peak biomass values (blooms). Our approach overcomes one of the problems inherent to statistical modeling of these organisms: the presence of a large proportion of zeros in data sets (Franks, 2018). For count data, such as cell abundance, hurdle models (e.g., Cha et al., 2014) assume that zeros occur from one process and the positive values from another, whereas zero-inflated models assume that "extra zeros" come from a second process (Cusack et al., 2015). However, for continuous data such as biovolume, this artificial categorization can impose an unwanted discontinuity in the data because in natural environments the same drivers often simultaneously influence absence (zeros) and presence (nonzero biomass) (Lecomte et al., 2013a). Contrary to most models for HABs, which use cell abundance as the response variable (e.g., Cha et al., 2014; Cusack et al., 2015), our approach is based on biovolume, which is the best indicator of phytoplankton biomass (Chorus and Cavalieri, 2000; Reynolds, 2006). Furthermore, the use of biovolume instead of other biological indicators can change model outputs and improve predictions of lake ecological status (Moe et al., 2016).

We found clear nonlinear, interactive effects of water temperature and conductivity on cyanobacterial biovolume. Growth of freshwater cyanobacteria is generally favored at higher temperatures, with well-defined thermal optima for growth at temperatures ranging between 20 and 30 °C (e.g., Fig. 5.3 in Reynolds, 2006), whereas high salinity tends to limit or inhibit cyanobacterial growth (Reynolds, 2006). The importance of these drivers for cyanobacterial blooms in estuaries has been well documented (temperature: Cha et al., 2014; Lehman et al., 2008; Robson and Hamilton, 2003; salinity: Hall et al., 2013; Robson and Hamilton, 2003; Taş et al., 2006). Models of cyanobacterial biomass have included interactions between environmental predictors (e.g., between temperature and nutrients in lentic water bodies; Taranu et al., 2012), but we found no previous examples of models including an interaction between temperature and conductivity. We suggest that inclusion of this interaction may lead to improvements in models for CyanoHABs in coastal environments.

Our model predicts that the probability of crossing the three threshold levels is greatest at 22.2 °C. Species from the genera *Microcystis* and *Dolichospermum* co-occur at our study site and frequently bloom together in the region (Aguilera et al., 2017; Haakonsson et al., 2017; O'Farrell et al., 2012) and elsewhere (Li et al., 2010; Te and Gin, 2011). In lentic ecosystems, mixed *Microcystis-Dolichospermum* blooms are commonly observed between 25 and 30 °C (Krienitz et al., 2002; O'Farrell et al., 2012; Te and Gin, 2011). However, in estuaries and coastal areas, such as the Baltic Sea and San Francisco Bay, cyanobacterial blooms are more frequent at temperatures nearer to 20 °C (Lehman et al., 2010; Pliński et al., 2007). A similar trend is found for coastal blooms in the Río de la Plata Estuary (5 out of 7 coastal blooms were

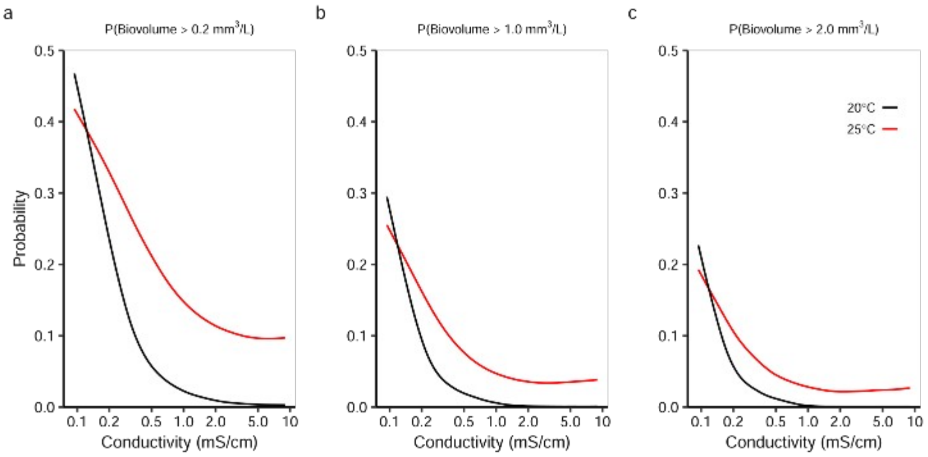

Fig. 8. Probability of exceeding three risk levels of exposure to cyanobacteria as a function of conductivity at two different temperatures: 20 °C (black curves) and 25 °C (red curves). (a) > 0.2 $mm^3 L^{-1}$; (b) > 1 $mm^3 L^{-1}$; (c) > 2 $mm^3 L^{-1}$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

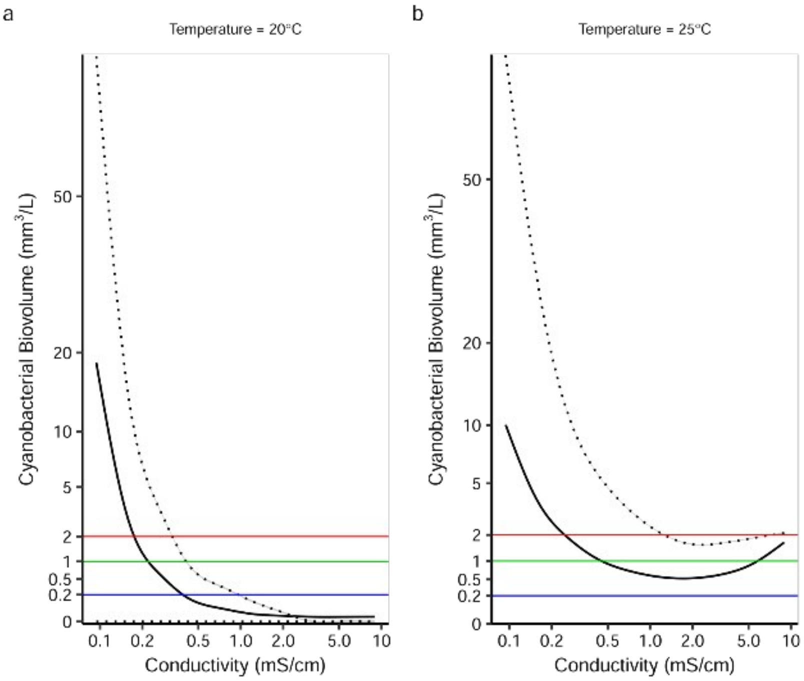

Fig. 9. Biovolume of cyanobacteria ($mm^3 L^{-1}$) as a function of conductivity at two water temperatures: (a) 20 °C; (b) 25 °C. Means (continuous black curves) and 25th and 75th percentiles (dotted curves) are shown. The horizontal lines represent the three risk levels of exposure to cyanobacteria (blue: 0.2 $mm^3 L^{-1}$; green: 1 $mm^3 L^{-1}$; red: 2 $mm^3 L^{-1}$). Note the square-root scale of the y axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

registered between 21 and 23 °C; Haakonsson et al., 2017). On the southern side of the estuary, cyanobacteria above WHO Guidance Level 1 (based on *Microcystis* cells) have been reported between 20 and 24 °C (Giannuzzi et al., 2012) (Supplementary Material Fig. S2).

These findings, and our own results, allow us to highlight the potential of our new model to detect changes in cyanobacterial biovolume in temperature ranges commonly found for CyanoHABs in the studied region.

The two explanatory variables in our model, temperature and conductivity, measured *in situ*, are normally recorded in basic monitoring programs and can be obtained in real time, which potentially allows for instantaneous, on site determination of exceedance probabilities. This is a comparative advantage over models that require time-consuming laboratory measurements of predictors such as nutrients. Our model can therefore be a useful tool for early warning of CyanoHAB events in monitoring programs in eutrophic coastal waters. Furthermore, the conductivity values covered in the present study are in the salinity range of the oligohaline areas of estuaries (Elliott and McLusky, 2002), where blooms often occur (i.e.: Lehman et al., 2005; Taş et al., 2006). Finally, the increasing availability of freely available environmental data (e.g.: https://www.dinama.gub.uy/oan/datos-abiertos/https://www.dinama.gub.uy/oan/datos-abiertos/) should promote the use of this type of model.

Our results suggest that the probability of cyanobacterial bloom occurrence at the study site, and possibly in most coastal areas in the Río de la Plata Estuary, is strongly dependent on two physical variables directly related to climate. Annual precipitation (annual and seasonal means) is projected to increase in this region (IPCC, 2007), which should lower the conductivity and favor the proliferation of cyanobacteria (Reichwaldt and Ghadouani, 2012). When extreme rainfall occurs in the Río de la Plata basin during summer, blooms are likely to appear in the estuary (Kruk et al., 2019). Furthermore, freshwater discharge from two large rivers (Uruguay and Paraná) enters the estuary, resulting in reduced conductivity and increased temperature, and thus favoring cyanobacterial blooms (Kruk et al., 2019). Cyanobacterial biomass is also flushed from reservoirs upstream into the estuary where it continues to grow and proliferate (Kruk et al., 2019). Extreme rainfall events in the southern Río de la Plata basin are projected take place through the twenty-first century (Barros et al., 2013) and therefore cyanobacterial blooms are expected to increase in intensity and duration in the future (Haakonsson et al., 2017).

Despite the fact that nutrient concentrations can be major determinants of cyanobacterial growth, they may not be primary predictors of biomass in nutrient-rich estuaries (Robson and Hamilton, 2004; Taş et al., 2006). Although strong reductions in nutrient loads (phosphorus and nitrogen) may help control cyanobacterial growth (Boesch, 2002; Harke et al., 2016), implementing an on-site nutrient monitoring system with adequate instrumentation and spatio-temporal coverage remains a challenging task in a large ecosystem such as the Río de la Plata Estuary.

5. Conclusions

- The proposed CPG approach to modeling cyanobacterial biovolume successfully handled the high proportion of zeros and the extreme values typically found in CyanHAB samples and provided accurate predictions of cyanobacterial biomass and probabilities of exceedance for alert thresholds of interest to management.
- The key predictors in our model, temperature and conductivity, readily measured *in situ*, are normally recorded in basic monitoring programs and can be obtained in real time, which potentially allows for instantaneous prediction of cyanobacterial biomass.
- Our model has comparative advantages over models that require time-consuming laboratory measurements of predictors such as nutrients.
- In the context of climate change predictions, our model is a useful tool for early warning systems in coastal eutrophic environments that are susceptible to developing CyanoHABs.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watres.2020.115710.

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SUPPLEMENTARY MATERIAL

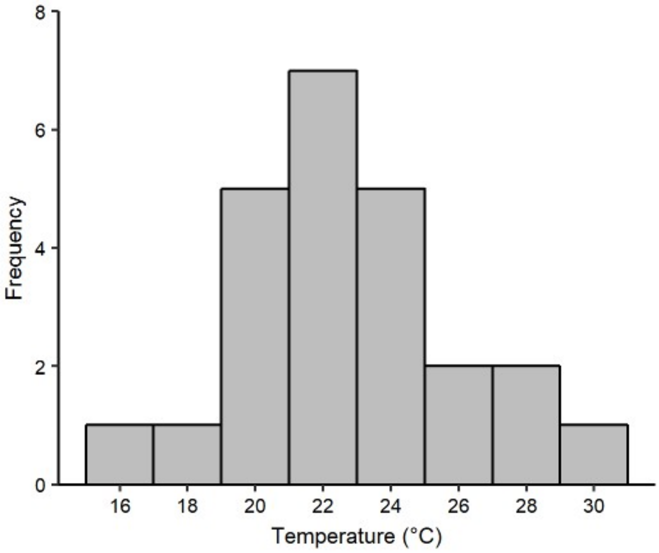
Table S1. List of cyanobacterial taxa present in quantitative samples during the sampling period.

Cyanobacterial taxa
Aphanocapsa spp.
Coelosphaerium sp.
Cyanodictyon sp.
Chrooccocus sp.
Cuspidothrix issatschenkoii
Dolichospermum crassum
Dolichospermum circinale
Dolichospermum uruguayense
Geitlerinema sp.
Merismopedia tenuissima
Microcystis aeruginosa
Microcystis flos-aquae
Microcystis panniformis
Microcystis novacekii
Microcystis protocystis
Microcystis wesenbergii
Pseudanabaena mucicola
Radiocystis fernandoi

Table S2. Components of variance for the random terms in the CPG model. Medians and quartiles (25%, 75%) are shown.

	Variance	Proportion of total
Spatial component (σ_η^2)	4.2 (1.9, 9.2)	0.19 (0.10, 0.36)
Temporal component (σ_ν^2)	16.9 (11.7, 25.1)	0.80 (0.63, 0.90)
Observation error (σ_ε^2)	0.15 (0.11, 0.20)	

Figure S1. Frequency of exceeding Guidance Level 1 for recreational waters of the WHO alert level framework (due to *Microcystis* cell counts; > 20.000 cells ml^{-1}). The data comes from three sampling points on the south coast of the Rio de la Plata Estuary, 60 Km south-west of the city of Buenos Aires. They were extracted from table 1 of Giannuzzi (2012).



5. Discusión general y conclusiones

Discusión

Este estudio permitió elucidar las principales forzantes antrópicas que explican la biomasa fitoplanctónica y la distribución de especies de cianobacterias y su biomasa en ecosistemas subtropicales. No obstante, los modelos desarrollados permitieron determinar que la magnitud del efecto fue dependiente del tipo de ecosistema, la estacionalidad y de las características de la cuenca hidrográfica.

5.1 El efecto de la agricultura depende de la geomorfología y de las precipitaciones.

Tanto a escala país como a escala cuenca nuestros resultados mostraron el mismo patrón: la eutrofización de los ecosistemas acuáticos continentales es una problemática creciente relacionada con el aumento de las actividades agropecuarias. El área de uso de suelo agrícola fue el principal factor en predecir la concentración del fósforo (P) en el agua de los ecosistemas lóticos estudiados, lo que coincide con otros estudios realizados en la región (Gorgoglione et al., 2020; Goyenola, 2017, Martínez, 2021) y en otras partes del mundo (Jones y Downing, 2009; Liu et al., 2014; Matej-Lukowicz et al., 2020). Los niveles de P en agua de los 50 ecosistemas de agua dulce analizados mostraron una tendencia clara de aumento en el tiempo, y en general estuvo asociada a la zona más agrícola del país, particularmente sistemas lóticos con embalses. En cuencas cabeceras con similares características geomorfológicas, baja actividad agrícola (<5%) y sin actividad lechera, la concentración de P se relacionó positivamente con las precipitaciones (Acumuladas, 7 días), mientras que esta relación no se encontró en la cuenca con importante actividad agrícola pero con una geomorfología diferente. Lo que indicó que en cuencas con suelos superficiales las características geomorfológicas en interacción con los forzantes climáticos también pueden promover una mayor llegada de nutrientes a los cursos de agua, incluso cuando las actividades agrícolas son reducidas. Esto implica que las cuencas difieren en su vulnerabilidad frente a los efectos causados por las actividades antrópicas y la variabilidad climática. Por lo tanto, es necesario realizar más estudios e intensificar los monitoreos para poder implementar planes de manejo adecuados que tomen en cuenta las características locales incluyendo los patrones climáticos regionales y locales.

5.2 El P es el nutriente principal para la predicción de la biomasa fitoplanctónica

La densa red hidrográfica de la región estudiada facilita que el P exportado de las actividades antrópicas llegue rápidamente a los ecosistemas acuáticos lénticos. Particularmente en los embalses y lagunas ubicadas en la costa, el P fue el nutriente principal para predecir la biomasa fitoplanctónica (chla). Estos resultados cuestionan uno de los paradigmas que ha permanecido en la literatura limnológica desde la década de los años 70 que plantea que en los climas más cálidos (subtropicales y tropicales), el nitrógeno (N) es el nutriente más prevalente en controlar la biomasa fitoplanctónica (Lewis, 2002, 2000). Asimismo, existen otras evidencias empíricas de regiones cálidas que tampoco apoyan la teoría de Lewis (Huszar et al., 2006; Muhid y Burford, 2012; Rowland et al., 2019). Sin embargo, en los lagos hipereutróficos que estudiamos (lagos urbanos), la chla respondió más al N que al P. Estos resultados apoyan la hipótesis propuesta por Schindler para climas templados (Schindler, 1977; Schindler et al., 2008), que afirma que la gran mayoría de los lagos están limitados por P y que el N solamente es importante en los lagos ya eutrofizados. Estudios de otras regiones climáticas también han demostrado la importancia del tipo de lago para modelar la chla (Dolman et al., 2016; Phillips et al., 2008) y aunque los criterios de definición del tipo de lago difiere entre estudios (profundidad, color, alcalinidad etc.), todos han demostrado que la respuesta de chla ante los nutrientes depende fuertemente del tipo de lago. Por lo tanto, los resultados de esta tesis indican que los factores locales como el estado trófico y la geomorfología (tipo de lago) son más relevantes que la región climática para predecir los efectos y la importancia relativa de los nutrientes sobre la biomasa fitoplanctónica.

5.3 La relación biomasa fitoplanctónica-nutrientes depende de la estacionalidad

La estacionalidad resultó ser una variable sumamente importante al momento de predecir la biomasa fitoplanctónica en esta región subtropical. Todos los tipos de ecosistema respondieron con mayores biomasa en la época cálida, y en los embalses la diferencia entre estaciones fue particularmente más marcada. En general, el análisis de los datos considerando la estacionalidad no es utilizada para el estudio de lagos cálidos, sino que por el contrario, se usan promedios anuales asumiendo un crecimiento del fitoplancton similar durante todo el año (Cunha et al., 2013; Huszar et al., 2006). Sin embargo, utilizar promedios y no considerar la estacionalidad puede enmascarar la variabilidad natural de dicha comunidad. La estacionalidad no solamente puede estar marcada por la temperatura como en las zonas subtropicales, sino que también por el período de lluvias o de vientos (zonas tropicales). Esto implica que los efectos de los nutrientes pueden ser malinterpretados y subestimados en los modelos predictivos. Por ejemplo, si no se consideraba la estacionalidad para los embalses, no se evidenciaba ningún efecto directo de los nutrientes. Por lo tanto, los cambios causados por la estacionalidad deben ser considerados para comprender y mejorar la predicción de las dinámicas ecológicas en los ecosistemas acuáticos subtropicales y tropicales. Además, quedó en evidencia que faltan más estudios en regiones cálidas para generar nuevas hipótesis sobre la dinámica fitoplancton-nutrientes.

5.4 Distribución y biomasa de las cianobacterias planctónicas en ecosistemas eutrofizados

En las regiones más cálidas, y en un contexto de altas concentraciones de nutrientes como vimos que ocurre en muchos ecosistemas del país, el crecimiento de las cianobacterias planctónicas y las floraciones de las mismas, se podrían esperar más frecuentes (Pick y Lean, 1987; Downing et al., 2001). Sin embargo, aun poco es sabido sobre su distribución y como influyen los forzantes climáticos en un marco eutrófico.

Microcystis es el género formador de floraciones de cianobacterias que ha sido más reportado en el mundo (Xiao et al., 2020) y en la región (Aguilera et al., 2017; González-Piana et al., 2011; Nagy et al., 2002), pero nuestro trabajo evidenció que el género *Dolichospermum* es el más distribuido y más frecuente en los cuerpos acuáticos del país. *Dolichospermum* podría tener una ventaja para lograr una mayor distribución, por su capacidad de formar acinetes que le permite sobrevivir en condiciones extremas, por ejemplo, siendo arrastrado aguas abajo por los cursos lóticos (Padisak et al., 2016), tipo de ecosistema dominante en la región. Además la capacidad de fijar nitrógeno es otra virtud que le podría brindar ventaja para su mayor distribución (Li et al., 2016). La amplia distribución y alta frecuencia de *Dolichospermum* apoya a su vez, la hipótesis sobre la expansión global de las especies formadoras de floraciones del orden Nostocales en el contexto del cambio climático global (Li et al., 2016; Sukenik et al., 2012), aunque es necesario realizar otros tipos de estudios para investigar si se trata de una expansión reciente. Por otro lado, la amplia coocurrencia de *Microcystis* y *Dolichospermum*, y su co-dominancia registrada en el mayor evento de floración ocurrido en el país (Aubriot et al., 2020, UTE-IMFIA, 2021), muestran que estos dos géneros son muy exitosos en ambientes eutróficos a estas latitudes. Sin embargo, los resultados también mostraron que responden de manera diferente frente a cambios en los forzantes climáticos. Esto implica que las cianobacterias no pueden ser consideradas un grupo único y que son necesarios más estudios de biogeografía y de fisiología para comprender la distribución de las cianobacterias más prevalentes en la región.

Encontraron relaciones directas e indirectas entre las precipitaciones y la biomasa de cianobacterias. En los ríos en general encontramos que las precipitaciones tuvieron el efecto más esperado de dilución (lavado) sobre la biomasa de cianobacterias. Sin embargo, también fue revelada la gran complejidad que existe entre las precipitaciones y las cianobacterias (Reichwaldt y Chadouani, 2012), ya que en la cuenca del Río Santa Lucía ocurrió el efecto contrario. Las cianobacterias se asocian a los eventos extremos de precipitaciones, dado que ocurre un lavado de las altas biomasas acumuladas en los embalses hacia el cauce principal del río (Somma et al., 2021). Por otro lado, en el estuario del Río de la Plata, encontramos que las precipitaciones tuvieron un efecto positivo (indirecto) sobre la biomasa de cianobacterias. El efecto fue indirecto porque fue a través de la conductividad, que tiene relación inversa con las precipitaciones en el estuario (Aubriot et al., 2020; Kruk et al., 2021). En el contexto del cambio climático global es fundamental conocer los efectos esperados según las predicciones climáticas para cada región geográfica (IPCC, 2021; Rodell et al., 2018). En esta región donde se esperan más lluvias, temperaturas más altas y más eventos de precipitaciones extremos (Díaz, 2018; IPCC, 2021), nuestros resultados mostraron que estas predicciones podrían resultar en más floraciones de cianobacterias en algunas cuencas particulares donde los niveles de nutrientes ya son altos (ecosistemas eutróficos), como en el estuario del Río de la Plata y en subcuencas del río Sta. Lucia.

5.5 Consecuencias y aportes para la gestión de los ecosistemas acuáticos

Los resultados de esta tesis demostraron que los cuerpos de agua agua límnicos del país se encuentran en una situación muy alarmante por los altos niveles de nutrientes, situación revelada ya hace décadas (Alonso et al., 2019; Bonilla et al., 2015; Conde y Sommaruga, 1999; Goyenola et al., 2021) y con tendencia al aumento en algunas zonas desde el año 2002. En la principal cuenca agrícola del país se demostró junto a otros trabajos, que la tendencia de los nutrientes está relacionada con la agricultura (Barreto et al., 2017; Diaz, 2013; Goyenola, 2017), como también se ha evidenciado a nivel global (Hart et al., 2004; Wurtsbaugh et al., 2019). A pesar de estas evidencias, aún persisten algunas ideas que minimizan el aporte que tiene la agricultura al aporte de nutrientes a los cursos de agua. Por ejemplo, Berreta y Carrasco (2021) concluyen que la agricultura no tiene efecto sobre los niveles altos de clorofila *a* encontradas en los embalses del Río Negro. Sin embargo, para esto utilizan evidencias parciales y se omiten estudios previos (Alcántara et al., 2021). Esto demuestra la importancia de seguir aportando evidencias claras sobre la relación de las actividades agropecuarios y la calidad del agua. Además, puede haber gran variabilidad de respuesta según las características de las cuencas hidrográficas. Incluso, las cuencas con muy poco uso agrícola pueden ser muy vulnerables al aporte de nutrientes, teniendo alto riesgo de eutrofización si se intensifica su uso. Por ello, se debe ampliar los estudios abarcando mayores áreas del país y extenderlos integrando análisis de usos de suelo con calidad del agua. Esto es aún más importante porque las proyecciones indican que tanto la intensificación del uso de las tierras, como otras actividades agropecuarias van a seguir aumentando en la región en las próximas décadas por la demanda de alimentos a nivel mundial (IICA, 2004; OPP, 2019; Zabel et al., 2019). Por lo tanto, para evitar que la calidad del agua siga empeorando se deben realizar grandes cambios, que requieren importantes decisiones políticas, con respecto a los aportes directos e indirectos de nutrientes a los cuerpos de agua del país. Asimismo, no hay reglamentación ambiental nacional para el monitoreo de cianobacterias en aguas superficiales, lo que podría ser un gran problema para la salud humana y animal, dado que el género *Dolichospermum* es potencial productora de toxinas, que en el momento no se analizan en los eventos de floraciones del país.

Conclusiones

- Muchas cuencas hidrográficas del país se encontraron comprometidas dado sus altos niveles de nutrientes en las aguas superficiales.
- El efecto de las actividades agropecuarias en los ecosistemas acuáticos, depende de las características geomorfológicas de cada cuenca y de la variabilidad climática.
- El P fue el nutriente principal para predecir la biomasa fitoplanctónica y el N fue solamente importante en sistemas eutrófico-hipereutróficos.
- Las cianobacterias planctónicas están altamente distribuidas en el país en todo tipo de ecosistema, siendo *Dolichospermum* el género más distribuido y más frecuente.
- La estacionalidad fue una variable fundamental para predecir la dinámica biomasa-nutrientes.
- Las variables climáticas-meteorológicas controlan la biomasa de cianobacterias en ambientes eutróficos .
- Los modelos jerárquicos Bayesianos mostraron ser muy efectivos para predecir los efectos de las variables forzantes sobre la biomasa del fitoplancton según el tipo de ecosistema y/o cuenca hidrográfica.
- Hay muchos vacíos de información y es necesario ampliar los programas de monitoreo (en cuanto a frecuencia y extensión geográfica) e incluir el seguimiento de las cianobacterias utilizando bioindicadores cuantitativos.

6. Perspectivas

Los resultados de la presente tesis permitieron plantear nuevas hipótesis y preguntas para continuar en proyectos futuros.

Las predicciones del cambio climático global para la región junto a los altos niveles de nutrientes en los cuerpos de agua aportados por las actividades agropecuarias, deja un escenario complejo donde se pueden esperar más floraciones de cianobacterias planctónicas. El modelo desarrollado para el biovolumen de cianobacterias (CPG) se esta aplicando en combinación con sistemas de sensores remotos para avanzar en sistemas de monitoreo y alerta temprana de floraciones en el estuario del Río de la Plata (Haakonsson et al. en prep).

Los cambios en los usos y coberturas del suelo mostraron tener una relevancia determinante en los niveles de nutrientes en agua en el proceso de eutrofización, pero también se reveló la importancia de tomar en cuenta factores geomorfológicos y climáticos para evaluar el agravamiento. En el contexto de mayor intensificación de los usos del suelo, en especial de la agricultura y la lechería, se requiere tener mejores evaluaciones sobre su efecto en la exportación de fósforo a los ecosistemas acuáticos. Los modelos jerárquicos Baysianos empleados en la tesis son una buena herramienta para seguir con esas evaluaciones ya que además permiten realizar predicciones según futuros escenarios tomando en cuenta la geomorfología de las cuencas hidrográfica.

Los resultados mostraron que altas biomasas de los géneros *Dolichospermum* y *Microcystis* estuvieron juntos en muchas oportunidades en eventos de floraciones. Durante la realización de esta tesis, se logró aislar una cepa de *Microcystis aeruginosa* (productora de microcistina) del estuario del Río de la Plata. Esta cepa permitirá en el futuro realizar experimentos para comprender mejor su distribución, coocurrencia y los factores que favorecen la producción de toxinas.

Es evidente la fragmentación de la información y el vacío de datos que no permiten representar adecuadamente la heterogeneidad ambiental de los ecosistemas acuáticos del país. La estadística Bayesiana, principal método de análisis durante la tesis, es una herramienta muy útil para estos desafíos, que además tiene ventajas frente al método frecuentista, ya que permite alcanzar estimaciones más exactas de los parámetros aún con pocos datos, lograr una interpretación de los resultados más fácil y directa (basada en probabilidad), incluir medidas de incertidumbre y diferentes niveles de variabilidad, entre otras ventajas. Por lo tanto, con la estadística Bayesiana por ejemplo se podrían analizar las bases de datos abiertos de la OAN (Observatorio Ambiental Nacional) combinando datos de caudales y de uso del suelo para identificar regiones críticas y predecir escenarios complejos a futuro.

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