

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

**INVASION STRATEGIES AND ESTABLISHMENT OF *CERATIUM*
DINOFLAGELLATE IN SUBTROPICAL WATERSHEDS OF
SOUTHERN BRAZIL AND ITS INTERACTION WITH
MICROCYSTIS CYANOBACTERIA**

RUAN DUTRA DA SILVA

PORTO ALEGRE

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Resumo

Ceratium furcoides é um dinofagelado que apresenta comportamento invasor nos ecossistemas aquáticos da América do Sul e vem ampliando sua distribuição nos últimos anos. Junto com *Microcystis* spp., podem coexistir, constituindo um grupo funcional em regiões temperadas. No entanto, interação entre eles, nas regiões subtropicais ainda não está clara. Neste estudo, monitoramos 151 municípios do sul do Brasil, com dados que variam de 2012 a 2022, com o objetivo de detectar e registrar a ocorrência e abundância de dinoflagelados no estado do Rio Grande do Sul, bem como examinar sua expansão e persistência padrão. Além disso, estudar sua interação com as comunidades locais, norteando-se pelas seguintes questões: esses organismos co-ocorrem nos ambientes estudados? se sim, como se dá essa co-ocorrência? e quais variáveis ambientais estão relacionadas aos padrões observados? *C. furcoides* foi registrada em 84,1% dos municípios monitorados, nas três regiões hidrográficas (RH) do estado. Especialmente, RH Guaíba apresentou as maiores densidades para a espécie ($10.912 \text{ cél.mL}^{-1}$); nas escalas temporais, 2014 e 2015 apresentaram picos de densidade, geralmente no verão. A área acumulada invadida por *C. furcoides* aumentou gradativamente, atingindo 266.625 km^2 em 2018, correspondendo a cerca de 94% do estado, porém a maior taxa de expansão ($3.142 \text{ km.ano}^{-1}$) e maior distância percorrida (40,4 km) ocorreram em 2012, durante a sua introdução. A expansão variou ao longo dos anos estudados, inicialmente rumo a RH Litoral e Guaíba (entre 2012 e 2014), seguida por um período estacionário (2015 a 2017), seguido de uma progressão em direção a RH Uruguai (2018). A análise de frequência mostrou que a persistência foi baixa na maioria dos municípios. Modelos de distribuição para *C. furcoides* e *Microcystis* spp. mostraram que ambos responderam de forma semelhante aos mesmos preditores, sendo os mais importantes a temperatura (sazonalidade, variação anual e variação média diurna), além do acúmulo de vazão. Apesar disso, a análise de co-ocorrência mostrou alta segregação em todas as escalas, impulsionada por mudanças de precipitação e temperatura proporcionadas pelo El Niño e La Niña, associadas ao aumento nutricional. No cenário subtropical, *C. furcoides* foi dominante, em termos de frequência e abundância, matéria orgânica sendo fundamental para o seu desenvolvimento e dominância; em oposição, *Microcystis* spp. foi muito sensível a perturbações, com florações esporádicas sustentadas por compostos nitrogenados e fosfatados. Dada a sua rápida expansão, dispersão em todo o estado, formação de florações extremamente grandes e domínio sobre as comunidades locais, o Rio Grande do Sul parece ser o segundo lar de *C. furcoides*.

Palavras-chave: Invasão biológica, co-ocorrência, competição, El Niño, La Niña, cianobactérias, dispersão

Abstract

Ceratium furcoides is a dinoflagellate that exhibits invasive behavior in the aquatic ecosystems of South America and has been expanding its range in recent years. Along with *Microcystis* spp., they may coexist, constituting a functional assemblage in temperate regions. However, their interaction in subtropics is still unclear. In this study, we monitored 151 municipalities in southern Brazil, with data ranging from 2012 to 2022, with the objective of detecting and recording the dinoflagellate occurrence and abundance in the state of Rio Grande do Sul, as well as to examine its expansion and persistence pattern. In addition, study its interaction with local communities, driving by the following questions: do these organisms co-occur in these environments? If so, how does this co-occurrence occur? what environmental variables are related to the observed patterns? *C. furcoides* was recorded in 84.1% of the monitored municipalities, in all three of the state's hydrographic regions (HR). Spatially, the Guaíba HR showed the highest densities for the species ($10,912 \text{ cell.mL}^{-1}$); in temporal scales, 2014 and 2015 displayed density peaks, usually in the summer. The cumulative area invaded by *C. furcoides* gradually increased, reaching $266,625 \text{ km}^2$ in 2018, corresponding to about 94% of the state, however the highest expansion rate ($3,142 \text{ km.year}^{-1}$) and longest distance covered (40.4 km) occurred in 2012, during its introduction. The expansion varied over the studied years, initially heading towards HR Littoral and Guaíba (between 2012 and 2014), proceeded by a steady period (2015 to 2017), followed by a progression toward HR Uruguay (2018). The frequency analysis showed that persistence was short in most of the municipalities. Distribution models for *C. furcoides* and *Microcystis* spp. showed that they responded similarly to the same predictors, the most important being temperature (seasonality, annual range and mean diurnal range), in addition to flow accumulation. Despite this, co-occurrence analysis showed high segregation in all scales, driven by shifts in precipitation and temperature provided by El Niño and La Niña, associated with nutritional increase. In subtropical scenario, *C. furcoides* was dominant, in terms of frequency and abundances, organic matter being key for its development and dominance; in opposition, *Microcystis* spp. was very sensitive to disturbances, with sporadic blooms supported by nitrogenous and phosphate compounds. Given its rapid expansion, statewide dispersibility, extremely large bloom formation, and dominance upon local communities, Rio Grande do Sul looks to be *C. furcoides*' second home.

Keywords: Biological invasion, co-occurrence, competition, El Niño, La Niña, cyanobacteria, dispersion

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General Introduction

The introduction of exotic species constitutes one of the most pervasive drivers of changes in natural habitats, responsible for a multitude of anthropic damages, such as biodiversity and habitat loss, fragmentation, and changes in ecosystem functioning and land-use (Tylianakis et al. 2008; Laurance et al. 2014; Kumschick et al. 2015; Bellard et al. 2016). In addition to negative impacts, the invasion process can act as a novel selective pressure on the organisms they interact with, as species with an invasive character tend to be excellent competitors, usually becoming dominant quickly, monopolizing resources, and consequently altering biological interactions (Mooney & Cleland 2001; Lee 2002; Didham et al. 2005).

Directly or indirectly, climate change is likely to influence biological invasions and give these organisms a chance: global rising temperatures, altered precipitation regimes, and extreme weather events are aspects relevant to distribution and prevalence of invasive species (Vilà et al. 2007; Thuiller et al. 2007; Richardson 2000). The hydrological cycle is expected to intensify in response to climate and increase the frequencies of the aforementioned extreme events (Huntington 2010). As pointed out by Trenberth et al. (2007), El Niño-Southern Oscillation events are coupled to ocean circulation and impact the climate of tropical and subtropical zones, as there is an irregularly periodic variation in winds and sea surface temperatures across the ocean. In this regard, two distinct phases occur, where the warmer one is known as El Niño, and the cooling phase is called La Niña. Historically, these events occur about every 3 to 7 years and alternate (Trenberth et al. 2007). Since 1950, there have been 20 and 22 El Niño and La Niña events respectively, with 2011/2012 (La Niña) and 2014/2015 (El Niño) being the last times these events occurred (Silva et al. 2022).

Hellmann et al. (2008) summarized that these events could have key consequences in invasive species, by: (I) altered mechanisms of transport and introduction, where mediated transport would enhance the survivorship of propagules; (II) altered climatic constraints, showing that non-native species would be able to colonize if conditions become more like the species' native range; (III) altered distribution of existing invasive species, as these species spread range would likely follow its temperature and hydrological constraints, selecting features in response to climate; (IV) altered impact of existing invasive species, given that the population densities of some invasive species would be reflected on native species; and (V) altered effectiveness of management strategies for invasive species, as tolerance and effectiveness of biocontrol's would be affected. In resume, in areas where individuals are killed by the disturbance, an increase the invasibility of the environment is expected (Davis et al. 2000) and is supported by reports that have linked extreme events to invasive species, such as wind (Pacheco et al., 2021), droughts (Crossetti et al., 2019; Queiroz et al., 2022) and floods (Mihaljević et al., 2010)

Among the known invading microorganisms in South America, the species of the genus *Ceratium* (Dinophyta) are in the forefront in terms of expansion. *Ceratium hirundinella* (O.F. Muller) Dujardin was first reported for the continent, colonizing Argentine and Chilean water bodies, starting in the 1990s (Boltovskoy et al., 1991, 2003, 2013; Guerrero & Echenique, 1997; Soto & Lembeye, 1999; Mac Donagh et al., 2005; Silverio et al., 2009). *Ceratium furcoides* (Levander) Langhans establishment is more recent, first invading areas previously unoccupied and subsequently replacing *C. hirundinella* (Boltovskoy et al., 2013; Salusso & Morana, 2014).

C. furcoides (Levander) dispersion models reveal that the continent is highly suitable to the invasive species (Meichtry-de-Zaburlín et al. 2016), which is corroborated by several reports in the region, such as in Argentina (Boltovskoy et al. 2013; Bordet et al. 2017; Daga et al. 2020), Peru (Mendoza-Carbajal et al. 2022), Colombia (Bustamante-Gil et al. 2012, 2022), Uruguay (Pacheco et al. 2021), and Chile (Almanza et al. 2016). Most notably, Brazilian environments have recorded the species the most, in many different aquatic ecosystems, such as lakes (Jati et al., 2014; Moreira et al., 2015, Campanelli et al., 2017; Silva et al., 2019), hydroelectric reservoirs (Santos-Wisniewski et al., 2007; Silva et al., 2012; Cassol et al., 2014; Cavalcante et al., 2017), urban reservoirs (Crossetti et al., 2019) and water-supply reservoirs (Matsumura-Tundisi et al., 2010; Nishimura et al., 2015; Cavalcante et al., 2016; Rojas-Castillo et al., 2023). The species can form blooms that are potentially harmful to the environment, leading to a significant pH increase, oxygen depletion, filter saturation in water treatment plants, changes in water color and odor, and the death of animals (Taylor et al. 1995; Matsumura-Tundisi et al. 2010; Almeida et al. 2016; Morales 2016; Pacheco et al. 2021).

Blooms of *Microcystis* spp. have been registered worldwide (Carmichael, 1986; Codd & Beattie, 1991), and is one of the most frequently found genera among the planktonic communities in South America (De León & Yunes 2001; Pérez et al., 2013; González-Piana et al., 2017; O'Farrell et al., 2019). According to Paerl (1988), they have undifferentiated dormant cells, being able to survive for several years, waiting for more favorable periods to its development and reproduction, making monitoring difficult. Many *Microcystis* spp. strains can produce microcystin, a potent hepatotoxin, which is associated with many environmental problems, such as death of animals (Carmichael, 1986; Codd & Beattie, 1991), in addition to odours and off-flavour compounds (Falconer, 2005). Thus, persistent blooms pose a risk to those who use impaired water resources for drinking water supplies, recreational activities, and fisheries (Harke et al., 2016).

Together with *Microcystis*, *Ceratium* species comprise Reynolds et al. (2002) L_M functional group, consisting of species that often co-occur in the summer epilimnia of eutrophic temperate lakes, being sensitive mostly to mixing, stratification and light. They are S-strategists, dealing extremely well in stressful situations, being able to migrate thought large distances to avoid light constraints or to access the more nutrient-rich deep-water layers and, in *Ceratium*'s case, use mixotrophy as nutrient alternative sources (Reynolds, 2006; Cavalcante et al., 2016).

This assemblage usually contributes to phytoplankton steady-states in temperate climate (Naselli-Flores & Barone, 2003), however, the interactions between both microorganisms is not fully understood in ecosystems where *Ceratium* species are considered invasive.

Algal invasions are poorly documented (Padisák et al. 2016), so studies addressing the introduction, establishment, and expansion of planktonic species, such as *C. furcoides*, are important for identifying dispersal routes and areas susceptible to invasion. Invasive species presence in aquatic environments may also influence the structure and dynamics of the phytoplankton community, so understanding its interactions with other species is of utmost importance.

As *C. furcoides* presents invasive behavior in the aquatic ecosystems of southern Brazil, reservoirs used to supply drinking water to human populations were monitored, in 151 municipalities, since the first occurrence of the dinoflagellate, with the following objectives: study the *C. furcoides* abundance and expansion pattern in Rio Grande do Sul and assess its temporal (eight years) and spatial distribution. The study also aimed to contribute to the understanding of the relationship between *C. furcoides* and *Microcystis* spp. in subtropical environments, being driven by the following questions: do *C. furcoides* and *Microcystis* spp. co-occur in the environments studied? if so, how does this co-occurrence occur? and what environmental variables are related to the observed distribution patterns?

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The second: “***Ceratium furcoides* and *Microcystis* spp. segregation patterns are ruled by nutrient availability and meteorological shifts in a Subtropical Region**” will be submitted to the scientific journal *Hydrobiologia*.

CHAPTER I

**Spread and persistence of the invasive dinoflagellate *Ceratium furcoides*
(Levander) Langhans through South America: watersheds in Rio
Grande do Sul, Brazil**



Spread and persistence of the invasive dinoflagellate *Ceratium furcoides* (Levander) Langhans through South America: watersheds in Rio Grande do Sul, Brazil

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Abstract

Ceratium furcoides is a dinoflagellate that exhibits invasive behavior in the aquatic ecosystems of South America and has been expanding its range in recent years. In this study, we monitored 151 municipalities in southern Brazil between 2012 and 2019 with the objective of detecting and recording the species' occurrence and abundance in the state of Rio Grande do Sul, as well as to examine its expansion and persistence pattern. *Ceratium furcoides* was recorded in 84.1% of the monitored municipalities, in all three of the state's hydrographic regions (HR). Spatially, the Guaíba HR showed the highest density for the species (10,912 cells mL⁻¹); in temporal scales, 2014 and 2015 displayed density peaks, usually in the summer. The cumulative area invaded by *C. furcoides* gradually increased, reaching 266,625 km² in 2018, corresponding to about 94% of the state; however, the highest expansion rate (3142 km year⁻¹) and longest distance covered (40.4 km) occurred in 2012, during its introduction. The expansion varied over the studied years, initially heading toward HR Littoral and Guaíba (between 2012 and 2014), followed by a steady period (2015–2017), and subsequently a progression toward HR Uruguay (2018). The frequency analysis showed that persistence was short in most of the municipalities. The results indicate that local environmental characteristics, especially temperature and precipitation, could be key for the invasion and development of the species. Given its rapid expansion, statewide dispersibility, and extremely large bloom formation, Rio Grande do Sul looks to be *C. furcoides*' second home.

Keywords Dispersion · Phytoplankton · Subtropical · Ecosystem services

Abbreviations

CORSAN	Companhia Riograndense de Saneamento
ETAs	Water treatment stations
FEPAM	Fundação Estadual de Proteção Ambiental
FO	Frequency of occurrence
HB	Hydrographic basins
HR	Hydrographic regions

IBGE	Instituto Brasileiro de Geografia e Estatística
IDW	Inverse distance weighted
MCP	Minimum convex polygon
MS	Meteorological stations
RS	Rio Grande do Sul

Introduction

The introduction of exotic species constitutes one of the most pervasive drivers of changes in natural habitats, responsible for a vast array of anthropic damage, such as biodiversity and habitat loss, fragmentation, and changes in ecosystem functioning and land use (Tylianakis et al. 2008; Laurance et al. 2014; Kumschick et al. 2015; Bellard et al. 2016). In addition to negative impacts, the invasion process can act as a novel selective pressure on the organisms they interact with, as species with an invasive character tend to be excellent competitors, usually becoming dominant quickly, monopolizing resources, and consequently altering

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biological interactions (Mooney and Cleland 2001; Lee 2002; Didham et al. 2005).

Microorganisms often have remarkable dispersal potential, and frequently, their spatial distributions are expressed by the “everything is everywhere but the environment selects” principle of Baas Becking (Wit and Bouvier 2006; Canfield 2015). This hypothesis suggests that only adapted organisms will flourish and proliferate in specific environments, and geographical patterns presented by these species would simply reflect an association between geography and ecology (Fuhrman 2009). Their dispersion is also dependent on a pool of organisms: the larger the population, the greater the chance of thriving. They may not succeed or proliferate at a given time and place, but some will survive long enough for immigration to secure a permanent presence (Fenchel and Finlay 2004). Thus, microorganisms are virtually everywhere, waiting for an opportunity to proliferate.

Directly or indirectly, climate change is likely to influence biological invasions and give these organisms a chance: rising global temperatures, altered precipitation regimes, and extreme weather events are aspects relevant to the distribution and prevalence of invasive species (Vilà et al. 2007; Thuiller et al. 2007; Richardson et al. 2000). The hydrological cycle is expected to intensify in response to climate and, increasing the frequency of the aforementioned extreme events (Huntington 2010). As pointed out by Trenberth et al. (2007), El Niño-Southern Oscillation events are coupled to ocean circulation and impact the climate of tropical and subtropical zones, as there is an irregular periodic variation in winds and sea surface temperatures across the ocean. In this regard, two distinct phases occur, where the warmer one is known as El Niño, and the cooling phase is called La Niña. Historically, these events occur about every 3–7 years and alternate (Trenberth et al. 2007). Since 1950, there have been 20 and 22 El Niño and La Niña events respectively, with 2011/2012 (La Niña) and 2014/2015 (El Niño) being the last times these events occurred (Silva et al. 2022).

In this context, species whose native ranges are warmer than their introduced ranges would be at an advantage, as the invader could withstand hotter temperatures and experience less mortality due to cold (Vilà et al. 2007). The same could be said about changes in precipitation patterns, as an increase in these rates could help an invasive species enhance its range (Vilà et al. 2007), because it can provide an input of nutrients from sediment (Cavalcante et al. 2016); may alter hydrological connectivity due to transfers of matter, energy, and organisms (Pringle 2001); and cause turbulence, altering species abundances in aquatic systems (Pollinger and Zemel 1981). Furthermore, the increasingly eutrophic world may favor the establishment and success of fast-growing invasive species (Vidal and Kruk 2008; Suke-nik et al. 2012), as an increase in nutrients is associated with algal blooms due to an increase in photosynthesis rates,

eventually causing oxygen depletion and an increase in pH to extreme levels, limiting light penetration, reducing growth, and causing the death of several organisms (Chislock et al. 2013).

Biological invasions by microscopic organisms often go unnoticed, as these species are small and, accordingly, their consequences for the environment are underestimated (Strayer 2010; Silva et al. 2012; Padišák et al. 2016).

Ceratium furcoides (Levander) Langhans 1925 is a freshwater dinoflagellate species native to the Northern Hemisphere (Carty and Parrow 2015) and has recently expanded its geographical distribution to South America, where it is considered invasive (Boltovskoy et al. 2013). Dispersion models reveal that the continent is highly suited to the invasive species (Meichtry-de-Zaburlín et al. 2016), which is corroborated by several reports in the region, such as in Argentina (Boltovskoy et al. 2013; Bordet et al. 2017; Daga et al. 2020), Peru (Mendoza-Carbajal et al. 2022), Colombia (Bustamante-Gil et al. 2012, 2021), Uruguay (Pacheco et al. 2021), and Chile (Almanza et al. 2016).

Ceratium furcoides can form blooms that, although not toxic, present harmful conditions that can include changes in water color and odor, filter saturation in water treatment plants, significant pH increase, oxygen depletion, and the death of animals (Taylor et al. 1995; Matsumura-Tundisi et al. 2010; Pitcher et al. 2011; Almeida et al. 2016; Morales 2016; Pacheco et al. 2021). Thus, the species' presence in aquatic systems is of critical concern because of compromised water quality and its high treatment cost.

Although unclear, the species' distribution in South America has been the subject of a growing number of reports. Aspects such as the stability of the water column (Bustamante-Gil et al. 2012), ideal temperature and precipitation (Cavalcante et al. 2016), and nutrient availability (Nishimura et al. 2015; Bustamante-Gil et al. 2012; Silva et al. 2012; Crossetti et al. 2019) are discussed as important to *C. furcoides*' expansion and colonization process. Furthermore, the dinoflagellate has competitive skills that make it superior to native phytoplankton, such as the ability to migrate vertically due to its flagellum, which enables access to areas with better light and more nutrients (Kruk et al. 2021), and the ability to form cysts when conditions are unfavorable, granting it survival for long periods in the sediment (Cavalcante et al. 2013). It is also herbivore-resistant owing to its horns and spines (Ollrik 1994), can make use of mixotrophy when necessary as a nutritional alternative (Cavalcante et al. 2013), and is able to store large amounts of nutrients (Bustamante-Gil et al. 2012).

In Brazil, the first report of *C. furcoides* was made in 2007 by Santos-Wisniewski et al. (2007) in Furnas Reservoir in the state of Minas Gerais. The invasions in Brazilian environments have often been preceded by disturbances that modify resource availability, thereby allowing *C. furcoides*

recruitment (Crossetti et al. 2019). The arrival and establishment of the species has been recorded in many aquatic ecosystems in Brazil, such as lakes (Moreira et al. 2015; Silva et al. 2019), hydroelectric reservoirs (Silva et al. 2012), and water supply reservoirs (Matsumura-Tundisi et al. 2010; Nishimura et al. 2015; Cavalcante et al. 2016; Rojas-Castillo et al. 2023).

Algal invasions are poorly documented (Padisák et al. 2016), so studies addressing the introduction, establishment, and expansion of planktonic species are important for identifying dispersal routes and areas susceptible to invasion. In South America, long-term studies concerning these species are scarce (Mac Donagh et al. 2005; Crossetti et al. 2019; Rojas-Castillo et al. 2023), as are those with high sampling frequency (Almanza et al. 2016; Bordet et al. 2017; Silva et al. 2019). Research incorporating a long time period, over an extensive area, with dispersal routes and their patterns is even rarer, the only one for *C. furcoides* being Severiano et al. (2021).

As *C. furcoides* presents invasive behavior in the aquatic ecosystems of southern Brazil, we monitored reservoirs used to supply drinking water to human populations in 151 municipalities for 8 years, since the first occurrence of the dinoflagellate, with the following objectives: (i) study the *C. furcoides* abundance and expansion pattern in Rio Grande do Sul and (ii) assess its temporal (8 years) and spatial (281,707.15 km²) distribution. This research represents the first of its kind for the state, where the species form the greatest blooms in the South American region (Silva et al. 2019; Rojas-Castillo et al. 2023). Furthermore, it is the first incorporating the species' dispersal patterns using its abundance in South America and not simply its presence/absence, following Baas Becking's principle (Wit and Bouvier 2006).

We hypothesize that the species' highest rate of expansion would occur in the first couple of years, as *C. furcoides* is known to be an aggressive invader (Crossetti et al. 2019; Silva et al. 2019; Severiano et al. 2022). Furthermore, we expected that an increase in temperature caused by global warming would be beneficial to the species, as its optimal growth occurs in temperatures around 25 °C (Butterwick et al. 2005; Cavalcante et al. 2016; Meichtry-de-Zaburlín et al. 2016). Moreover, *C. furcoides* would profit by phenomena like the El Niño-Southern Oscillation, by taking advantage of disturbances in the homeostasis of the phytoplankton community prompted by droughts (Crossetti et al. 2019), and enhance its dispersion and range whenever the precipitation increased, as heavy rainfall promotes connectivity among aquatic environments (Lesschen et al. 2009). Finally, the preferable regions for the species' blooms would be those close to large cities and industrial centers, as increased nutrient levels in water bodies are associated with anthropic influence (Dodds et al. 2009), and the growth of planktonic

species is the primary biological response to nutrient enrichment (BoQiang et al. 2013).

Materials and methods

Study site

Rio Grande do Sul (RS) is Brazil's southernmost state (Fig. 1). It has 497 municipalities, a total area of 281,707.15 km², and 11,422,973 inhabitants, representing approximately 5.4% of the Brazilian population (Rio Grande do Sul 2023).

Rio Grande do Sul is divided into three hydrographic regions (HR): HR Uruguay, which is located in the national basin of Uruguay, and HR Guaíba and HR Littoral, which are located in the HR South Atlantic (ANA 2015) (Fig. 1). According to SEMA [Secretaria do Meio Ambiente e Infraestrutura] (2018), the HRs are divided into hydrographic basins (HB) and can be identified by the region initial and its specific number (Fig. 1).

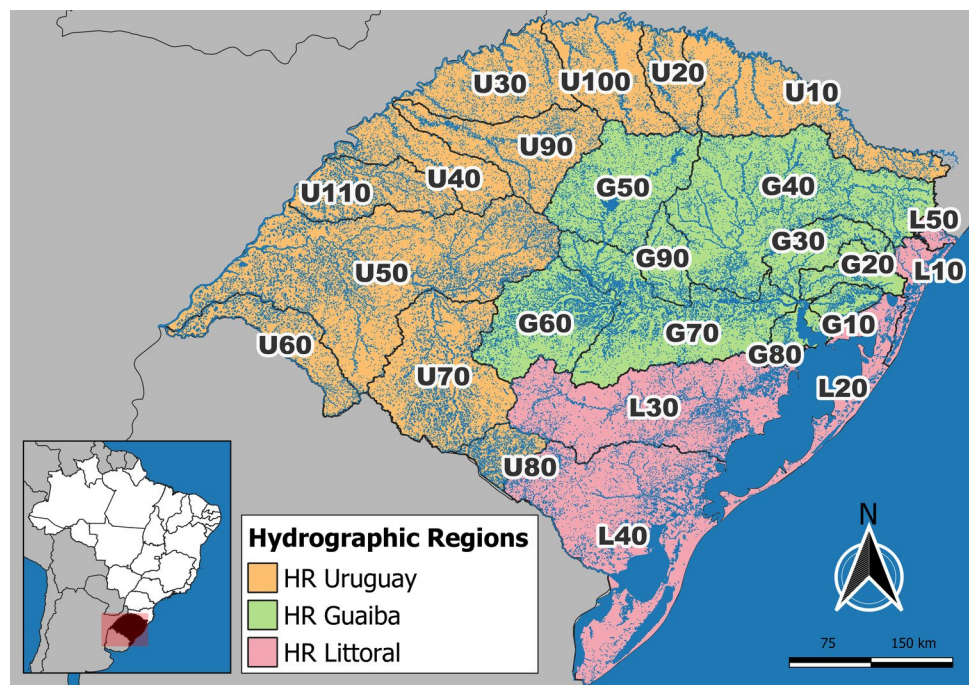
HR Uruguay is in northern RS, extending into the state of Santa Catarina and the neighboring countries of Argentina and Uruguay (BRASIL 2006), with a total area of 385,000 km², 174,000 km² of that being in Brazil and encompassing 286 municipalities (FEPAM 2022). Oxisols and chernosols are predominant in the region, which favors agricultural, livestock, and agro-industrial practices (BRASIL 2003).

HR Guaíba lies in northeastern RS and covers an area of 84,763.54 km², corresponding to about 30% of the state's total area. Two-hundred and fifty-one municipalities, supporting more than 60% of the state's population, are fully or partially situated in the region. The vegetation of the area is characteristic of RS, i.e., mixed and seasonal ombrophilous forest, in addition to fields (FEPAM 2022). The main economic practices are based on agriculture, livestock, and industry. These factors, associated with a large population, cause HR Guaíba many environmental problems, such as pollution from domestic sewage and industrial waste, contamination by pesticides, and the erosion and silting of water bodies (FEPAM 2022).

HR Littoral covers an area of approximately 69,000 km² and includes 58 municipalities, which are distributed along a NE–SW line near the Atlantic Ocean. The landscape consists of moving dunes, interconnected coastal lagoons and marshes, and dunes fixed by arboreal vegetation. The use and occupation of the land changes along the coastal region, but the main economic practices are agricultural and industrial (FEPAM 2022; Haase et al. 2003).

The state climate is classified as Cfa and Cfb, according to the Köppen system, which together operate as a temperate climate region where the temperature of the coldest month varies between –3 and 18 °C (Kottek et al. 2006). The rainfall is evenly distributed over the year, with

Fig. 1 Location of the hydrographic regions (HR) of Rio Grande do Sul state, southern Brazil, its hydrographic basins (HB), and their specific numbers. *U* Uruguay, *L* Littoral, *G* Guaíba, *U10* HB Apuaê-Inhandava, *U20* HB Passo Fundo, *U30* HB Turvo-Santa Rosa-Santo Cristo, *U40* HB Piratinim, *U50* HB Ibicuí, *U60* HB Quaraí, *U70* HB Santa Maria, *U80* HB Negro, *U90* HB Ijuí, *U100* HB Várzea, *U110* HB Butuí-Icamaquã, *L10* HB Tramandaí, *L20* HB Médio, *L30* HB Camaquã, *L40* HB Mirim-São Gonçalo, *L50* HB Mampituba, *G10* HB Gravataí, *G20* HB Sinos, *G30* HB Caí, *G40* HB Taquari-Antas, *G50* HB Alto Jacuí, *G60* HB Vacacaí-Vacacaí Mirim, *G70* HB Baixo Jacuí, *G80* HB Guaíba, *G90* HB Pardo



the accumulation ranging from 1000 mm to more than 2000 mm (Kottek et al. 2006; Rio Grande do Sul 2023).

Meteorological data

Climate data (temperature and precipitation) from each HB were obtained through the historical series of INMET (Instituto Nacional de Meteorologia) from automated stations throughout Rio Grande do Sul (<https://portal.inmet.gov.br/>) for the eight sampled years (2012–2019). For this approach, the daily temperature averages and accumulated precipitation were used, as the series provides 24 readings/day of these data (hourly measurement). There are 44 meteorological stations (MS) in RS; however, only 38 were used, as they provided the most complete dataset (Supplementary Material 1).

To better visualize the climate's spatial and temporal variation, the dataset was transformed into a raster using QGIS software version 3.22.5 (QGIS Development Team 2023). For this purpose, the inverse distance weighted (IDW) interpolation method was used, in which cell values are determined using a linearly weighted combination of a set of sample points, assigning values to non-sampled points based on the average of sampled points within the neighborhood (Lu and Wong 2008). The geospatial and vector database used for the construction of the maps was in the geographic information system (GIS) shapefile format made available by Fundação Estadual de Proteção Ambiental (FEPAM 2018).

Phytoplankton sampling and identification of *Ceratiurn furcoides*

CORSAN (Companhia Riograndense de Saneamento) is the company responsible for most of the water supply and treatment in RS, covering 96% of the state (317 municipalities). A total of 151 municipalities with phytoplankton data were monitored between 2012 and 2019 (Supplementary Material 2).

Phytoplankton data sampling (weekly, monthly) was carried out using 1 L polyethylene bottles in places near the water catchments or a raw water tap at the water treatment stations (ETAs), depending on the municipality (Supplementary Material 2), on the subsurface of the water column. These samples were concentrated by centrifugation and quantified using the Sedgewick-Rafter technique (CETESB 2005), a quantification protocol for counting cells in a large volume, with the results expressed in cells mL⁻¹.

Identification of *C. furcoides* was made based on studies of its genus, which had been previously identified on a regional scale and documented by Cavalcante et al. (2013).

Analysis of the spatial and temporal distribution of *C. furcoides*

Descriptive statistical analyses (STATISTICA® software version 7.1) were performed with the aim of exploring spatial and/or temporal variations in biotic and meteorological data. For this approach, data were spatially organized according to the corresponding municipality, and these

arranged according to their respective HB (SEMA 2020). For temporal analyses (January 2012–September 2019), samples were organized annually (2012–2019) and seasonally (summer, fall, winter, spring).

A distribution map of *C. furcoides* occurrence was produced from the geographical position of the municipality (latitude, longitude) using the FEPAM cartographic database (<https://fepam.rs.gov.br/inicial>) as a reference.

To calculate the cumulative invaded area (km²), a minimum convex polygon (MCP) was drawn around the geographical positions of the municipalities. The MCP is drawn considering the smallest polygon in which no internal angle exceeds 180° and contains all the occurrence sites. To obtain the area of the polygon in square kilometers, the coordinate system used (longitude, latitude) was converted using the Albers equal-area projection system, following instructions from the Instituto Brasileiro de Geografia e Estatística (IBGE) (2022). The expansion rate of *C. furcoides* (km year⁻¹) was calculated, as described by Preuss et al. (2014), by plotting the square root of the occupied area against time (years).

The distance (km) and direction of the expansion of *C. furcoides* between consecutive years were also calculated, considering the distance between the areas of consecutive years and direction of centroids from MCP. The values obtained for the expansion direction were categorized according to Severiano et al. (2022), where cardinal points (north: 0°; south: 180°; east, 90°; and west: 270°), collateral points (northeast: 45°; southeast: 135°; northwest: 315°; and southwest: 225°), and sub-collateral points (north-northeast: 22.5°; east-northeast: 67.5°; east-southeast: 112.5°; south-southeast: 157.5°; south-southwest: 202.5°; west-southwest: 247.5°; west-northwest: 292.5°; and north-northwest: 337.5°) were used. Analyses were performed using the SIRGAS2000 projection reference system using QGIS software version 3.22.5 (QGIS Development Team 2023). The geospatial and vector database used for the construction of the maps was in GIS shapefile format, made available by FEPAM (2018).

Frequency of *C. furcoides* occurrence

To assess the persistence of *C. furcoides* in invaded municipalities, the frequency of occurrence (FO in %) was calculated. To define FO, samples for each municipality were grouped for each year by season (e.g.: summer of 2012, fall 2012, winter 2012, spring 2012, and so on) and then transformed into a presence/absence matrix. In the resulting matrix, the following equation was applied: $FO = \frac{px100}{P}$, where p is the number of samples in which the species was recorded, and P is the total number of samples collected. The following ranges were considered for the FO (Matteucci and Colma 1982): very frequent (FO ≥ 70%), frequent (40%

≤ FO < 70%), infrequent (10% ≤ FO < 40%), and sporadic (FO < 10%).

Statistical analysis

To evaluate whether the meteorological conditions (precipitation and temperature) were significantly associated with *C. furcoides* throughout the sampling period, multiple regression was performed. Analysis of variance (ANOVA) was carried out to analyze the meteorological variation within and among the HRs and years, to fully verify whether the meteorological variables presented statistically significant differences on temporal and spatial scales. To explore the possible relationships between HRs and their specific meteorological conditions, breakdown and one-way ANOVAs were carried out. A t test was conducted to assess whether the meteorological variables between HRs were significantly different in each sampled year. The multiple regression analysis was performed in the R environment, version 4.3.1 (R Core Team 2023); all the other analyses were performed in STATISTICA® software version 7.1.

Results

In general, the temperature followed a subtropical pattern, with spring and summer as the warmest seasons (Fig. 2). The years 2012 and 2014 presented the highest temperatures (for both maxima and averages), while the lowest occurred in 2012 (minima) and 2013 (averages), which indicated a large fluctuation in this climatic variable (Fig. 2; Supplementary Material 1) exactly during the introduction and expansion of the invasive species in Rio Grande do Sul.

For the precipitation, the maxima and the highest averages were found mostly in spring, especially in 2015, when the effects of El Niño were quite intense in the region, whereas fall exhibited the lowest averages, particularly in 2012 (Fig. 3; Supplementary Material 1).

ANOVA results revealed significant differences among the three HRs for temperature ($F = 3.39$; $p < 0.001$) and precipitation ($F = 2.29$; $p = 0.01$). The breakdown ANOVA showed that, for temperature, HR Uruguay was significantly different from the other two HRs ($F = 2.3$; $p < 0.03$), whereas for precipitation there were dissimilarities among all HRs (Uruguay $F = 7.19$; $p < 0.001$; Guaíba $F = 11.77$; $p < 0.001$; Littoral $F = 3.38$; $p = 0.004$).

Temporal differences for the meteorological variables were evidenced by t tests (Table 1). The temperature differed significantly in the HRs in all eight sampled years ($p \leq 0.001$), while significant differences in precipitation were observed only in 2012 and 2015, the years of the *C. furcoides* invasion and blooms, respectively.

Fig. 2 Mean temperature (°C) of INMET meteorological stations by year (from 2012 to 2019)

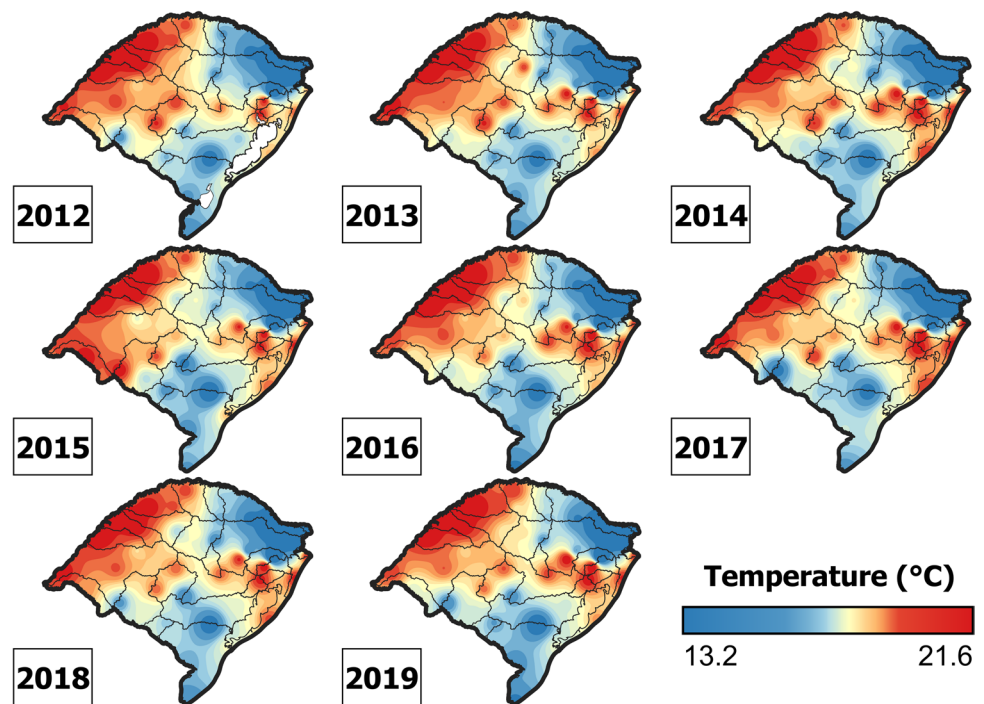
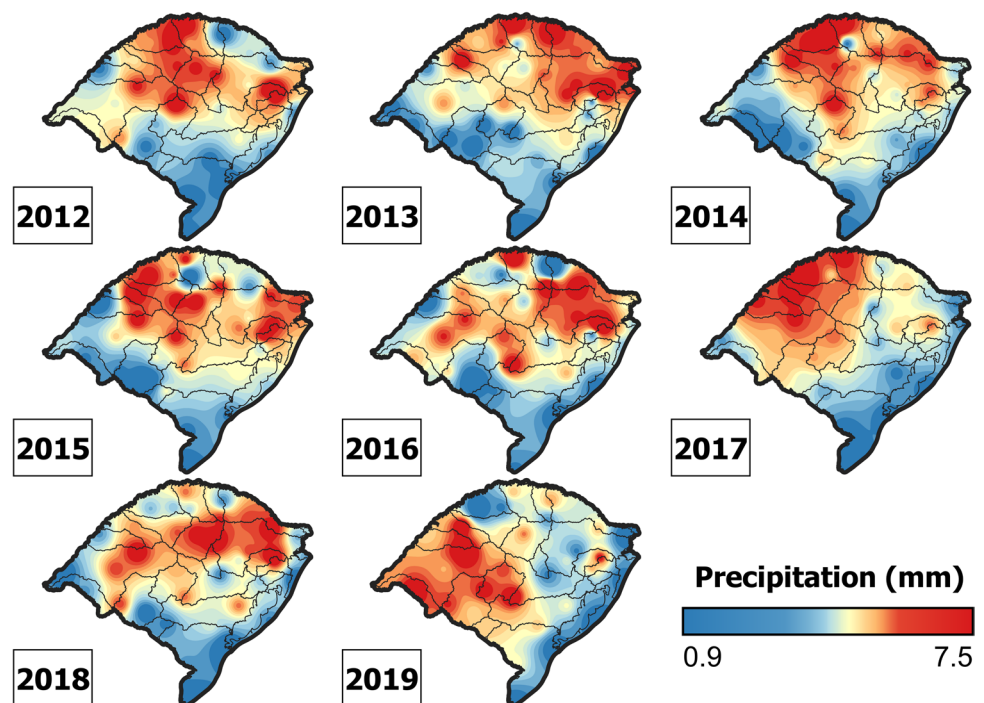


Fig. 3 Mean precipitation (mm) of INMET meteorological stations by year (from 2012 to 2019)



From 2012 to 2019, a total of 127 municipalities (84.1%) recorded the presence of *C. furcoides* (99 quantitatively and 28 only qualitatively) in the three Rio Grande do Sul hydrographic regions. The *C. furcoides* occurrence frequency analysis showed that the species was very frequent in only six municipalities (Bento Gonçalves, Aceguá, Farroupilha, Santa Maria, São Marcos, and Santa Cruz do Sul) (Fig. 4).

It was frequent in 14 municipalities and infrequent in 43. The other municipalities with a record of *C. furcoides* (36 municipalities) were considered sporadic (Fig. 4). Thus, in 20 municipalities we can consider the species as having been established, at least until the spring of 2019.

Multiple regression showed relationships among precipitation and temperature significantly associated with

Table 1 Results of *t* tests for temperature (TP) and precipitation (PR) for each sampled year (2012–2019)

Variable	Year	df	<i>t</i> value	<i>p</i>
TP	2012	74	64.13	<0.001
	2013	74	60.32	<0.001
	2014	74	64.21	<0.001
	2015	74	63.57	<0.001
	2016	74	63.30	0.001
	2017	74	65.35	<0.001
	2018	74	62.52	<0.001
	2019	74	64.93	<0.001
	PR	2012	74	12.34
2013		74	14.53	0.732
2014		74	16.56	0.115
2015		74	12.89	<0.001
2016		74	14.96	0.317
2017		74	15.52	0.099
2018		74	13.07	0.494
2019		74	14.31	0.787

the occurrence of *C. furcoides* in the municipalities with higher frequency: very frequent ($r^2 = 0.016$; $F = 6.85$; $p = 0.001$) and frequent ($r^2 = 0.015$; $F = 4.36$; $p = 0.013$). For those considered infrequent or sporadic, these meteorological variables were not significantly related to the species ($p > 0.05$).

The Guaíba HR showed the highest density of *C. furcoides* (10,912 cells mL⁻¹) in Bento Gonçalves (summer of 2015), while the highest averages were found in HR Littoral (202.79 cells mL⁻¹) (Fig. 5). In temporal scales, 2014 and 2015 presented the highest-density peaks, with the greatest density for the species usually occurring in the summer (Fig. 5).

Ceratium furcoides was first recorded in Rio Grande do Sul in January 2012, in Ácegua, located in HR Littoral, followed by another nine new records during the same year across all three hydrographic regions (Fig. 6). The highest number of new occurrences was found in 2013 (26 municipalities), predominantly in spring (10), followed by 2014 (22) and 2015 (19) (Fig. 6). *Ceratium furcoides* was recorded 22 more times in the remaining sampled years (2016–2019). This means that the expansion still continued, even if more slowly and less aggressively than during its introduction.

The cumulative area invaded by *C. furcoides* gradually increased over the sampled years, starting at 154,261 km² in the first year of its expansion (2012), which represents more than 50% of the state (281,707 km² in total), and peaking in 2018 with an area of 266,625 km², corresponding to about 94% of RS (Fig. 7). The highest rate of expansion occurred in 2012 (3142.087 km year⁻¹), followed by 2013 (408,659 km year⁻¹) and 2014 (185,210 km year⁻¹) (Fig. 7).

This shows the expansive behavior of *C. furcoides* during the introduction as it sought ideal locations to establish itself.

The non-cumulative invaded area showed that *C. furcoides* steadily spread over RS from 2012 to 2015, usually increasing every other season. From 2016 onward, the species did not expand its range, remaining stable throughout the remaining sample period (except for the winter 2018) (Fig. 8). On an annual scale, by 2016, *C. furcoides* had already found the ideal environments for its establishment, and its expansion slowed.

Considering the distance between centroids from the MCPs, the longest distance covered by *C. furcoides* was 40.4 km, in the first year of invasion (from 2012 to 2013) (Fig. 9), confirming its aggressive behavior during its introduction and initial expansion. The species' expansion direction varied significantly over the studied years (Fig. 9), heading east-southeast in 2013 and 2016, east-northeast in 2014, north-northwest in 2015, west in 2017, and west-southwest in 2018. In 2019, *C. furcoides* did not expand (Fig. 7), as the species area peaked in 2018 (Fig. 8). Initially, the direction indicated a rapid advance toward HR Guaíba and Littoral (between 2012 and 2014), followed by a steady period (2015–2016), and subsequently by progression toward HR Uruguay (2017–2018).

Discussion

The arrival of *Ceratium* species in South American aquatic systems is a fairly recent event. *Ceratium hirundinella* was first reported for the continent, colonizing Argentine and Chilean water bodies in a northward direction starting in the 1990s (Boltovskoy 1991; Boltovskoy et al. 2003, 2013; Guerrero and Echenique 1997; Soto and Lembeye 1999; Mac Donagh et al. 2005; Silverio et al. 2009) (Fig. 10). Establishment of *C. furcoides* is more recent, first invading areas previously unoccupied and subsequently replacing *C. hirundinella* (Boltovskoy et al. 2013; Salusso and Morana 2014) (Fig. 10).

Several processes provoke natural climatic variability, and one of the most important is the El Niño-Southern Oscillation (Clarke 2008). These episodes are linked to changes in precipitation and temperature, thereby triggering or amplifying drought and flooding (Cai et al. 2020). Events like these are changing not only in frequency, but also in magnitude, timing, and duration (Easterling et al. 2000; Diez et al. 2012), and a widespread expectation is that these shifts favor an increase in the number of biological invasions (Dukes and Mooney 1999; Walther et al. 2009). The phytoplankton community is affected by climate variability, responding differently depending on the phase of the El Niño-Southern Oscillation, as a shift in productivity is associated with both phases (Rousseaux and Gregg 2012),

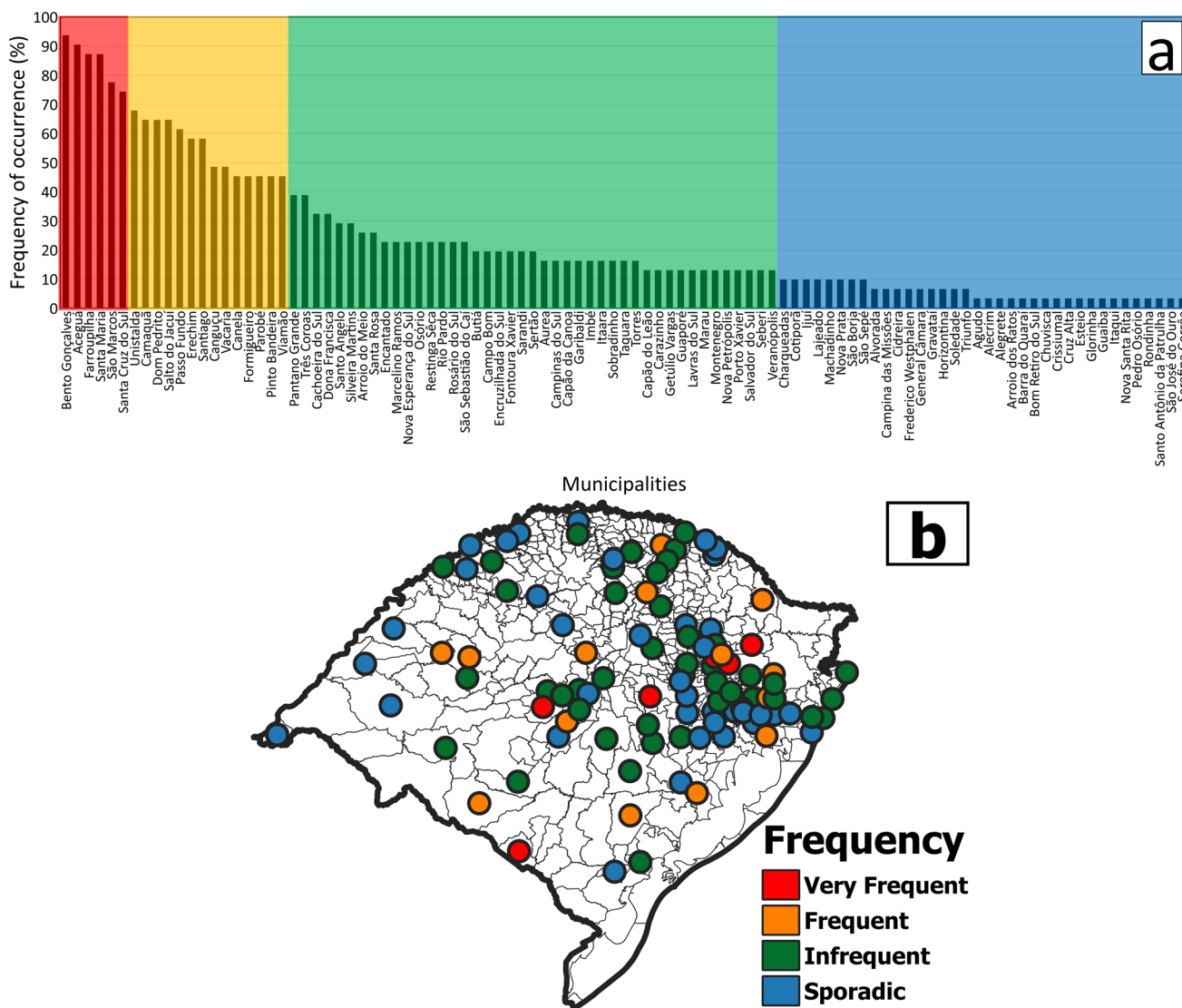


Fig. 4 Frequency of *C. furcoides* occurrence (FO) in municipalities of Rio Grande do Sul state, southern Brazil. Very frequent (FO ≥ 70%), frequent (40% ≤ FO < 70%), infrequent (10% ≤ FO < 40%), and sporadic (FO < 10%). **a** Municipalities with quantitative record of *C. furcoides*; **b** spatial distribution of the municipalities with quantitative record of *C. furcoides*

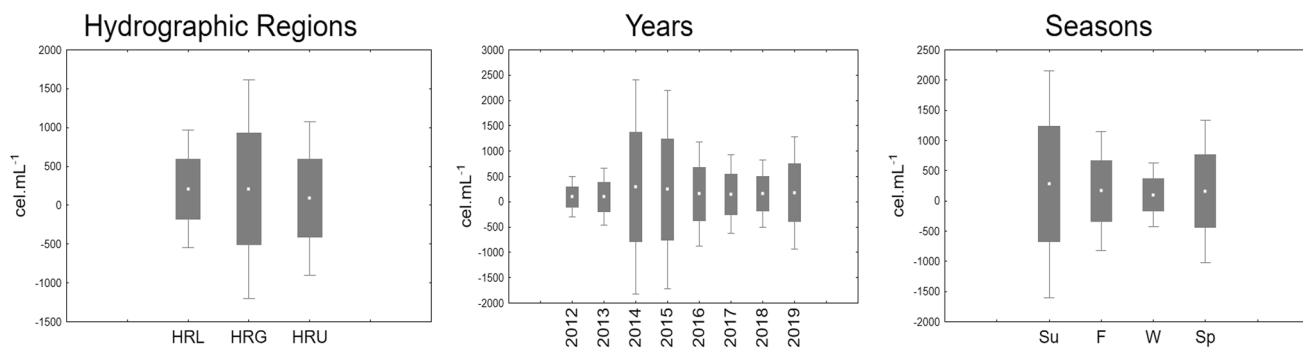


Fig. 5 Density values (cells mL⁻¹) of *C. furcoides* in spatial (hydrographic regions) and temporal scales (years and seasons). *HR* hydrographic regions, *U* Uruguay, *L* Littoral, *G* Guaíba, *Su* Summer, *F* Fall, *W* Winter, *Sp* Spring

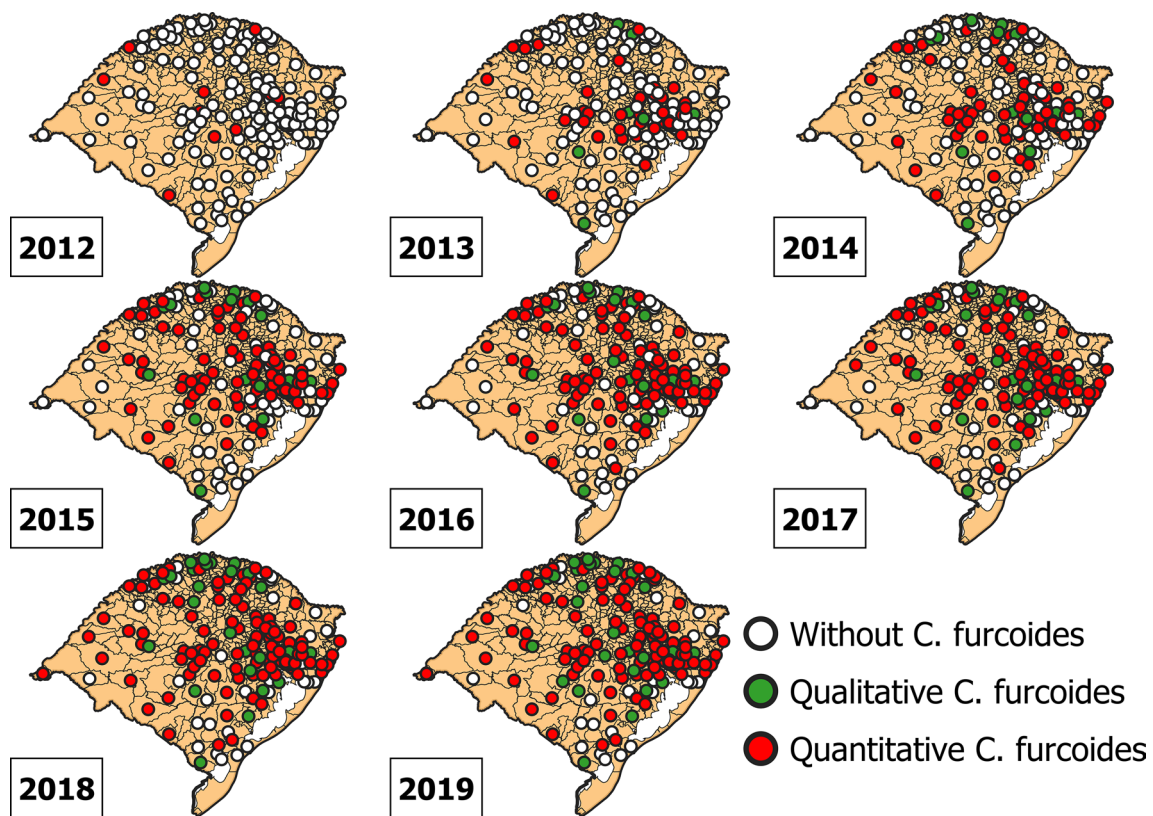


Fig. 6 Cumulative distribution of *C. furcoides*, during the eight monitored years, in municipalities of Rio Grande do Sul state, southern Brazil

related to changes in the supply of nutrients necessary for phytoplankton photosynthesis (Masotti et al. 2011). Studies in the subtropical region revealed that the El Niño-Southern Oscillation led to different limnological conditions and variation in phytoplankton biomass compared with more typical years (Wieliczko et al. 2021). The authors found that higher chlorophyll *a* concentrations were recorded during La Niña events, while El Niño was related to higher values of dissolved oxygen, nitrogen, and phosphorus. These events clearly showed that, when compared with typical years, the El Niño-Southern Oscillation increased the availability of resources relevant to opportunistic invasive species.

In South America, global warming looks to benefit the establishment of invasive *Ceratium* species. Both *C. hirundinella* and *C. furcoides* often take advantage of increased precipitation rates (Rodríguez et al. 2005; Cavalcante et al. 2016) and warm water temperature (between 15 and 26 °C) (Mac Donagh et al. 2005; Rodríguez et al. 2005; Crossetti et al. 2019) to grow their populations by increasing their metabolism (Cavalcante et al. 2016). Furthermore, disturbances in the steady state of the phytoplankton caused by droughts (an increase in mortality of native biota) provide a window of opportunity for these species (Crossetti et al. 2019). In short, the changing climate can relax factors that prevent these species from becoming dominant and limit

their range, with negative impacts on native biota (Rehage and Blanchard 2016).

South America is susceptible to invasion by *C. furcoides*, and the species is still expanding (Meichtry-de-Zaburlin et al. 2016; Accattatis et al. 2020), as our records proved for Rio Grande do Sul, Brazil. *Ceratium furcoides* was first observed in RS by Cavalcante et al. (2013) in Aceguá in 2012, and considering that this is the database that started this study, we can confirm that the species became established in the state, as it was found throughout the sample period (2012–2019). The areas suitable for *C. furcoides* are mainly located in the subtropical regions of South America (Meichtry-de-Zaburlin et al. 2016), which corroborates our results. Since its introduction in Rio Grande do Sul, *C. furcoides* has not only been recorded but also established with high densities in reservoirs (Cavalcante et al. 2016; Rojas-Castillo et al. 2023) and shallow lakes (Silva et al. 2019). In addition to the high density of *C. furcoides* in Brazilian environments, a large number of occurrences have been noted as well (especially in RS) (Supplementary Material 3), contrasting with *C. hirundinella*, which seems to have a preference for Argentine environments (Fig. 10).

Ceratium furcoides' invasion into southern Brazil was most probably driven by the highly variable meteorological conditions present in the year of its invasion, 2012, when a

Fig. 7 Cumulative invaded area (km²; **a**) and rate of range expansion (km year⁻¹; **b**) of *C. furcoides* during the years monitored (from 2012 to 2019) in municipalities of Rio Grande do Sul state, southern Brazil

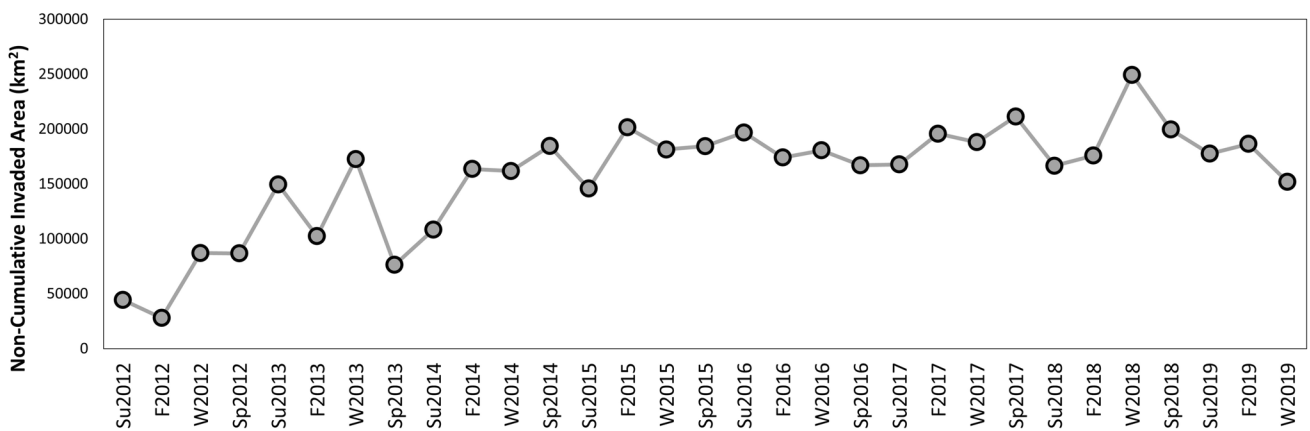
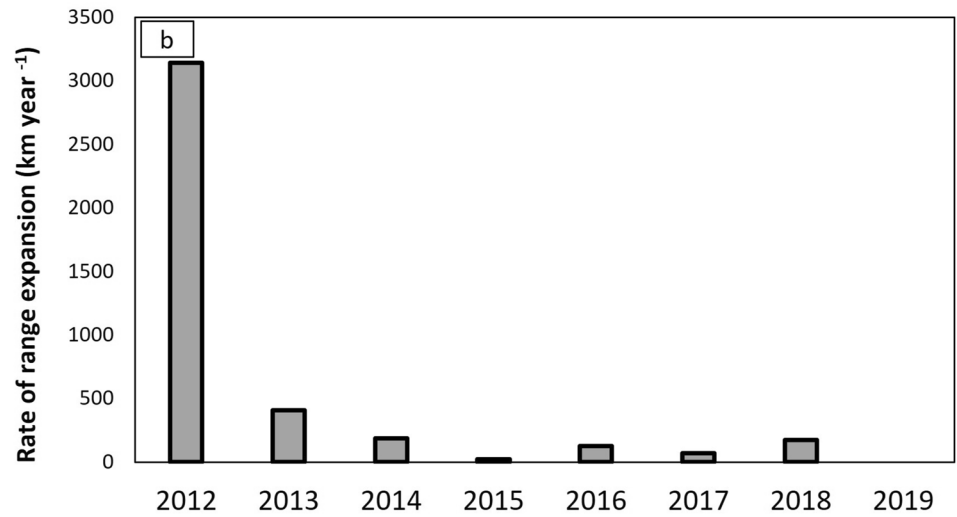
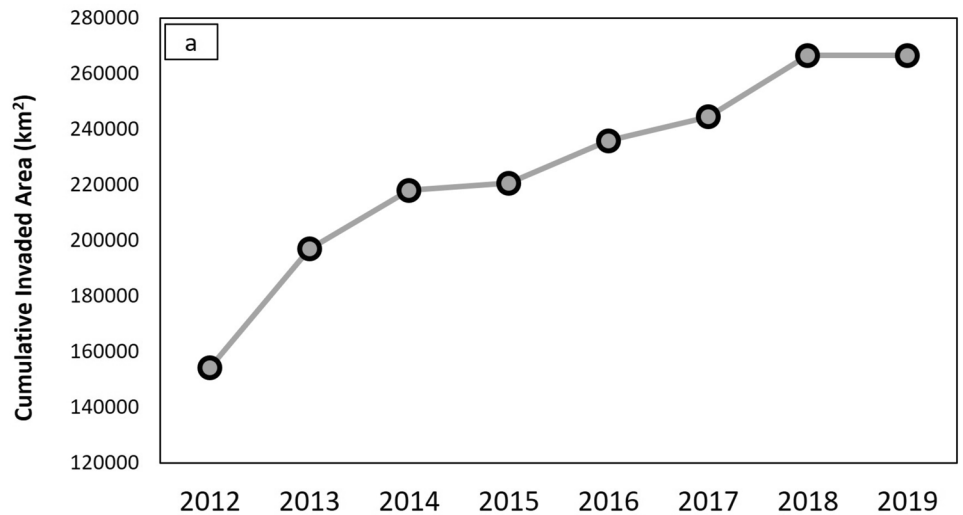


Fig. 8 Non-cumulative invaded area (km²) of *C. furcoides* on a seasonal scale (*Su* summer, *F* fall, *W* winter, *Sp* spring) in municipalities of Rio Grande do Sul state, southern Brazil, from 2012 to 2019

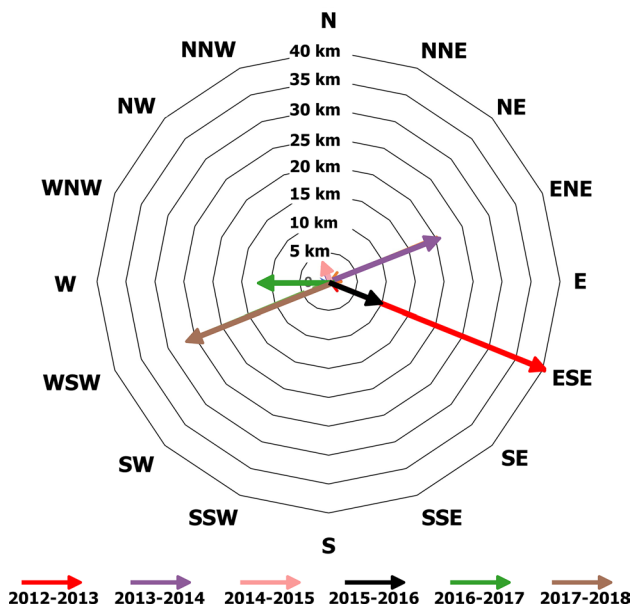


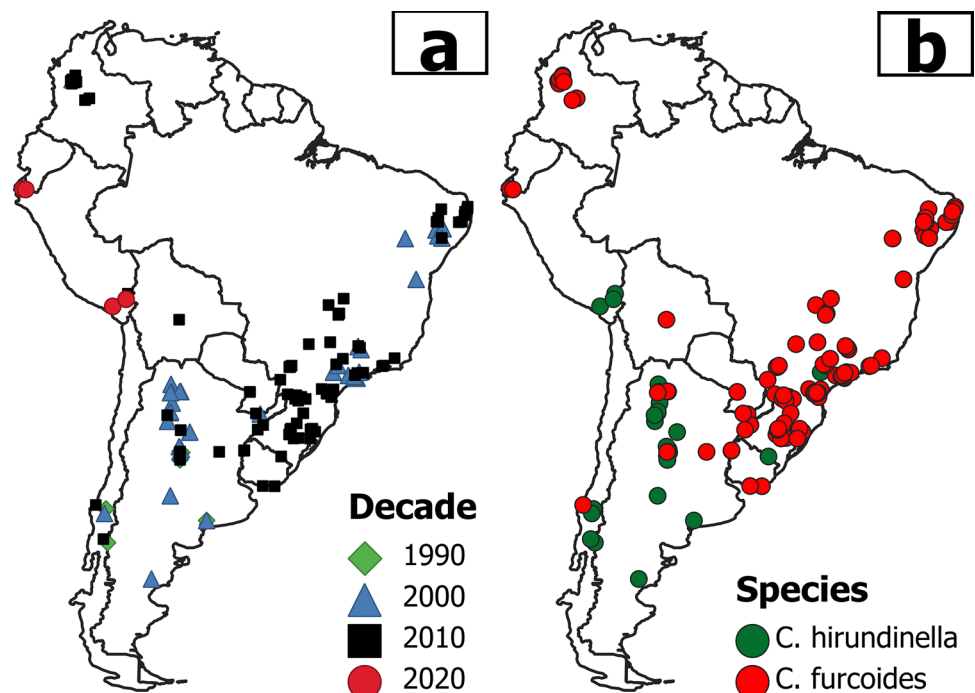
Fig. 9 Distance (km) and direction of *C. furcoides* expansion between consecutive years in municipalities of Rio Grande do Sul state, southern Brazil. N north, S south, E east, W west, NE northeast, SE southeast, NW northwest, SW southwest, NNE north-northeast, ENE east-northeast, ESE east-southeast, SSE south-southeast, SSW south-southwest, WSW west-southwest, WNW west-northwest, and NNW north-northwest

large fluctuation in temperature and relative drought existed. The bloom and fast expansion might indicate that *C. furcoides* was already present in the state before this study,

but not registered in water samples. Instead, it could have colonized from cysts already in the sediment (Bustamante-Gil et al. 2012), potentially facilitated by the aforementioned meteorological changes, as these factors may stress native species and alter the interactions between their groups, thus allowing non-native species to establish themselves and spread into regions where they had been absent (Strayer 2010; Engel et al. 2011). Climate shifts such as drought (Crossetti et al. 2019) and extreme wind (Pacheco et al. 2021) have been reported as possible causes of *C. furcoides* invasion in South America.

As mentioned, the species displayed aggressive invasive behavior, quickly covering a large area early on in its expansion, as well as reaching relatively high density. Similar results were found in Paraíba (Brazil), where the highest rate of expansion for the species occurred in the second sampled year (Severiano et al. 2021), but without density data for comparison. Additionally, Rojas-Castillo et al. (2023) reported a *C. furcoides* bloom (15,865 ind. mL⁻¹) immediately after a new reservoir filling in Caxias do Sul (Rio Grande do Sul, Brazil), the highest peak in South America. *Ceratium* species are effective under limiting conditions, competing for nutrients using vertical migration over long distances to microenvironments with greater availability of resources, such as light and nutrients, using mixotrophy when necessary (Reynolds 2006; Reynolds et al. 2002). Additionally, the genus is resistant to herbivores due to its horns and spines (Van Ginkel et al. 2001), which allow it to compete extremely well against native phytoplankton, except other dinoflagellates (SenckenbergDZMB 2018). Although

Fig. 10 *Ceratium furcoides* and *Ceratium hirundinella* records in South American aquatic systems, by decade (a) and by species (b)



it has reached a large part of the state, the dispersion pattern initially exhibited was that of “jump dispersal,” where the species expands its occurrence area irregularly, through jumps over long geographical distances (Wilson et al. 2009). The following years (2013 onward) showed that *C. furcoides* tended to spread through “concentric rings,” where the invasive species colonized from geographically close basin to basin (Wilson et al. 2009; Moreira et al. 2015; Silva et al. 2018; Pacheco et al. 2021). Wind, animals, and humans can also be highly effective dispersal mechanisms and help the expansion of the dinoflagellate, as its propagules persist in the water (Padišák et al. 2016).

The direction of expansion suggests that *C. furcoides* was initially heading toward the Guaíba and Littoral Hydrographic Regions (from 2012 to 2014). We believe that this may be a direct consequence of the regions’ environmental problems, as they provide almost ideal conditions for the proliferation of the dinoflagellate due to eutrophication of water bodies through domestic and industrial sewage as well as erosion and silting (BRASIL 2006). The growth of phytoplankton species is the primary biological response to nutrient enrichment in aquatic environments, arising from industrialization, agricultural modernization, and urbanization (Devlin et al. 2011; BoQiang et al. 2013). The notion that the dinoflagellate was looking for an ideal environment to establish itself and form blooms is further evidenced by the fact that the highest density of *C. furcoides* (2014 and 2015) coincided with a decrease in the distance covered by the species (from 2015 to 2017). Many studies associate *C. furcoides* with eutrophication (Meichtry-de-Zaburlin et al. 2014; Almanza et al. 2016; Pacheco et al. 2021). Migratory birds could also provide a mechanism to disperse *C. furcoides* cysts, as the coastal area of the Rio Grande do Sul is well known as a refuge for thousands of migrants (WHSRN 2023). Migratory species of birds can act as long-distance dispersants, as they can overcome major geographical barriers and stop at sites with similar habitat characteristics, which increases the probability of successful establishment of dispersed propagules (Viana et al. 2016). The direction of expansion recorded in 2018 hints that *C. furcoides* was heading west–southwest, toward HR Uruguay. However, it looks like the extreme portion of the region does not have ideal conditions for the establishment of the species, as the dinoflagellate quickly disappeared from most of the municipalities in this extreme area, including Itaqui, Alegrete, and Barra do Quaraí, and the municipality of Quaraí did not register *C. furcoides* at all. The Quaraí and Santa Maria River basins (U60 and U70 hydrographic basins, respectively) suffer from low oxygen availability, as the high population density is associated with low water availability in addition to high demand from rice plantations (BRASIL 2006). This could explain the non-establishment of the species in the area, given that the dinoflagellate has been associated with

well-oxygenated water bodies in Rio Grande do Sul (Cavalcante et al. 2016; Rojas-Castillo et al. 2023). Moreover, these river basins are in an area that exhibited unusually high temperatures throughout the sampling period (usually 1 to 2 °C above the mean temperature for the state), and this could be a thermal barrier to *C. furcoides* establishment. Finally, we believe that proximity to already invaded countries, such as Argentina and Uruguay (Meichtry-de-Zaburlin et al. 2014; Pacheco et al. 2021), could be a gateway for the species into the region, through colonization from cysts in nearby water bodies.

Although *C. furcoides* was recorded in most areas of the state, the frequency analysis showed that the species was frequent or very frequent in only 20 municipalities monitored. Studies in different aquatic ecosystems in South America reveal that its presence could range from a single record (Silva et al. 2018; Macêdo et al. 2021) to a permanent presence (Silva et al. 2012, 2019). Most of the municipalities with quantitative records of *C. furcoides* belong to HR Guaíba (56 out of 99), as do those with higher frequency (11 out of 20), suggesting that this hydrographic region has better conditions for the development of the dinoflagellate. The establishment of species into new environments is dependent on the local characteristics (abiotic conditions and biotic interactions), as these features can act as ecological filters, determining whether the species can survive, reproduce, and persist in the habitat (Incagnone et al. 2015).

Studies in Caxias do Sul (Rojas-Castillo et al. 2023) and Porto Alegre (Silva et al. 2019), in HR Guaíba, revealed two of the highest densities for the species in South America (15,865 ind. mL⁻¹ and 10,170 ind. mL⁻¹ respectively), indicating that this area is extremely suitable for *C. furcoides*.

Likewise, these municipalities with higher frequency were the ones where the species was significantly associated with an increase in temperature and shifts in precipitation patterns. Considering that an increase in intensity and frequency of meteorological changes is expected (Huntington 2010), the dinoflagellate would profit not only in reaching new areas but also in forming blooms more often. In this scenario, subtropical (and possibly tropical) regions would be those with ideal conditions for *C. furcoides* and, accordingly, most vulnerable to its permanent residence. Even though its invasive presence has been recorded in Asia (Wu and Chou 1998; Haochen et al. 2020), Africa (El-Otify et al. 2003) and Oceania (Cassie 1978), subtropical regions of South America reveal the highest number of *C. furcoides* invasions (Silva et al. 2012, 2019; Cavalcante et al. 2016; Rojas-Castillo et al. 2023) (Supplementary Material 3), which suggests that these regions have better conditions for its permanency.

The temperature range for the occurrence of the species also looks to be much wider than expected (between 18 and 22 °C, according to Meichtry-de-Zaburlin et al. 2016), as

C. furcoides was found in environments with temperatures as high as 30.7 °C and as low as 3.7 °C. Recently, Severiano et al. (2022) reported evidence of the species in warm temperatures (around 26–28 °C) in Paraíba (in the tropical zone of Brazil); in an Uruguayan lake, Pacheco et al. (2021) reported a *C. furcoides* occurrence in temperatures ranging from 18 to 28.4 °C; and in Colombia, the species was found in environments with temperatures as high as 25.5 °C (Bustamante-Gil et al. 2021). Studies outside South America have also highlighted a wide range of temperatures, such as in Taiwan, 25 °C (Wu and Chou 1998), Poland, around 20 °C (Stefaniak et al. 2007), Spain, below 15 °C (Sendra et al. 2022), and Italy, between 2 and 8.5 °C (Naselli-Flores 2003).

Furthermore, large densities have occurred in years where high temperatures were associated with high precipitation rates, suggesting that this combination may spark the growth of *C. furcoides*. Cavalcante et al. (2016) associated the occurrence and blooms of the species in reservoirs in Caxias do Sul (RS) with ideal temperature conditions as well as high precipitation rates, which can lead to nutrient suspension in water bodies via the sediment flow from the soil. The authors mentioned that the combination of both can result in a metabolic increase in these organisms, eventually causing blooms.

Conclusions

The spread of *C. furcoides* has accelerated in recent years in South America in general and in Brazilian environments in particular, having been recorded in many states (Matsumura-Tundisi et al. 2010; Crossetti et al. 2019; Severiano et al. 2022), indicating an ongoing expansion process (Meichtry-de-Zaburlin et al. 2016) (Supplementary Material 3). Eutrophication, global warming, and meteorological changes seem to favor *C. furcoides* invasion and dominance (Crossetti et al. 2019; Macêdo et al. 2021; Kruk et al. 2021).

The dinoflagellate benefited from climate shifts, entering the RS region at the end of a La Niña event (the drought in 2011–2012) and forming blooms while the state was affected by expressive amounts of rain caused by the extreme El Niño of 2015 (Silva et al. 2022; NOAA 2023). These events are predicted to increase in intensity and frequency (Huntington 2010), and with a concomitant rise in global temperature, the subtropical regions of the world would be the most vulnerable to *C. furcoides* invasion and establishment.

The Guaíba hydrographic region showed the largest number of municipalities with the occurrence of the species as well as the highest densities, making this an area of interest for water management bodies, as *C. furcoides* blooms can have a variety of impacts including a significant increase in pH (Almeida et al. 2016), death of animals (Pitcher et al.

2011), and oxygen depletion (Matsumura-Tundisi et al. 2010). As the municipalities' reservoirs supply water to human populations, mitigating actions against the species should be implemented. As *Ceratium* is relatively large and not toxic, physical treatment is quite efficient at removing it, as demonstrated by Almeida et al. (2016), but some chemical treatment is necessary to eliminate the taste and odor. However, for CORSAN, a water treatment company, it would be a small problem relative to toxic cyanobacteria, where the protocols of the potability ordinance are more restrictive. Another plan of action should be to implement monitoring on an international scale, at the Mercosur level, since this species arrived in our state, most probably, via neighboring countries.

After the bloom events, *C. furcoides* densities decreased considerably, with the persistence tending to be low in most invaded municipalities. Based on this, a more stable state of the phytoplankton community appears to have been reached; however, further studies integrating the native community are needed to clarify planktonic interactions in the aquatic systems of RS. This need for research (*Ceratium* versus native biota) on this topic was highlighted by Silva et al. (2019): the authors found that the presence of *C. furcoides* in an urban and shallow lake was beneficial to the community, bringing more diversity in sites previously dominated by cyanobacteria. This contrasts with most studies in that regard, which emphasize the harmful conditions brought by the species (Matsumura-Tundisi et al. 2010; Pacheco et al. 2021).

The distribution map of *Ceratium* species in South America showed that *C. hirundinella* have a preference for Argentine environments, while *C. furcoides* prefers Brazilian ones. This difference in their distribution and environmental preference indicates the need for more studies incorporating both species in order to understand the causes of these patterns. Both species invaded the RS via Aceguá (Cavalcante et al. 2013), but only *C. furcoides* was dispersed and established, which makes us question these patterns even more.

Lastly, although we showed that *C. furcoides* blooms were both highly abundant and dispersed, our results could well be an underestimation, since CORSAN monitoring frequency is determined by Cyanobacteria densities, because it is more important given its association with health concerns (production of toxins) (Komárek et al. 2002). To fully understand the species autecology, detailed and prolonged studies focusing on *C. furcoides* are needed to achieve a robust plan of action against the dinoflagellate.

Given the rapid expansion and impacts of *C. furcoides* in South America, monitoring and long-term studies are key to really understanding the effects of the species' invasion into these environments. Considering its dispersion in the state (occupying more than 94%) and its ability to form the largest blooms in the South American region (greater than 10,000

cells mL⁻¹; Silva et al. 2019; Rojas-Castillo et al. 2023; and the present study), we believe that the Rio Grande do Sul could become *C. furcoides*' second home.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-024-01042-5>.

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Author contributions RDS: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing—Original draft, Writing—Review & editing, Visualization; LMR: Methodology, Resources, Data curation; LSC: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing—Review & editing, Funding acquisition, Project administration, Supervision.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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CHAPTER II

***Ceratium furcoides* and *Microcystis* spp. segregation patterns are ruled by nutrient availability and meteorological shifts in a Subtropical Region**

***Ceratium furcoides* and *Microcystis* spp. segregation patterns are ruled by nutrient availability and meteorological shifts in a Subtropical Region**

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Abstract

Ceratium furcoides is a dinoflagellate that exhibits invasive behavior in aquatic ecosystems of South America and its presence alters local phytoplankton communities. Along with *Microcystis*, they may coexist, constituting a functional assemblage in temperate regions. However, their interaction in subtropics is still unclear. In this study, 151 municipalities were monitored in southern Brazil between 2012 and 2022, aiming to understand whether both species co-occur, and given the co-occurrence, how it happens, as well as investigate which variables drive the observed patterns. The results indicated that both present similar spatial preferences, occurring and blooming in the same hydrographic regions. Distribution models showed that they responded similarly to the same predictors, the most important being temperature (seasonality, annual range and mean diurnal range), in addition to flow accumulation. Despite this, co-occurrence analysis showed high segregation in all scales, driven by shifts in precipitation and temperature provided by El Niño and La Niña, associated with nutritional increase. In subtropical scenario, *C. furcoides* was dominant, in terms of frequency and abundance, organic matter being key for its development and dominance; in opposition, *Microcystis* was sensitive to disturbances, with sporadic blooms supported by nitrite and nitrate.

Keywords: Biological invasion, co-occurrence, competition, El Niño, La Niña, cyanobacteria

Introduction

Freshwater communities are shaped not only by abiotic factors, but also by biotic interactions among organisms, fluctuating across environmental gradients (De Bernardi, 1981; Thompson, 1988). These interactions can alter populations' fitness, growth, and properties, being highly dependent on the context in which they occur (Chamberlain et al., 2014), challenging the understanding of how multiple interactions affect the community (Tylianakis et al., 2008).

The Competitive Exclusion Principle (Tilman, 1977, 1980, 1981) is one of the best-known examples of interactions among phytoplankton species, in which the superior competitor would be more efficient at capturing the shared resource, being able to sustain a viable population at minimum resource level and,

eventually, competitively exclude other species. According to Böhn et al. (2008), the competition is supported if shows: niche shifts; density reduction or extinction; reduced growth of organisms; reduced nutritional intake; altered community composition and altered size structure of prey populations.

Another fundamental question is raised by the Paradox of the Plankton (Hutchinson, 1961), which questions how the coexistence of several species is possible if only a handful of limiting resources are available. This could be explained by mechanisms other than the competitive exclusion, and can involve temporal heterogeneity, by environmental shifts due to seasonal changes (Hutchinson, 1961; Levins, 1979; Bracco et al., 2000); spatial heterogeneity, by altered resource supply (Tilman, 1980); spatial competition, as organism affects mostly its local neighborhood, generating opportunities for novel ecological strategies and multispecies coexistence (Klausmeier & Tilman, 2002) and chaotic fluctuations in abundances induced by competition, as it was shown that species invasion, replacement and dominance patterns rarely repeat themselves (Huisman & Weissing, 1999).

Phytoplankton abundance and the community structure are directly impacted by how species fare in relation to selective pressures and, to avoid potential losses, they developed several mechanisms (Reynolds, 1984). Some groups tend to have significantly higher maximum uptake rates of nutrients (Litchman et al., 2006), others have developed the ability to migrate vertically, enabling access to areas with more resources (Kruk et al., 2021), some form cysts, guaranteeing their survival for long periods in the sediment (Cavalcante et al., 2013). Therefore, when associated with environmental variables, these abilities ensured by different functional traits may provide basis for diverse ecological strategies of phytoplankton groups and could explain global patterns of their distribution (Litchman et al., 2007).

Biological invasions can be defined as the introduction of species beyond their natural dispersal potential and outside their natural range (Olenin et al., 2010), exerting substantial negative impact on native biota, economic values, and/or human health (Lodge et al., 2006). The invasion process can be divided into a series of stages, in which there are barriers that need to be overcome for a species to pass on to the next stage (Blackburn et al., 2011; Lodge et al., 2006), making biological invasions a complex subject. Firstly, invasive species need to disperse and survive until reaching a location outside the geographic area where they previously occurred. Most of the species will go extinct in this new location, but some will establish a self-sustaining population, which will remain localized and undetected. A proportion of established populations will then spread steadily and widely, eventually becoming abundant at many locations. Due to their abundance, ecological changes will be detectable and felt, and finally, the species would be considered invasive.

Several factors influence biological invasions: number of propagules, as the larger the population, the greater the chance of thriving, making it possible for some to survive long enough for immigration to secure a permanent presence (Fenchel & Finlay, 2004); the characteristics of the species, as the invasive ones tend to be great competitors, having broad ecological requirements and tolerances, therefore becoming dominant rapidly (Mooney & Cleland, 2001; Lee, 2002; Didham et al., 2005); the susceptibility of the environment to invasion, as they often include geographical and historical isolation, lower diversity of native species and high levels of disturbances (Elton, 1958).

Many studies have reported that invading species are particularly successful in disturbed habitats, especially those affected by extreme weather events, as there are changes in stratification patterns, nutrient

concentrations, and light availability (Kasprzak et al., 2017; Crossetti et al., 2019; Salmaso & Tolotti, 2021; Silva et al., 2024). One such event is the El Niño–Southern Oscillation cycle (ENSO), that are coupled to ocean circulation and may influence the climate of tropical and subtropical zones, by unusual precipitation fluctuations, leading to heavy rainy phase (El Niño) or droughts phases (La Niña) in the south hemisphere (Clarke, 2008; Trenberth et al., 2007). Hellmann et al. (2008) summarized that these extreme events could have key consequences in invasion processes, by: altered mechanisms of transport and introduction, where mediated transport would enhance the survivorship of propagules; altered climatic constraints, showing that non-native species would be able to colonize if conditions become more unlike the native species' range; altered distribution of existing invasive species, as these species spread range would likely follow its temperature and hydrological constraints, selecting features in response to climate; altered impact of existing invasive species, given that the population densities of some invasive species would be reflected on native species; and altered effectiveness of management strategies for invasive species, as tolerance and effectiveness of biocontrol's would be affected. In resume, in areas where individuals are extinct by disturbances, an increase in environmental invasiveness is expected (Davis et al. 2000) and is supported by reports that have linked extreme events to invasive species occurrence, such as events related to winds (Pacheco et al., 2021), droughts (Crossetti et al., 2019; Queiroz et al., 2022) and floods (Mihaljević et al., 2010; Silva et al., 2024).

Among the known invading microorganisms in South America, the species of the genus *Ceratium* (Dinophyta) are in the forefront in terms of expansion. *Ceratium hirundinella* (O.F. Muller) Dujardin was first reported for the continent, colonizing Argentine and Chilean water bodies (Thomasson, 1963; Boltovskoy et al., 1991, 2003, 2013; Guerrero & Echenique, 1997; Soto & Lembeye, 1999; Mac Donagh et al., 2005; Silverio et al., 2009). *Ceratium furcoides* (Levander) Langhans establishment is more recent, first invading areas previously unoccupied and subsequently replacing *C. hirundinella* (Boltovskoy et al., 2013; Salusso & Morana, 2014).

In the South American continent, *C. furcoides* is the one that received more attention recently, due to its rapid dispersion and establishment with extremely high bloom formations (Silva et al., 2019; Rojas-Castillo et al., 2023; Silva et al., 2024). Many countries have been reported its invasive presence in the region, such as Chile (Almanza et al., 2016), Colombia (Bustamante-Gil et al., 2012, 2022), Argentina (Boltovskoy et al., 2013; Meichtry-de-Zaburlín et al., 2014; Bordet et al., 2017), Paraguay (Meichtry-de-Zaburlín et al., 2014) and Uruguay (Pacheco et al., 2021). Most notably, Brazilian environments have recorded the species the most, in many different aquatic ecosystems, such as lakes (Jati et al., 2014; Moreira et al., 2015, Campanelli et al., 2017; Silva et al., 2019), hydroelectric reservoirs (Santos-Wisniewski et al., 2007; Silva et al., 2012; Cassol et al., 2014; Cavalcante et al., 2017), urban reservoirs (Crossetti et al., 2019) and water-supply reservoirs (Matsumura-Tundisi et al., 2010; Nishimura et al., 2015; Cavalcante et al., 2016; Rojas-Castillo et al., 2023; Silva et al., 2024). The species can form blooms that are potentially harmful to the environment, leading to a significant pH increase, oxygen depletion, filter saturation in water treatment plants, changes in water color and odor, and the death of animals (Taylor et al. 1995; Matsumura-Tundisi et al. 2010; Almeida et al. 2016; Morales 2016; Pacheco et al. 2021).

Blooms of *Microcystis* spp. have been registered worldwide (Carmichael, 1986; Codd & Beattie, 1991), and is one of the most frequently found genera among the planktonic communities in South America (De

León & Yunes 2001; Pérez et al., 2013; González-Piana et al., 2017; O'Farrell et al., 2019). According to Paerl (1988), they have undifferentiated dormant cells, being able to survive for several years, waiting for more favorable periods to its development and reproduction, making monitoring difficult. Many *Microcystis* spp. strains can produce microcystin, a potent hepatotoxin, which is associated with many environmental problems, such as death of animals (Carmichael, 1986; Codd & Beattie, 1991), in addition to odours and off-flavour compounds (Falconer, 2005). Thus, persistent blooms pose a risk to those who use impaired water resources for drinking water supplies, recreational activities, and fisheries (Harke et al., 2016).

Together with *Microcystis*, *Ceratium* species comprise Reynolds et al. (2002) **LM** functional group, consisting of species that often co-occur in the summer epilimnia of eutrophic temperate lakes, being sensitive mostly to mixing, stratification and light. They are S-strategists, dealing extremely well in stressful situations, being able to migrate through large distances to avoid light constraints or to access the more nutrient-rich deep-water layers and, in *Ceratium*'s case, use mixotrophy as nutrient alternative sources (Reynolds, 2006; Cavalcante et al., 2016).

This assemblage usually contributes to phytoplankton steady-states in temperate climate (Naselli-Flores & Barone, 2003), however, the interactions between both microorganisms is not fully understood in ecosystems where *Ceratium* species are considered invasive. Crossetti et al. (2019) have shown that no co-occurrence between *C. furcoides* and *Microcystis* spp. happened, suggesting that the environmental conditions were more important to their niche segregation, in a tropical shallow eutrophic reservoir in southeast Brazil. The study performed by Silva et al. (2019), demonstrated that *C. furcoides* invasion contributed to a more diverse phytoplankton community in subtropical, shallow lake (southern Brazil), in sites previously dominated by *Microcystis* spp. So, even though studies exploring *C. furcoides* invasions in Brazilian environments are growing, the species effects upon local communities, especially those composed by cyanobacteria, are still unclear.

As *C. furcoides* presents invasive behavior in the aquatic ecosystems of southern Brazil and its presence may influence the structure and dynamics of the phytoplankton community, understanding its interactions with other species is of utmost importance. Then, a long-term monitoring dataset (11 years) of drinking water supply systems from 151 municipalities was used, aiming to contribute to the understanding of the relationship between *C. furcoides* and *Microcystis* spp. in subtropical environments, being driven by the following questions: (I) do *C. furcoides* and *Microcystis* spp. co-occur in the environments studied?; (II) if so, how does this co-occurrence occur?; and (III) what environmental variables are related to the observed distribution patterns?

Materials and methods

Study sites

Rio Grande do Sul (RS) is Brazil's southernmost state (Fig. 1). It has an area of 281,707.15 km² with 497 municipalities in total, and a population of 11,422,973 inhabitants, representing about 6% of Brazil's population (Rio Grande do Sul, 2023). There are three hydrographic regions (HR) in the state: HR Uruguay, which is located in the national basin of Uruguay, HR Guaíba and HR Littoral, which are located in the HR South Atlantic (Agência Nacional de Águas - ANA, 2015) (Figure 1). The HRs are divided into

hydrographic basins (HB; SEMA, 2018) and are identified by the initial letter of the HR to which they belong (Fig. 1). A complete characterization of the HRs can be found in Silva et al. (2024).

According to the Köppen system, the state climate is classified as Cfa and Cfb, operating as a temperate climate region where the temperature of the coldest month varies between -3 and 18°C (Kottek et al., 2006). The rainfall is evenly distributed over the year, with the accumulation ranging from 1000 mm to more than 2000 mm (Kottek et al., 2006; Rio Grande do Sul, 2023).

Meteorological Data

During the eleven sampled years (2012 to 2022), climatic data (temperature and precipitation) were obtained through the historical series of INMET (Instituto Nacional de Meteorologia), from automated stations throughout Rio Grande do Sul state (<https://portal.inmet.gov.br/>). This series provides 24 readings/day of these data (hourly measurement), and for this approach, daily temperature averages and accumulated precipitation were used (**Supplementary Material 1 and 2**).

During the sampling period, the region endured a series of climate induced phenomena. In the end of 2011 and beginning of 2012, the south region of Brazil experienced a prolonged drought prompted by extreme La Niña event, with more than 300 municipalities declaring a state of emergency, having great impact in the agriculture and socioeconomic (Anderson et al., 2015, 2016; Rio Grande do Sul, 2021). This event also recurred in mid-late 2020, going through 2021, where the hydrological regime was 70% bellow of its long-term averages (Operador Nacional do Sistema Elétrico - ONS, 2024). In contrast, 2015 recorded severe flooding in the wake of heavy summer rains brought on by El Niño, affecting more than 100,000 people in the bordering areas of Paraguay, Uruguay, Brazil and Argentina (The Guardian, 2015).

Following the concept of Borics et al. (2013), in the present study, the flood and drought events brought by La Niña and El Niño were considered disturbances.

Sampling

CORSAN (Companhia Riograndense de Saneamento) is the regional sanitation company responsible for most of the water supply and treatment in the studied region, covering 96% of the state (317 municipalities) and provided the water abiotic and biotic data for the present study. A total of 151 municipalities with phytoplankton data (total phytoplankton, total cyanobacteria, *C. furcoides* and *Microcystis* spp.) were monitored between 2012 and 2022 (see **Supplementary Material 3**), with the results expressed in cel.mL⁻¹. The aquatic systems sampled were ETAs (water treatment stations), dams, rivers, lakes, streams, canals, and lagoons. For more detailed sampling methods, see Silva et al. (2024).

Physical and chemical analyses were carried out in the water treatment stations' laboratories of each municipality (American Public Health Association - APHA, 2012) and included pH, organic matter, apparent color, turbidity, alkalinity, and dissolved oxygen. Nutrient analyses (total phosphorus, nitrite, and nitrate) (Environmental Protection Agency - EPA, 1997; APHA, 2012) were performed in CORSAN's central water laboratory.

Biovolume transformations (mm³/L) were performed for *C. furcoides* and *Microcystis* spp. density data, according to Cavalcante et al. (2018) and Hillebrand et al. (1999) respectively, to better evaluate the contribution of each genus.

Modeling of susceptible areas

Models of the potential distribution of *Ceratium furcoides* and *Microcystis* spp. were estimated by using a Maximum Entropy algorithm in the *MaxEnt* software version 3.4.3 (Phillips et al., 2006, 2017; Phillips & Dudík, 2008). This algorithm models species by checking the relationship between the locations of its known presence and the environmental characteristics of that region and then extrapolating to areas where similar conditions occur in the study area (Vogler et al., 2013, Beltramino et al., 2015).

A total of twenty-three variables were used in the model: nineteen climatic, three hydrological and one topographic. Environmental variables were obtained from WorldClim (<http://www.worldclim.org>) and HydroSHEDS (<https://www.hydrosheds.org/>) at a spatial resolution of 30 arc seconds (~1 km²). WorldClim provides climatic data resulted from weather stations spanning 1950–2000 (Fick & Hijmans, 2017); HydroSHEDS data are derived from a Shuttle Radar Topography Mission (SRTM) digital elevation model (Lehner et al., 2008).

Seventy-five percent of the species occurrences were randomly selected and employed in the Training Model whilst the other twenty-five percent were applied in the Test Model. The logistic output was chosen and returns continuous values, with an estimated probability of presence between 0 (no probability of the species presence) and 1 (high probability of presence). The Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC curves analyses; Fielding & Bell, 1997) was used to evaluate the resulting Model. According to Vogler et al. (2013), the AUC is a threshold independent measure that ranges from 0.5 (no predictability) to 1 (perfect prediction) and, as pointed out by Loo et al. (2007), values above 0.8 often indicate a strong prediction. This algorithm and settings were chosen because it have shown good performance in relation to microscopic, aquatic species (Meichtry-de-Zaburlín et al., 2016). Models were processed in QGIS software, version 3.22.5 (QGIS Development Team, 2023).

The similarity of the models was quantified by Schoener *D*, and Hellinger *I* distances (Schoener, 1968; Warren et al., 2008). These metrics were obtained by comparing the estimates of habitat suitability calculated for each grid cell of the study area and range from 0, when species predicted environmental tolerances do not overlap at all, to 1, when all grid cells are estimated to be equally suitable for both species (Warren et al., 2008). To assess the significance of the values obtained, the Identity Test was conducted. In this test, the species occurrences are randomized, creating pseudopopulations and permuted values of *D* and *I*. If the observed results are significantly lower than those of the randomized, the models are interpreted to be different (Warren et al., 2010). Analysis were performed in *ENMTools* software, version 1.3 (Warren et al., 2010).

Biotic and abiotic spatial and temporal analysis

To investigate the spatial and/or temporal variations of biotic and abiotic data, descriptive analyses (STATISTICA® software version 14.0.1, StatSoft, 2020) were performed. For this approach, data were spatially organized according to the corresponding municipality, and these data arranged according to their respective HB. For temporal analyses (January 2012 to December 2022), samples were organized annually (2012 to 2022) and seasonally (summer, fall, winter, spring).

To better visualize the spatial variation of *C. furcoides* and *Microcystis* spp., distribution maps (mean biovolume) were produced from the geographical position of the municipality (latitude, longitude), using the cartographic database of the regional environmental protection foundation (Fundação Estadual de

Proteção Ambiental Henrique Luis Roessler – FEPAM; <https://fepam.rs.gov.br/inicial>) as a reference. HR distribution maps were also produced using the same database, both being processed in QGIS software, version 3.22.5 (QGIS Development Team, 2023).

As the algae size varies considerably from one group to another (Bellinger & Sigee, 2010), biovolume estimations (Hillebrand et al., 1999; Cavalcante et al., 2018) were employed in these analyses, to better visualize the actual contribution from each genus.

Frequency of the *C. furcoides* and *Microcystis* spp. occurrence

To assess the persistence of *C. furcoides* and *Microcystis* spp. in the municipalities, the frequency of occurrence (FO, in %) was calculated. The FO account for the number of samples in which the organism occurred in relation to the total number of samples collected, using the equation: $FO = \frac{px100}{P}$, where p is the number of samples in which the species was recorded, and P is the total number of samples collected. For this approach, the samples for each municipality were grouped for each year seasonally (e.g.: summer of 2012, fall 2012, winter 2012, spring 2012, and so on) according to Silva et al. (2024) and then transformed into a presence/absence matrix and, finally, applied to aforementioned equation. The following ranges were considered for the FO (Matteucci & Colma, 1982): very frequent ($FO \geq 70\%$), frequent ($40\% \leq FO < 70\%$), infrequent ($10\% \leq FO < 40\%$), and sporadic ($FO < 10\%$).

Statistical Analysis

In order to analyze the coexistence patterns between *C. furcoides* and *Microcystis* spp., Stone & Robert's (1990) *C*-score metric was used, which is based on the mean number of checkerboard units (CUs) among all possible pairs of species in a matrix. This index is calculated as follows: $CU = (R_i - S)(R_j - S)$, where R_i and R_j are the row totals for species i and j , and S is the number of sites containing both species. For any particular species pair, the larger the *C*-score, the more segregated the pair, with fewer shared sites (Stone & Roberts, 1990; Gotelli & Ulrich, 2010). This metric was chosen because it showed strong statistical power to detect nonrandomly structured communities (Gotelli, 2000).

The significance of the *C*-score was tested using null models with simulated random matrices (5,000 simulations). The algorithm used in this model preserved differences in the commonness and rarity of species, using fixed rows–equiprobable columns, randomizing the species occurrences between sites and was chosen because showed low susceptibility to Type I error (Gotelli, 2000). For this approach, the abundances matrices were transformed into presence/absence matrices and then these patterns analyzed in five scales: global (all samples), yearly, seasonally, hydrographic regions, and type of aquatic system. Analyses were performed in the R environment using *EcoSimR* package (Gotelli et al., 2015).

For the municipalities with higher frequency of *C. furcoides* and *Microcystis* spp. (very frequent; $FO \geq 70\%$), Generalized linear models (GLMs) were performed to evaluate the importance of the predictors. To select the best approximating ordinary least square GLM for each response variable, the Akaike Information Criterion (AIC) (Akaike, 1974) was estimated. The AIC provides an evaluation of the information that would be lost if a particular model were used and can be calculated by applying the following equation: $AIC = n \cdot \ln(\sigma^2) + 2k$, where n is the number of data, σ the sum of squared residuals for the model under evaluation, and k the number of its free parameters. The best model is the one characterized by the lowest

AIC. To test the relative quality of the model, ΔAIC was estimated by computing the difference between the AIC for each model. Finally, Akaike's weights (ω) of each model were calculated, to provide evidence that the model is the best explanatory one. Values of ω are standardized by their sum across all evaluated models, so they are highly dependent on the set of models used (Burnham & Anderson, 2002). These analyses were carried out using the *MuMIn* package (Bartoń, 2023) in R environment, version 4.3.1 (R Core Team, 2023). To identify the relative importance of the predictors for each GLM model, *glimm.hp* function (Lai et al., 2022) was applied, also in R environment. This analysis decomposes the models marginal R^2 , quantifying the contribution of each predictor to the total marginal R^2 .

The Redundancy Analysis (RDA) was also performed in the municipalities with higher frequency, to observe how the sampling units varied in function of the environmental variables, using density matrix (cel.mL^{-1}), as this analysis also included data from total phytoplankton and total cyanobacteria. The dataset constructed and employed followed the same principles as the FO, although using mean values from the groupings. Analysis were performed was PC-Ord 6 (McCune & Mefford, 2011).

Results

The subtropical seasonal pattern was confirmed, where the warmest seasons were spring and summer (see **Supplementary Material 1**). The mean temperature for the sampling period was about 18°C , with peaks (for both averages and maxima values) usually being found in 2012 and 2022, and to a lesser extent, 2014, while the lowest in 2012 (minima) and 2013 (averages). Precipitation was well distributed, with most of the peaks being found in 2015 (averages), during an El Niño event, and 2016 (maxima); on the other hand, the lowest averages occurred mostly in fall of 2012 and 2021 (La Niña years) (**Supplementary Material 2**).

There was a clear spatial pattern regarding abiotic data (physical, chemical and nutrients), where Bento Gonçalves, Farroupilha, and Santa Cruz do Sul (all in HR Guaíba) stood out for having the peaks for most of the variables (Table 1). In temporal scale, 2021 showed the highest averages for all nutrients, as well as higher values of these variables; on the other hand, 2022 presented low nutritional amounts.

The distribution models generated had a very good performance, with AUCs above 0.9 (training data) and 0.8 (test data) (Fig. 2). The area's most susceptible to both species are mainly located in the North-northeast and part of the Central region of the state, as well as the majority of HR Guaíba (Fig. 2). In addition to these areas, the *Microcystis* spp. model suggested that large parts of the HR Littoral are susceptible to the genus distribution, especially those close to the Atlantic Ocean and Patos Lagoon (L20).

The jackknife test of variable importance showed that temperature seasonality, temperature annual range and mean diurnal range were the predictors that most influenced the development of the models for both organisms (Fig. 3; **Supplementary Material 4**). Flow Accumulation was the variable that decreases the gain the most when it was omitted in these models, indicating the most information that isn't present in the other variables (Fig. 3; **Supplementary Material 4**).

The similarity of the distribution models was very high in both the Schoener D (0.82) and Hellinger I (0.97) indexes and it was confirmed for both metrics by the Identity test ($D=0.83 \pm 0.02$, $I=0.98 \pm 0.007$; $p > 0.05$). The *C. furcoides* occurrence frequency analysis showed that the species was very frequent in eight municipalities (Bento Gonçalves, Aceguá, Farroupilha, Santa Maria, São Marcos, Santa Cruz do Sul,

Camaquã, and Unistalda) (Fig. 4; **Supplementary Material 5**). On the other hand, *Microcystis* spp. was very frequent only in Passo Fundo, Bento Gonçalves, Santa Maria, and Salto do Jacuí (Fig. 4; **Supplementary Material 5**).

The Guaíba HR revealed the highest biovolumes of *C. furcoides* (2.6×10^8 mm³/L) and *Microcystis* spp. (8.9×10^6 mm³/L), both in the same municipality (Bento Gonçalves, G40 HB) (Figs. 5 and 6). The average peaks, however, were found in the HBs G90 (*C. furcoides*), G40 and L40 (*Microcystis* spp.) (Fig. 6). In temporal scales, 2014 and 2015 presented the peaks for the dinoflagellate, while the cyanobacteria higher biovolumes were found in 2014 (Fig. 5). Summer was the preference for *C. furcoides*, in contrast with *Microcystis* spp., which occurred mostly in fall (Fig. 5). Their blooms occurred primarily in dams (Fig. 5). The coexistence analysis evidenced that, in all cases, the populations of *C. furcoides* and *Microcystis* spp. tended to be significantly more segregated than expected by chance ($p \leq 0.002$) (Fig. 7). Even though both organisms presented similar spatial patterns, they still rarely co-occurred, exhibiting a greater degree of segregation in HR Guaíba, especially in the summer of 2013 and 2014 (Fig. 7). The aquatic systems with the highest segregation were ETAs, followed by dams (Fig. 7).

GLM results obtained for *C. furcoides* indicated that the best models always included organic matter and, to a lesser degree, total phosphorus and nitrate (Table 2). For *Microcystis* spp., the best models were compound by dissolved oxygen and pH (Table 2), as well as total phosphorus, nitrite, and nitrate.

The first two axes from the RDA carried out with the data where *C. furcoides* presented higher frequencies of occurrence explained 25.4% of the total variability (Fig. 8). The variables that contributed most to the ordination in axes 1 were color (0.78), pH (-0.54) and NO₃ (-0.43), while in axis 2 organic matter (0.69) and dissolved oxygen (-0.52) were the most important variables. When *Microcystis* spp. was very frequent, pH (-0.86), dissolved oxygen (-0.56), and alkalinity (-0.56) were the most important predictors in axes 1, whilst the axes 2 were related to organic matter (0.61) and turbidity (-0.35) (Fig. 8), explaining 35.2% of the total variability.

In spatial scales, considering the municipalities, it was possible to identify four different groups: one that always had very high phytoplankton in general (Bento Gonçalves and Farroupilha), one more related to *C. furcoides* (Aceguá, Santa Cruz do Sul and São Marcos) (Fig. 8), other with intermediate biovolume (Camaquã, Santa Maria), and another linked to *Microcystis* spp. (Passo Fundo, Salto do Jacuí, and Unistalda) (Fig. 8).

Temporally, *C. furcoides* leaned towards 2014, 2015 and 2016 (Fig. 8b), while *Microcystis* spp. to 2014, 2021 and 2022 (Fig. 8). In the seasonal scale, *C. furcoides* was related to summer and spring, whilst *Microcystis* spp. to fall and summer (Fig. 8).

Discussion

Evidence suggests that the classic co-occurrence between *Ceratium* and *Microcystis* spp. that often take place in temperate zones (Reynolds et al., 2002; Nasselli-Flores & Barone, 2003; Grigorszky et al., 2019) occurred to a minimal in subtropical region based on the observed results. Even though they tended to co-occur less often than expected by chance, all the results showed a high degree of segregation in both spatial and temporal scales. According to Grigorszky et al. (2019), two major processes play a role in determining

the coexistence of species in the same trophic level: environmental filtering and interspecific competition, where due to an inability to survive and/or reproduce, certain species are excluded from the community.

The distribution models showed that *C. furcoides* and *Microcystis* spp. share similar areas of susceptibility, as they seem to have some similar environmental preferences. Both thrive at temperatures above 20°C, in freshwater waterbodies, in environments with well-balanced nutrients proportions (Yunes et al., 1996; Bustamante-Gil et al., 2012; Cavalcante et al., 2016). Model's results are supported by a high number of *C. furcoides* occurrences (Cavalcante et al., 2013; Silva et al., 2019; Rojas-Castillo et al., 2023; Silva et al., 2024), as well as historical presence of *Microcystis* spp. blooms in the studied region (Kantin & Baumgarten, 1982; Odebrecht et al., 1987; Yunes et al., 1996; Matthiensen et al., 1999; Carvalho et al., 2008; Lemes & Yunes, 2017). Meanwhile, the model also suggested that HB Littoral Médio (L20) would have a high susceptibility to cyanobacteria, which is supported by reports in the area (Matthiensen et al., 1999; Yunes, 2009).

The climate-driven processes that influence mixing seems to strongly influence the diversity and abundance of phytoplankton (Falkowski & Oliver, 2007), and species undergo physiological changes in anticipation of seasonal environmental shift, in order to maximize their fitness (Liu et al., 2022). *C. furcoides* and *Microcystis* spp. habitat suitability tended to increase with low to moderate shifts in seasonality, as in these periods an influx and resuspension of nutrients, cysts, and dormancy structures may occur (Naselli-Flores & Barone, 2003; Matsumura-Tundisi et al., 2010). On the other hand, turbulent and fast transition tended to reduce models' suitability, due to potential lower light availability (Jungo et al., 2001), reduced cell viability (Regel et al., 2004), potential colonies collapse due to stress (O'Brien et al., 2004; Xiao et al., 2016), and potential reduce in their competitive advantages, by preventing vertical migration (Ibelings et al., 1991; Wallace & Hamilton, 1999; Oliver & Ganf, 2000). In contrast, the association with changes in annual range of temperature in subtropical regions tended to always reduce their habitat suitability, as observed in the present study. In aquatic environments, organisms often specialize in a range of temperatures due to metabolic tradeoffs between the structure and function of their enzymes and cell membranes (Bijma et al. 2013), and as reported (Macêdo et al., 2021; Ganf, 1974), these groups are related to warmish, isothermal environments, which indicates that subtropical regions already have optimal conditions for their development, and any change in these localities would be detrimental.

Additionally, the mean diurnal range association may be due to the daily fluctuations in temperature within the water column. In a stable water column, *Microcystis* spp. often show a daily pattern of vertical migration, being explained by a decrease in cell density due to carbohydrates use in dark periods and an increase in cell density due to carbohydrate accumulation in the light (Kromkamp & Mur, 1984). It could also depend on external factors causing changes in buoyancy, due especially to the density of gas vesicles (Thomas & Walsby, 1985). Likewise, *C. furcoides* could use vertical migration through the water column due to its flagellum, which enables access to areas with better light and more nutrients (Kruk et al., 2021). In the present study, sampling was restricted to the subsurface. However, given the recognized ecological abilities of these organisms, spatial niche segregation cannot be ruled out, that is, surface with a prevalence of *Microcystis* spp. while *C. furcoides* is recorded in deeper layers.

According to the model, *Microcystis* spp. habitat suitability tended to be higher with moderate increase in diurnal range, while *C. furcoides*'s tended to decrease to a certain extent. Villamaña et al. (2019) pointed

out that planktonic species growth is regulated by the availability of light and nutrients, yet these variables often present opposite vertical distribution in the water column, so optimal photosynthesis rate occur where light and nutrients coexist. The results suggest that vertical migration is more impactful and relevant for cyanobacteria, as the ability to migrate vertically and scavenge for nutrients is advantageous and may offer a more favorable strategy to maximize light capture (Brookes et al., 1999; Brookes & Ganf, 2001). However, it may require a large fraction of energy that would be used for growth when compared to other mechanisms (Raven & Lavoie, 2021), and this may explain later decrease of suitability. As for *Ceratium*, the ability to use mixotrophy as nutritional alternative (Reynolds, 2006; Cavalcante et al. 2016) and store large amounts of nutrients (Bustamante-Gil et al. 2012) may mitigate the need for vertical migration.

Flow accumulation also was variable important in both models, although acting in opposite ways. Corroborating with most reports for the species in South America, *C. furcoides* benefited from the potential disturbances caused by an increase in flow accumulations (Cavalcante et al., 2016; Crossetti et al., 2019; Silva et al., 2024), as its habitat suitability tended to increase in higher levels of this variable. Likewise, an increase in flow accumulations could be one of the responsible to its state-wide dispersion, as Rio Grande do Sul is drained by a dense hydrographic mesh (Rio Grande do Sul, 2021) and its occurrence is reported in more than 94% of the state (Silva et al., 2024). The positive association with this variable could also be explained by its well distributed rainfall, as was demonstrated. In opposition, *Microcystis* spp. environmental suitability tended to decrease with higher levels of flow accumulation, as with increase in disturbance there is lower light availability and an increase in colonies collapse (Jungo et al., 2001; O'Brien et al., 2004; Xiao et al., 2016).

Their spatial preferences also tended to agree with the distribution models, as their blooms and higher frequencies occurred, mostly, in the same hydrographic regions. As an increase in biomass is expected in response to nutrient enrichment in aquatic environments (Devlin et al. 2011; BoQiang et al. 2013), their blooms could well be associated with eutrophication of water bodies, as HR Littoral and, specially, HR Guaíba suffer from anthropogenic pressures. The HR Guaíba support most of the populations state, with a large industrial concentration, where several activities occur, such as agricultural, livestock, agro-industrial, commercial and services (Rio Grande do Sul, 2021), and according to FEPAM (2023), this region regularly exceeded the established limit for nutrient intake (total phosphorous, in special), thus corroborating with the present findings, where most physical, chemical and nutrients peaks were found in this region municipalities. The HR Guaíba drains directly to HR Littoral, particularly through Patos Lagoon (G80 in direction of L20), providing approximately 80% of its freshwater (Yunes et al., 1996), causing organic materials to flow towards this region. Its waters are also used for domestic water supply, fishing, leisure, navigation, agriculture and, consequently, receive domestic and industrial sewage (Yunes et al., 1996). Furthermore, this water discharge in North-South direction is facilitated by intense rainfall and North or Northeast winds (Yunes 2009).

In terms of seasonal patterns, *C. furcoides* dictated the interactions within the local planktonic community, as when it achieved its peaks, a higher segregation was found, highlighting its invasive character, tending to be an excellent competitor, monopolizing resources and, accordingly, having negative effect on species of the phytoplankton. Also, the dinoflagellate highest abundance usually occurred in the summer, which agrees with studies that related the species consequences on communities, as in this season, the association

of high residence and high temperature may improve its fitness (Kruk et al., 2021), and therefore, increase the segregation.

Yearly, both species' patterns were directly linked to nutrients fluctuations associated with climate shifts. Higher segregation was initially observed in 2013 and 2014 and may be linked to a drought prior to their blooms (La Niña of 2012), high temperatures and an accumulation of total phosphorous. Phytoplankton species are sensitive to shift in water column stability promoted by this phenomenon, and an increase in this factor often increase phytoplankton biomass, being no different for cyanobacteria (Zhang et al., 2019) and flagellates (Becker et al., 2010). Species of cyanobacteria also are known to have a high affinity for phosphates compounds, absorbing and storing this nutrient, then moving towards the intense light at the surface, generating blooms (Reynolds et al., 1981; Jacobson & Halmann, 1982), the same could be said for *C. furcoides*, as its blooms are associated with the combination of ideal temperature and nutrient availability (Cavalcante et al., 2016; Crossetti et al., 2019). These patterns repeat themselves, as fairly low precipitation rates in 2021 associated with high temperatures in 2022 prompted by La Niña made it possible for *Microcystis* spp. develop blooms, thus increasing segregation.

In 2015, the strongest El Niño in the studied region, a higher degree of coexistence was observed, coinciding with an increase in rainfall and lower abundance of *Microcystis* spp. In subtropical regions, blooms of *C. furcoides* often are concomitant with increase in rainfall, due to an increase in organic material and destabilization of native planktonic species (Cavalcante et al., 2016; Silva et al., 2024). In these situations, when the species of *Ceratium* bloom, they tend to dominate, as in Brazil, where Rojas-Castillo et al. (2023) found a negative relation between *C. furcoides* and species richness; similarly, in Japan, *Ceratium* spp. end up being responsible for about 90% of the phytoplankton when blooming (Baek et al., 2007); in Chile, Almanza et al. (2016) found that the species richness and diversity were lower during its colonization.

The results also evidenced a clear spatial segregation in relation to HRs, where the competition for nutrients was evident, particularly in HR Guaíba. Phytoplankton communities are regulated by several mechanisms, and one of the most important is nutrient enrichment arising from industrialization, agricultural modernization, and urbanization, and the expected response is their growth (Devlin et al. 2011; BoQiang et al. 2013). In this scale, *C. furcoides* tended to be more related to organic matter, suggesting that, in subtropical regions, unique strategies such as mixotrophy are imperative in its development and success. Similarly, the positive association with this variable could be related to cyst resuspension, as these structures are deposited in surface sediments and can germinate during periods of mixing, when environmental conditions become favorable (Bustamante-Gil et al., 2012; Cavalcante et al., 2016; Crossetti et al., 2019; Pacheco et al., 2021). According to Chan et al. (2008), degradation of organic matter can reduce the water column dissolved oxygen, leaving aquatic environments vulnerable to hypoxia and/or anoxia, especially in the bottom layer (Pitcher & Probyn, 2011). This may explain the high segregation between the dinoflagellate and *Microcystis* spp., as these cyanobacteria photosynthetic production is related to oxygen (Huang & Chen, 2013), also highlighting their close relation with light availability (Brookes et al., 1999; Brookes & Ganf, 2001).

Segregation patterns were also much more evident in aquatic systems with higher water retention, such as dams and ETAs. In reservoirs, the residence time is manipulated to balance the need of water storage and water renewal for maintaining quality requirements and can influence stratification processes and nutrient

availability and may be determinant in the interaction between planktonic species (Straškraba 1999; Londe et al., 2016). The increased stability and the consequent higher stratification in these systems may explain their preference for these environments, as total cyanobacteria biomass is often higher when this factor is raised, developing faster in vertically stable environments that allow their colonies to rise to the surface (Reynolds, 1997; Romo et al., 2012; Huisman et al., 2014); *C. furcoides* fitness is reported to be higher under high residence time, usually outcompeting other species (Kruk et al., 2021), enabling blooms rapidly (Cavalcante et al., 2016; Rojas-Castillo et al., 2023; Silva et al., 2024). At the same time, the mechanism that grant their segregation is vertical migration and differences in their ecological niches, as species of *Microcystis* frequently occupy the water surface, while *Ceratium* is distributed below the surface (Kruk et al., 2021).

Likewise, segregation was demonstrated by how the sampling units were distributed, as in both scenarios, *Ceratium* and *Microcystis* spp. were plotted in the extreme opposite sides of the RDA biplot. Aceguá and Santa Cruz were highly related to the dinoflagellate, and again, it can be explained by its dominance, as in these municipalities *C. furcoides* frequency and abundances were much higher than *Microcystis* spp. That is the opposite of reports in Mediterranean, that showed cyanobacteria dominance over other species (Moustaka-Gouni et al., 2006), different from studies in Asian (Chen et al., 2003), and also differ from those in other temperate regions that reported coexistence (Reynolds et al., 2002; Nasselli-Flores & Barone, 2003; Grigorszky et al., 2019). The segregation pattern could also be explained by climate variability related to El Niño and La Niña, as in rainy years (2015 and 2016), most of the sampling units were related to *C. furcoides*, in opposition to *Microcystis*, that often leaned towards dry years (2012 and 2021), highlighting that disturbances are beneficial to the former and stability to the latter.

For both, the GLM models underlined intimate relationships with alkalinity and pH. However under non-limited nutrient conditions, the development of blooms can result in changes in these variables (Hansen, 2002; Hinga, 2002; Raven et al., 2020), which may be attributed in this case. Beyond these variables, the best models also emphasized the importance of nitrite, nitrate, and total phosphorus, and is in accordance with many reports, that describe their occurrence in wide range of nutrient concentrations (Baek et al., 2007, 2008; Matsumura-Tundisi et al., 2010; Cavalcante et al., 2016; Crossetti et al., 2019; Kim et al., 2020; Zhou & Wang, 2022).

Conclusions

In the northern hemisphere, species of *Microcystis* and *Ceratium* often constitute a functional assemblage (Naselli-Flores & Barone, 2003), and may coexist as they possess similar sensitivities and tolerances (Reynolds et al., 2002). In subtropical regions, segregation patterns were much more evident, as the results proved to southern Brazil, and observed elsewhere in South America (Bordet et al., 2017).

The results strongly suggested that, in a subtropical region, the environmental scenario conditioned by climatic phenomena drove interaction between both *Ceratium furcoides* and *Microcystis* spp., as the dinoflagellate was often related to disturbances of El Niño, while the stability provided by La Niña usually benefited the cyanobacteria.

In all scales (spatial and temporal), the results here presented suggest high degree of segregation, where the dinoflagellate bloomed and maintained its abundance throughout the sampling period, in contrast with

Microcystis spp., that sporadically had high abundances. Considering that shifts in precipitation and temperature are expected to increase in a global climate change scenario (Huntington, 2010), the habitual dominance by cyanobacteria bloom-forming species may give up some space in *Ceratium*'s favor, and subtropical regions may be strongly affected in this way.

Blooms of *C. furcoides* and *Microcystis* spp. are typically associated with eutrophic and nutrient-rich environments (Paerl, 1988; et al., 2016; Crossetti et al., 2019; Grigorszky et al., 2019;) and, accordingly, it might have harmful consequences. On one hand, *Microcystis* spp. blooms may generate health concern due to its toxins (Komárek et al., 2002), on the other, *Ceratium furcoides* could cause significant increase in pH (Almeida et al., 2016), death of animals (Pitcher et al., 2011) and oxygen depletion (Matsumura-Tundisi et al., 2010; Pacheco et al., 2021). Considering that HR Guaíba was the preference for both, in terms of abundances and frequencies, it is extremely eutrophic, and supports most of the population of the studied region, this local should be in focus for future studies and management authorities.

Finally, only a handful of studies explored the interactions between *C. furcoides* and local communities in South American environments (Matsumura-Tundisi et al., 2010; Nishimura et al., 2015; Bordet et al., 2017; Crossetti et al., 2019; Silva et al., 2019; Rojas-Castillo et al., 2023). Then, more studies and monitoring of the behavior of this species will provide valuable information to identify occurrence patterns and/or new ecotypes in regions where this organism is invasive.

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Author contributions

RDS: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing—Original draft, Writing—Review & editing, Visualization; **LCO:** Conceptualization, Methodology, Validation, Writing—Original draft, Writing—Review & editing, Visualization; **LMR:** Methodology, Resources, Data curation; **LSC:** Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Writing—Review & editing, Funding acquisition, Project administration, Supervision.

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Data availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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Figure Caption

Fig. 1 Location of the Hydrographic Regions (HR) of Rio Grande do Sul state, Southern Brazil, its Hydrographic Basins (HB), and their specific numbers. *U* Uruguay; *L* Littoral; *G* Guaíba; *U10* – HB Apuaê-Inhandava, *U20* HB Passo Fundo, *U30* HB Turvo-Santa Rosa-Santo Cristo, *U40* HB Piratinim, *U50* HB Ibicuí, *U60* HB Quaraí, *U70* HB Santa Maria, *U80* HB Negro, *U90* HB Ijuí, *U100* HB Várzea, *U110* HB Butuí-Icamaquã; *L10* HB Tramandaí, *L20* HB Médio, *L30* HB Camaquã, *L40* HB Mirim-São Gonçalo, *L50* HB Mampituba; *G10* HB Gravataí, *G20* HB Sinos, *G30* HB Caí, *G40* HB Taquari-Antas, *G50* HB Alto Jacuí, *G60* HB Vacacaí- Vacacaí Mirim, *G70* HB Baixo Jacuí, *G80* HB Guaíba, *G90* HB Pardo.

Fig. 2 Potential distribution of *Ceratium furcoides* (a) and *Microcystis* spp. (b), in Rio Grande do Sul state, Southern Brazil. Blue areas indicate low susceptibility regions and red areas indicate high susceptible regions. Areas Under the Curve (AUC) for Training (Tr) and Test (Te) data.

Fig. 3 Response curves of the four strongest environmental predictors for *Ceratium furcoides* (a to d) and *Microcystis* spp. (e to h).

Fig. 4 Frequency of occurrences (FO; $n = 44$; 11 years x 4 seasons) of *Ceratium furcoides* (a) and *Microcystis* spp. (b) in municipalities of Rio Grande do Sul state, Southern Brazil. **Very frequent** ($FO \geq 70\%$), **Frequent** ($40\% \leq FO < 70\%$), **Infrequent** ($10\% \leq FO < 40\%$), and **Sporadic** ($FO < 10\%$). See **Supplementary Material 5** for raw data.

Fig. 5 Biovolume values (mm^3/L) of *Ceratium furcoides* and *Microcystis* spp. in spatial (Hydrographic Regions) and temporal scales (years and seasons), and by aquatic systems. *HR* Hydrographic Regions; *U* Uruguay, $n = 1,033$; *L* Littoral, $n = 459$; *G* Guaíba, $n = 1,948$; *Su* Summer, $n = 1,079$; *F* Fall, $n = 849$; *W* Winter, $n = 647$; *Sp* Spring, $n = 865$; *ETA* Water Treatment Station, $n = 2,032$; *Dm* Dam, $n = 1,132$; *Lk* Lake, $n = 70$; *Riv* River, $n = 171$; *Str* Stream, $n = 41$; *Oth* Others, $n = 44$.

Fig. 6 Mean biovolume values (mm^3/L) of *Ceratium furcoides* and *Microcystis* spp. in spatial scale, by Hydrographic Basins (a and b) and municipalities (c and d). $n =$ range from 1 to 461; for Hydrographic Basins codes, see Fig. 1.

Fig. 7 Observed (box) and simulated (line) C-score values in spatial (Hydrographic Regions) and temporal scales (years and seasons), and by aquatic systems. *HR* Hydrographic Regions; *U* Uruguay; *L* Littoral; *G* Guaíba; *Su* Summer; *F* Fall; *W* Winter; *Sp* Spring; *ETA* Water Treatment Station; *Dm* Dam; *Lk* Lake; *Riv* River; *Str* Stream; *Oth* Others; for number of samples, see Fig. 5

Fig. 8 Redundancy Analysis (RDA) in municipalities with higher frequency of occurrence ($FO \geq 70\%$) to *Ceratium furcoides* (a to c; $n = 290$) and *Microcystis* spp. (d to f; $n = 135$). *CE* *Ceratium furcoides*, *FT* total phytoplankton, *CN* cyanobacteria, *MC* *Microcystis*; *Alk* alkalinity, *DO* dissolved oxygen, *Tur* turbidity, *OM* organic matter; *BG* Bento Gonçalves, *AC* Açegua, *FA* Farroupilha, *SW* São Marcos, *SZ* Santa Cruz do Sul, *SM* Santa Maria, *CQ* Camaquã, *UN* Unistalda, *PF* Passo Fundo, *SJ* Salto do Jacuí.

Table Caption

Table 1 Mean (maximum – minimum) values of abiotic variables of the municipalities with higher frequency ($FO \geq 70\%$) of *Ceratium furcoides* and *Microcystis* spp. *OM* organic matter; *DO* dissolved oxygen; *Turb* turbidity; *Alk* alkalinity; *TE* temperature; *TP* total phosphorous; *PR* precipitation; *BG* Bento Gonçalves, $n = 794$; *AC* Açegua, $n = 135$; *FA* Farroupilha, $n = 669$; *SW* São Marcos, $n = 140$; *SZ* Santa Cruz do Sul, $n = 545$; *SM* Santa Maria, $n = 563$; *CQ* Camaquã, $n = 254$; *UN* Unistalda, $n = 92$; *PF* Passo Fundo, $n = 397$; *SJ* Salto do Jacuí; $n = 147$; *ND* not detected; $<LQ$ below the analytic limit.

Table 2 Information-theory results for ten best candidates Generalized Linear Models (GLM) for *Ceratium furcoides* (CE) and *Microcystis* spp. (MC). *AIC* Akaike information criterion; ΔAIC difference between models; ω Akaike weight; *OM* organic matter; *DO* dissolved oxygen; *Turb* turbidity; *Alk* alkalinity; *TE* temperature; *TP* total phosphorous; *PR* precipitation.

Fig.1

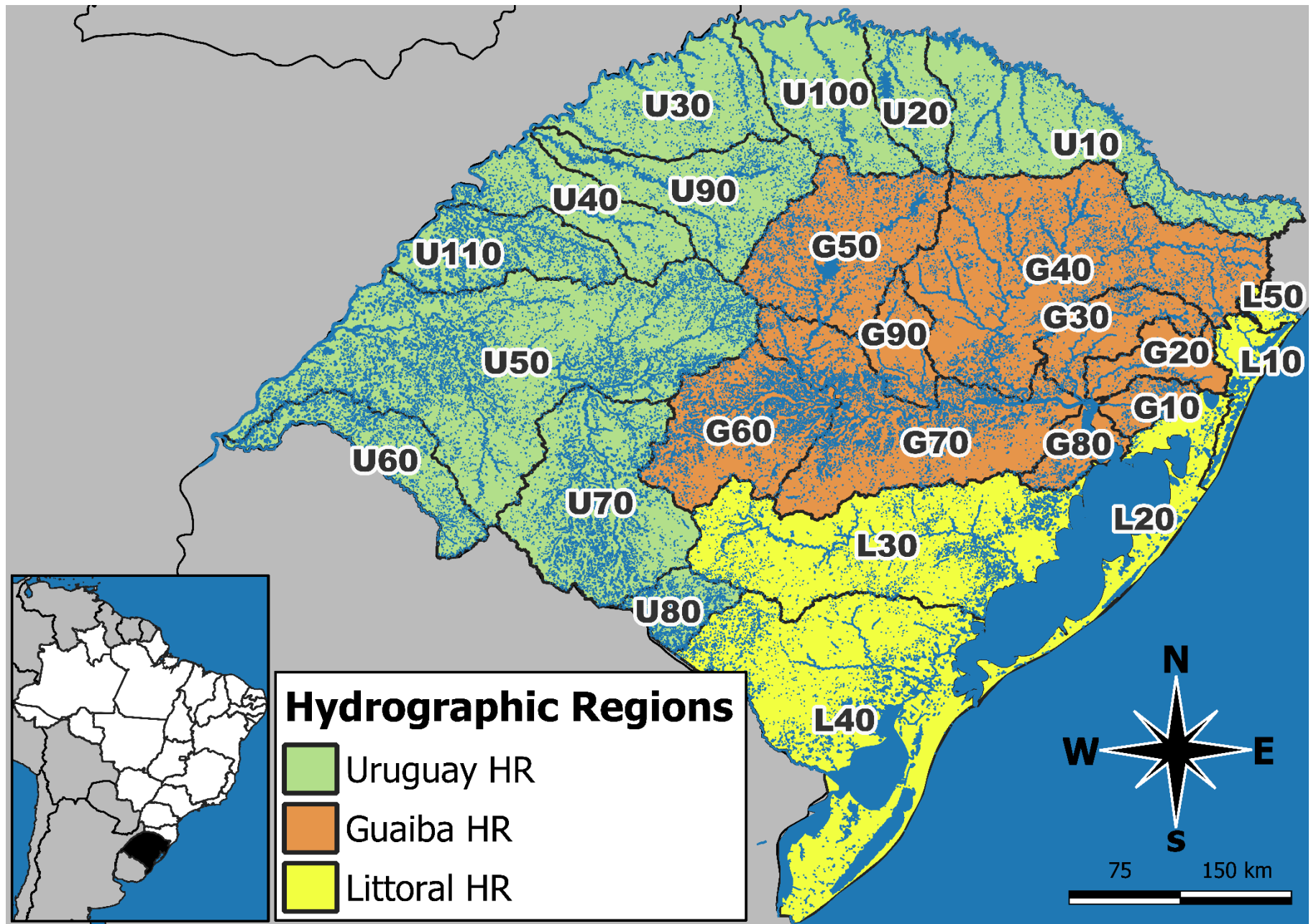


Fig.2

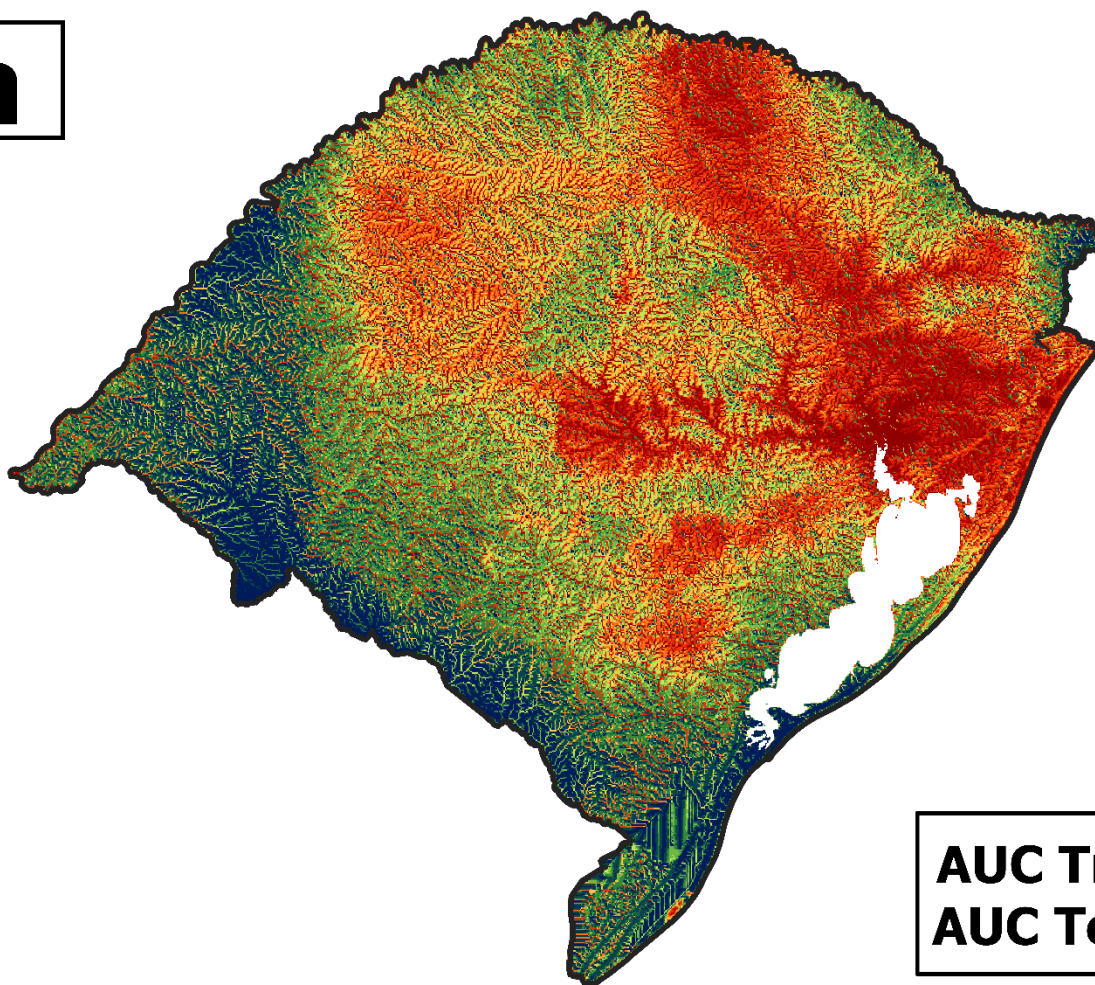
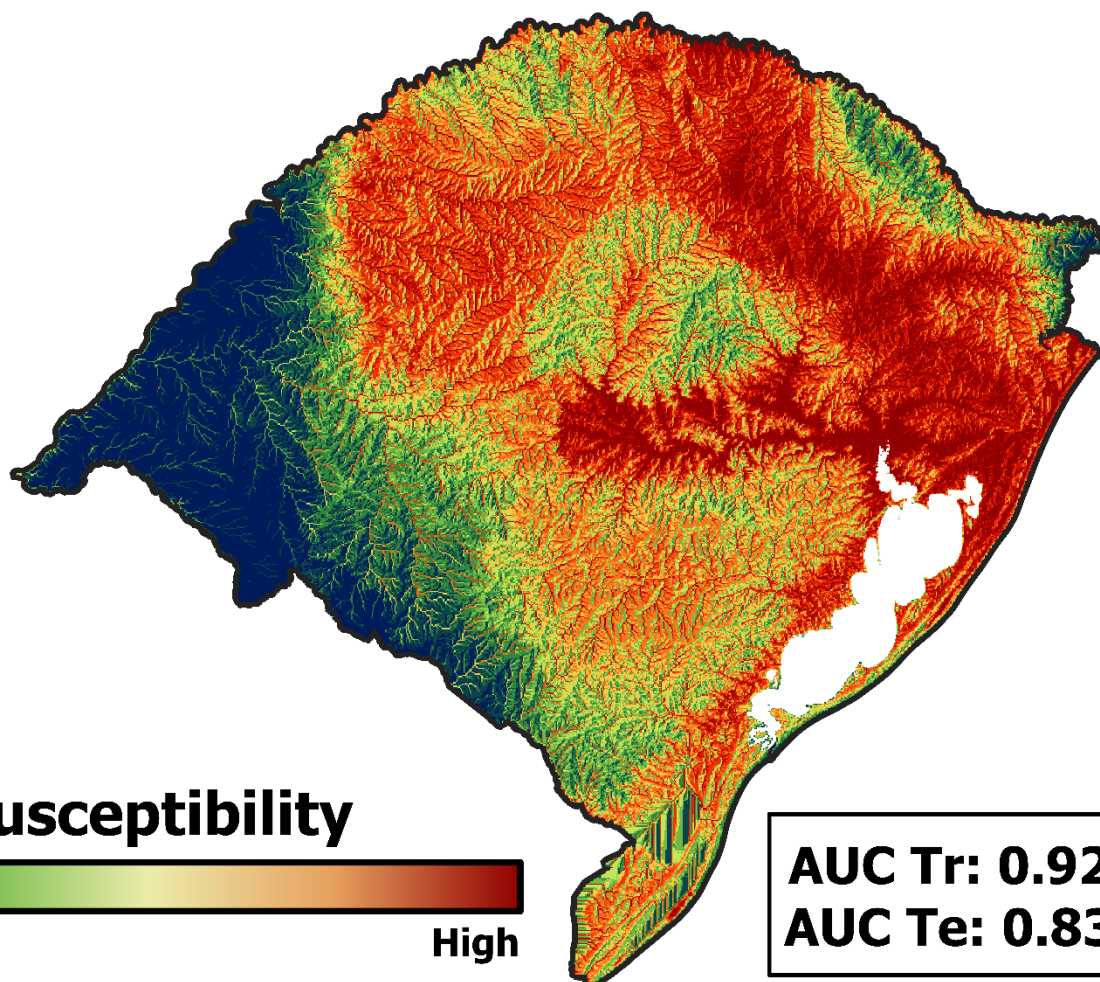
a**b****Susceptibility**

Fig.3

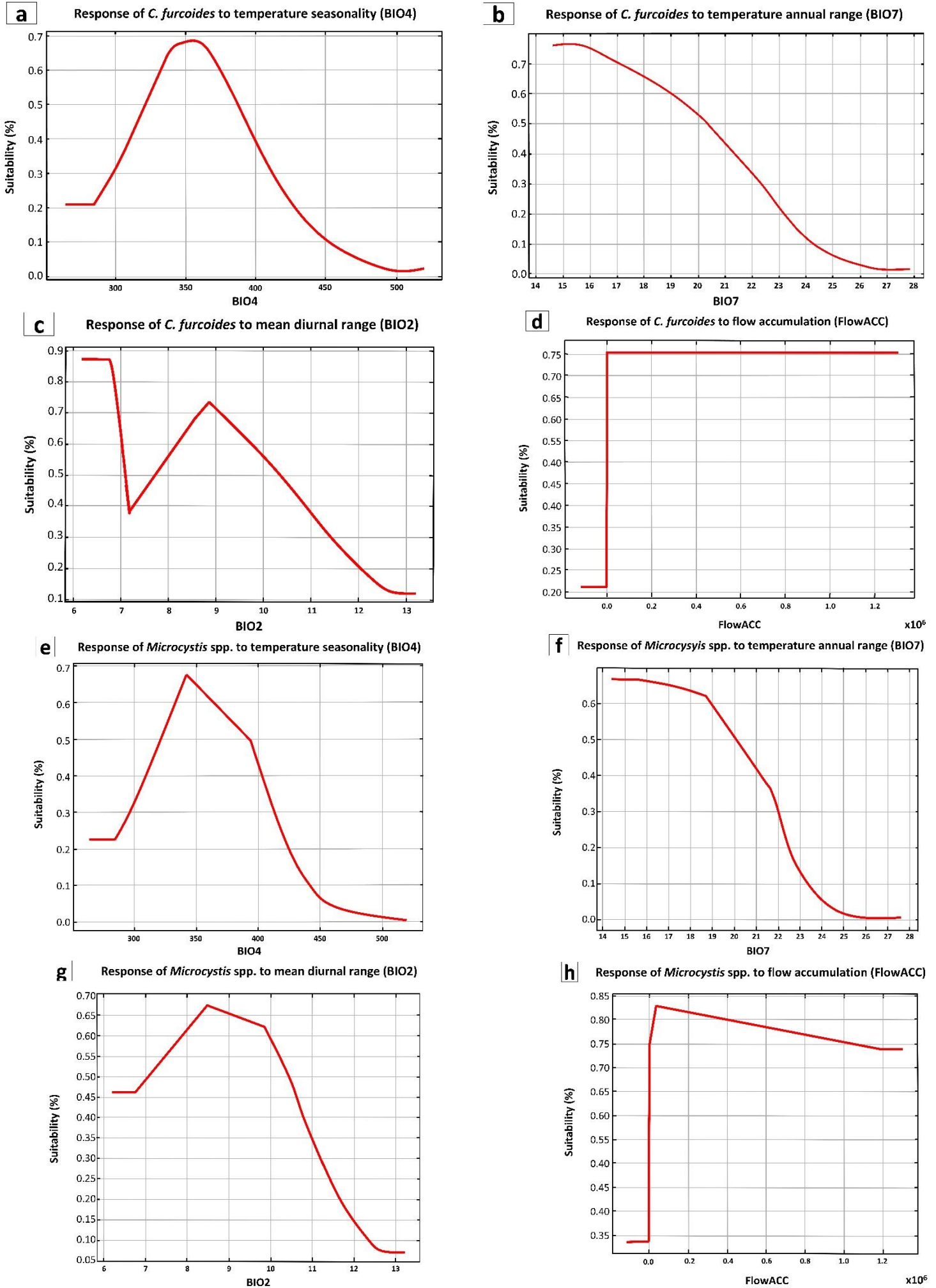
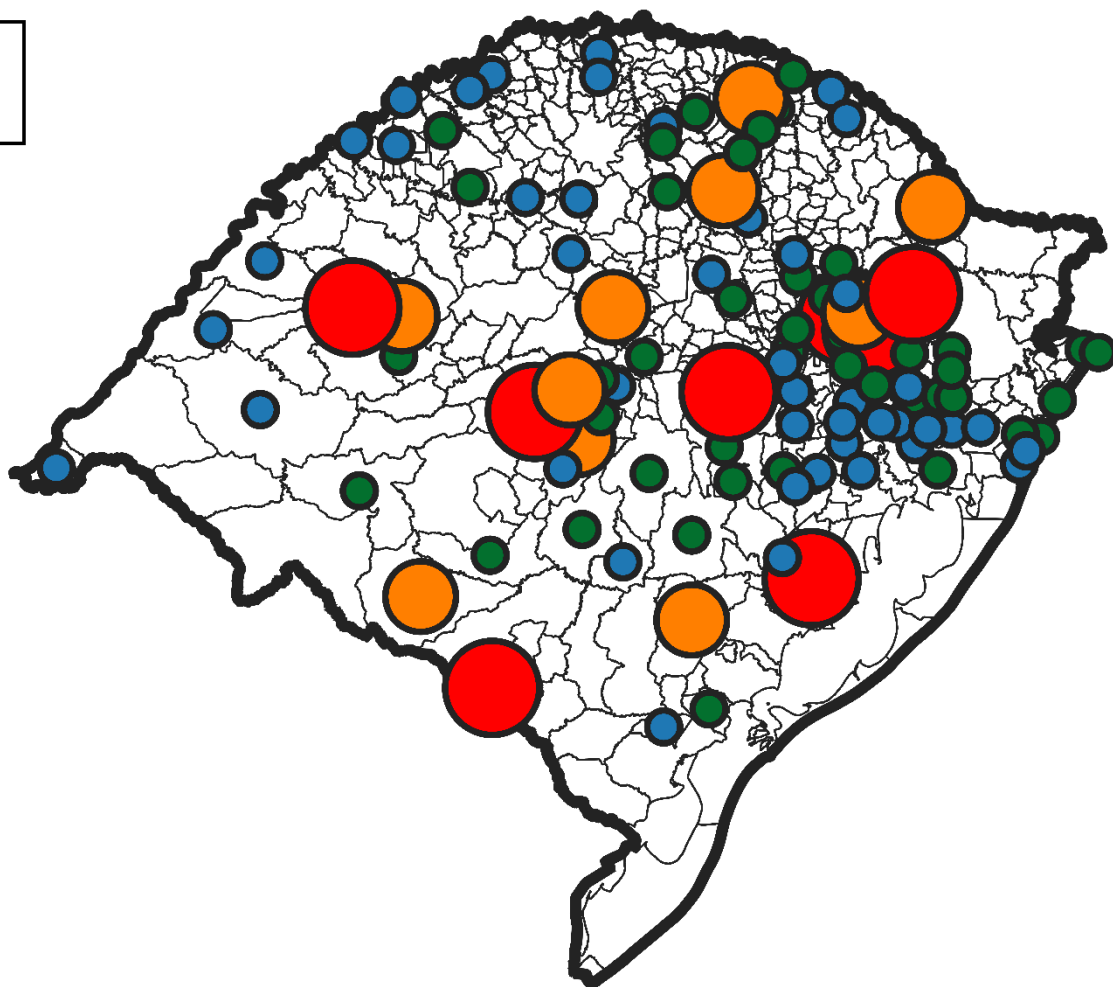
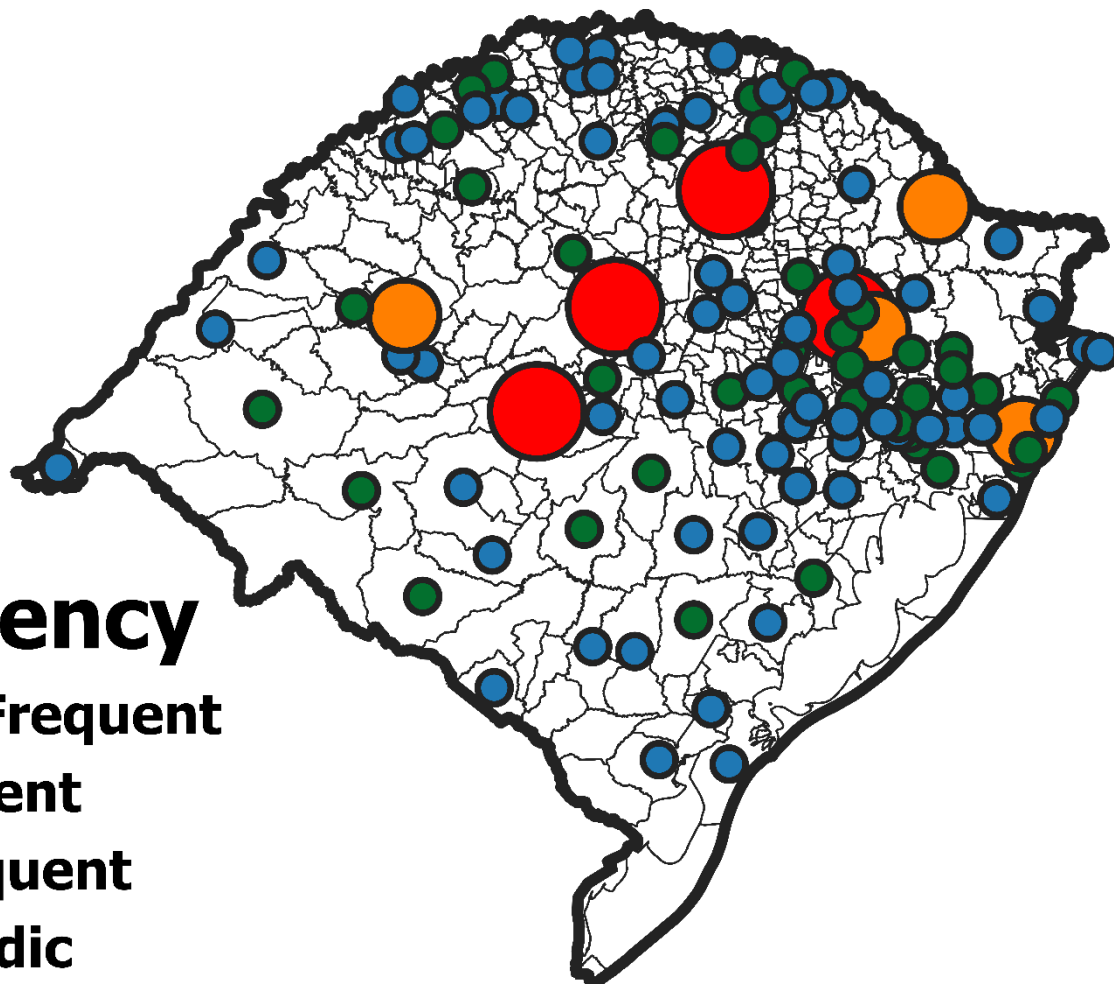


Fig.4

a**b**

Frequency

Very Frequent

Frequent

Infrequent

Sporadic

Fig.5

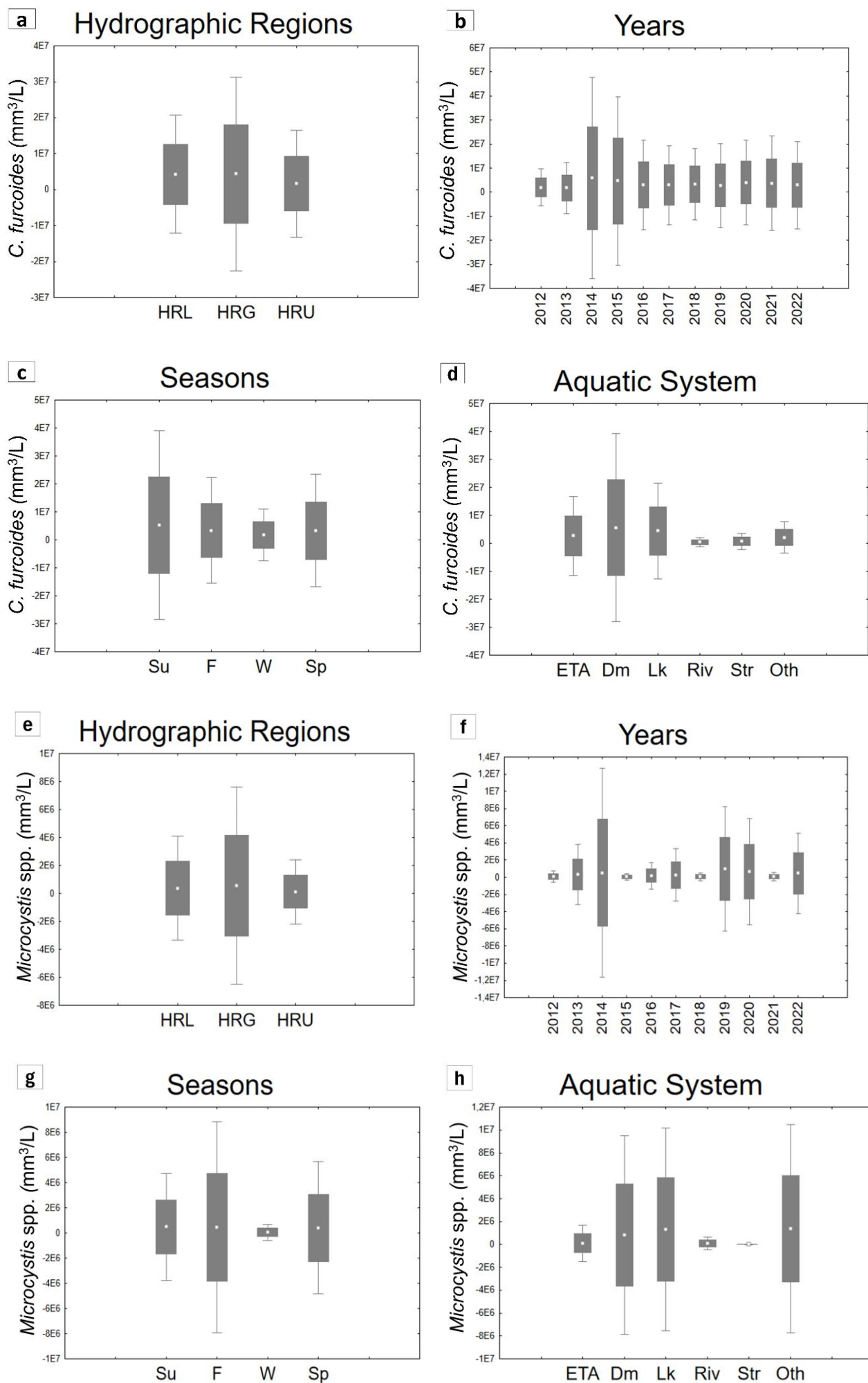


Fig.6

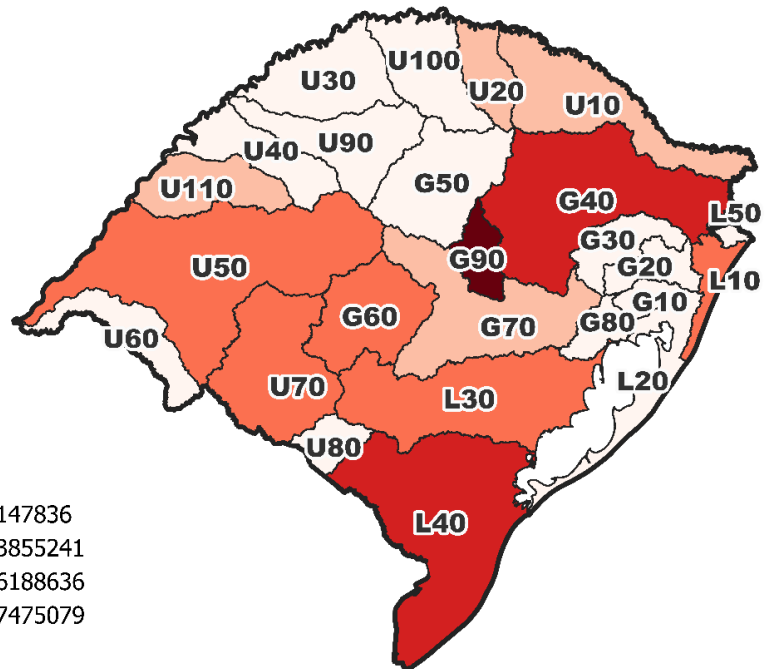
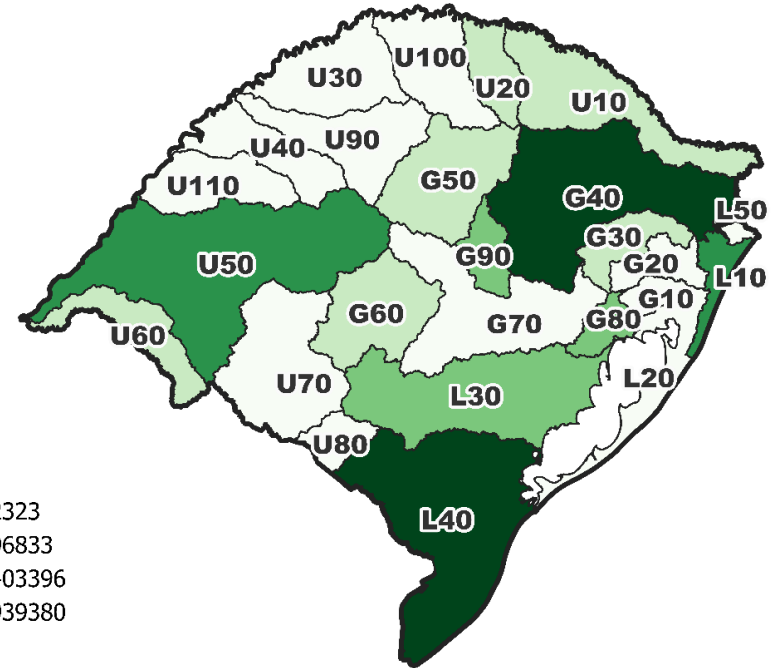
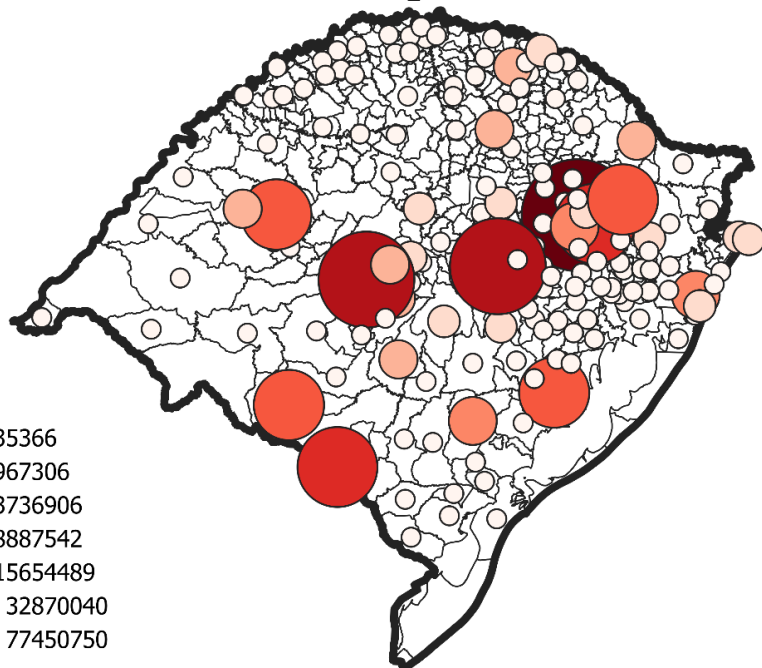
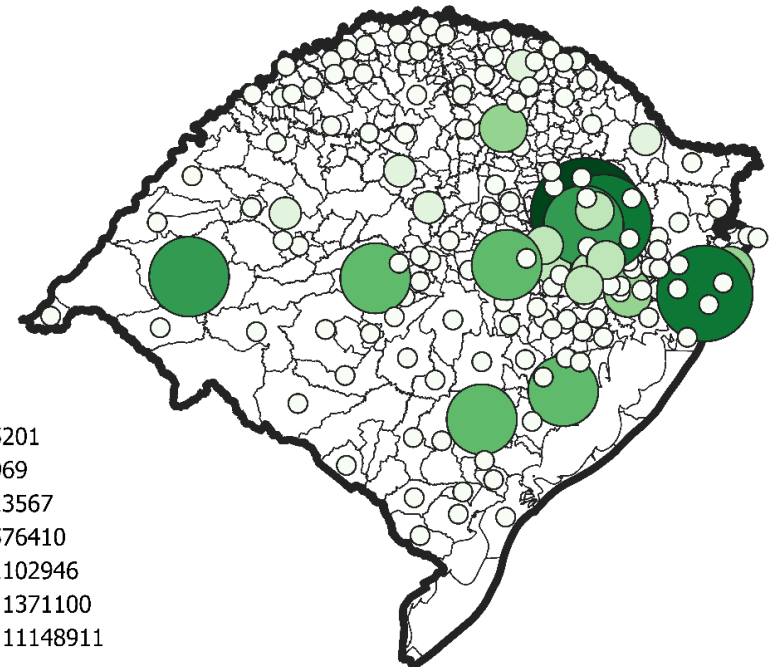
a**b****c****d**

Fig.7

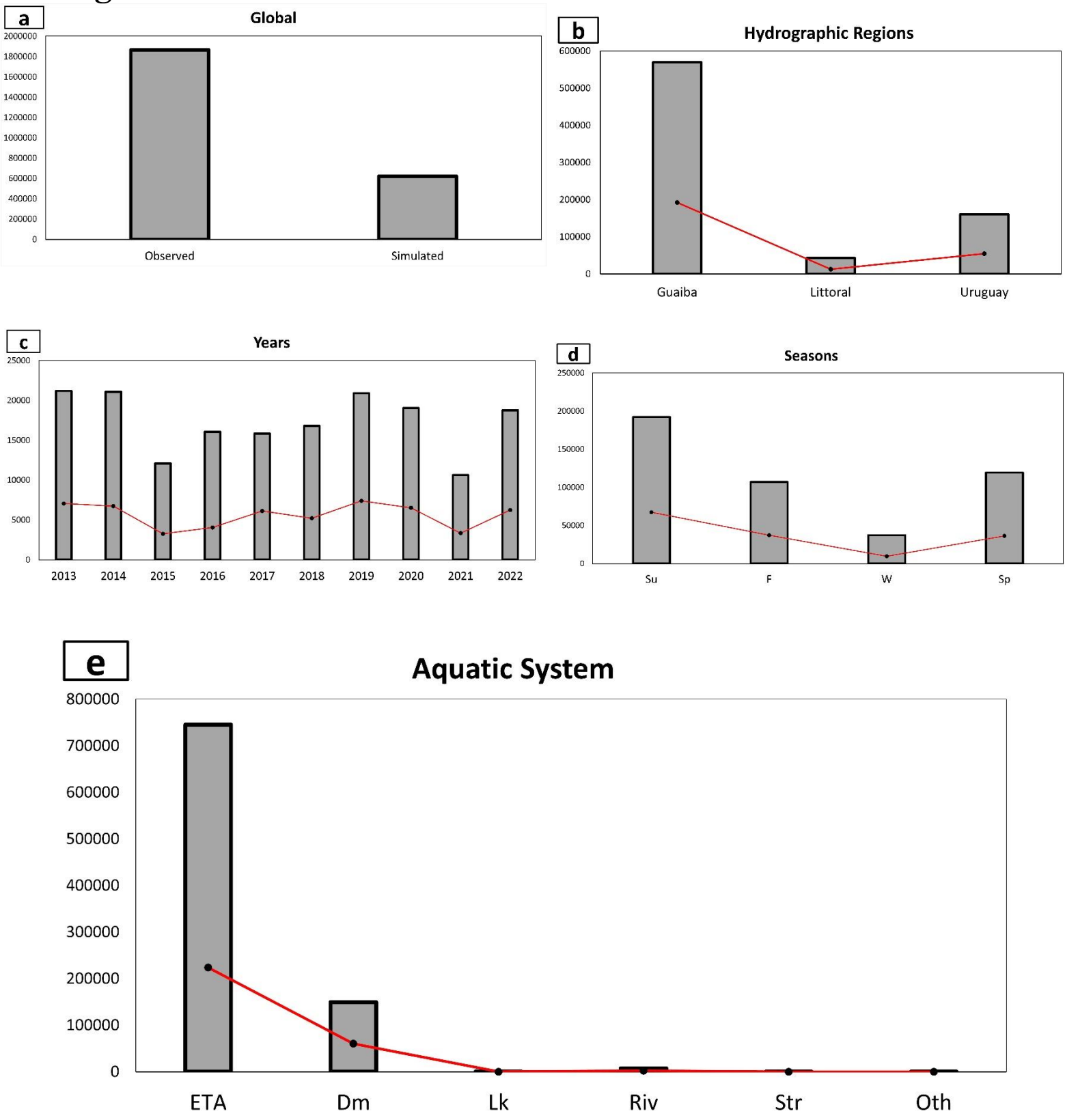


Fig.8

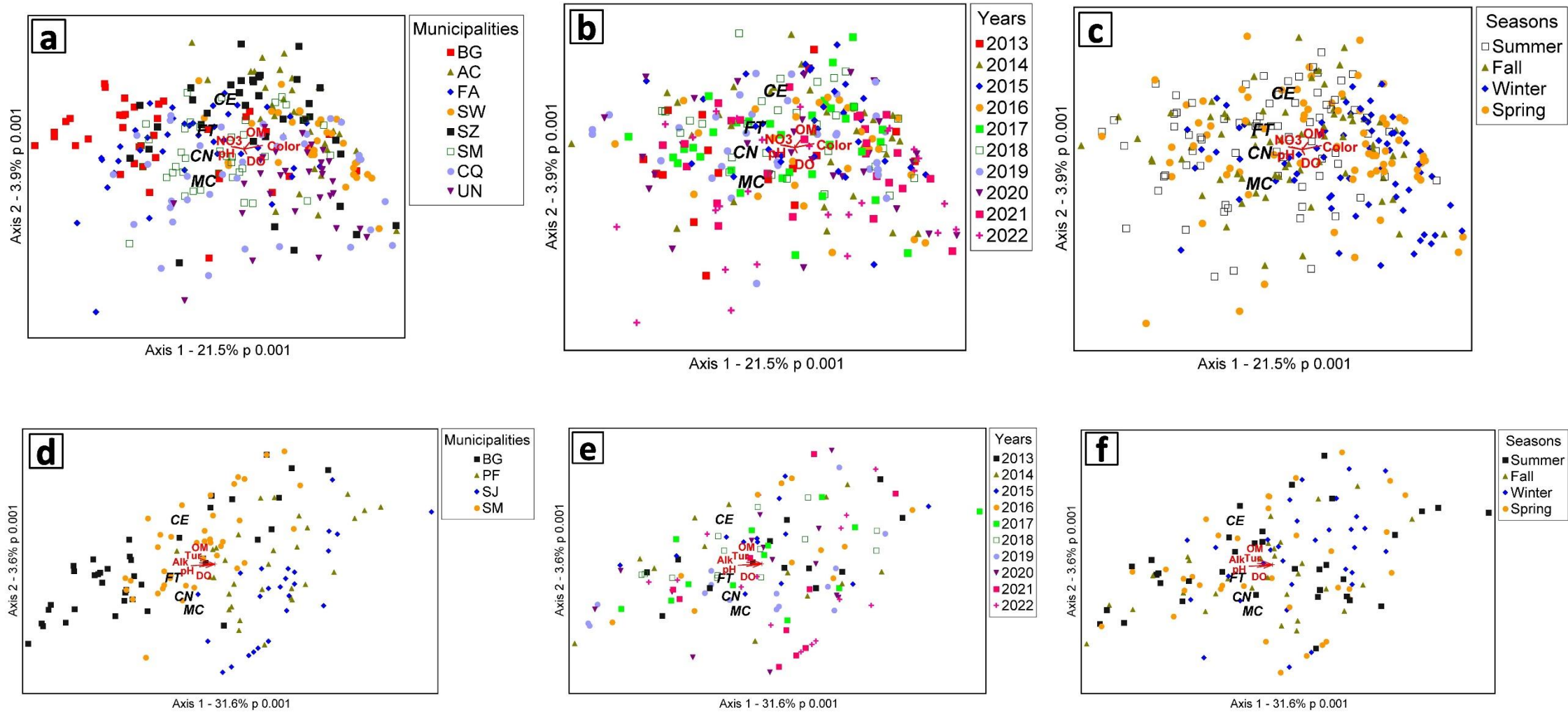


Table 1

	Alk	Color	OM	DO	pH	Turb	NO2	NO3	TP	TE	PR
AC	32.5 (59 - 10)	98.8 (220 - 35)	11 (24 - 5)	5.4 (14 - 0.8)	7.2 (8.5 - 6.5)	18.6 (106 - 3.4)	ND (ND - ND)	0.085 (0.49 - ND)	0.043 (0.116 - <LQ)	17.9 (31.2 - 3.7)	4.1 (165 - 0)
BG	25.1 (176 - 2)	42.4 (550 - 0)	5 (66 - 0)	7.6 (14 - 0.8)	7.4 (10.3 - 5.7)	18.2 (322 - 0.2)	0.022 (0.33 - ND)	1.78 (6.3 - ND)	0.203 (0.889 - ND)	17.8 (29.1 - 2.2)	4.7 (133.6 - 0)
CQ	20.6 (49 - 10)	51.2 (220 - 2)	5 (49 - 2)	7.3 (10 - 0.9)	7.2 (8.2 - 6.1)	25.3 (147 - 1.1)	0.0014 (<LQ - ND)	0.39 (1.48 - ND)	0.053 (0.32 - ND)	18.5 (29.7 - 5.7)	4.2 (162 - 0)
SM	24.9 (224 - 2)	27.4 (186 - 0)	4 (25 - 0)	6.8 (12 - 0.4)	7 (9.2 - 4.5)	9.7 (329 - 0.2)	0.0049 (0.13 - ND)	0.419 (2.08 - ND)	0.06 (0.396 - ND)	19.4 (35.2 - 4.3)	4.9 (151.8 - 0)
FA	20.6 (94 - 2)	24.9 (100 - 0)	5 (54 - 0)	4.3 (28 - 0.2)	6.9 (10 - 5.7)	8.1 (94.5 - 0.2)	0.0445 (0.7 - ND)	1.08 (3.6 - ND)	0.074 (0.174 - ND)	17.8 (29.1 - 2.2)	4.7 (133.6 - 0)
SZ	46.4 (207 - 3)	52 (204 - 0)	3 (39 - 0)	7.1 (12.3 - 1.2)	7.3 (9.6 - 6.1)	22.6 (369 - 0.2)	0.0016 (0.05 - ND)	1.058 (3.53 - 0.04)	0.085 (0.996 - ND)	19.5 (34.8 - 5)	4 (238.6 - 0)
SW	10.2 (14 - 5)	114.4 (180 - 2)	6 (10 - 1)	6 (9.6 - 0.4)	6.6 (7.6 - 5.9)	23.9 (51 - 0.3)	ND (ND - ND)	0.086 (0.36 - ND)	0.038 (0.083 - 0.017)	16.1 (29.9 - 1.4)	5.6 (149.6 - 0)
PF	15.7 (60 - 2)	68.3 (450 - 9)	5 (37 - 2)	5.8 (16 - 0.7)	6.8 (8.1 - 6.1)	22.5 (332 - 4)	0.011 (0.11 - ND)	0.839 (5.5 - 0.11)	0.075 (0.339 - ND)	18 (28.4 - 2)	4.9 (120.4 - 0)
SJ	16.5 (23 - 8)	48.3 (200 - 5)	2 (18 - 1)	5.9 (9.2 - 2)	7 (7.5 - 6.2)	14.5 (81 - 2.1)	0.0004 (0.05 - ND)	0.79 (1.5 - 0.44)	0.021 (0.113 - ND)	18.9 (30.3 - 3)	5 (117.8 - 0)
UN	21.3 (27 - 10)	49.5 (135 - 7)	8 (75 - 4)	7.2 (9.6 - 2.6)	7.1 (7.8 - 6.4)	8.1 (81 - 2.7)	0.016 (0.1 - ND)	0.163 (1.05 - ND)	0.018 (0.053 - ND)	19.1 (34.3 - 2.7)	5 (150.8 - 0)
2013	19 (150 - 3)	49.6 (550 - 2)	5 (66 - 0)	6.9 (16 - 0.4)	7 (9.1 - 5.7)	16.7 (329 - 0.2)	0.008 (0.12 - ND)	0.789 (3.37 - ND)	0.111 (0.889 - ND)	17.7 (30.1 - 1.4)	4.6 (238.6 - 0)
2014	25.5 (195 - 2)	59.6 (280 - 2)	5 (26 - 0)	6.2 (12 - 0.4)	7 (9.5 - 6)	14.6 (99 - 0.2)	0.016 (0.24 - ND)	1.182 (3.27 - 0.15)	0.063 (0.209 - ND)	18.7 (34.8 - 4.1)	5.7 (133.6 - 0)
2015	23.7 (183 - 2)	62.7 (245 - 2)	2 (29 - 0)	6.2 (14 - 0.4)	7 (9.5 - 5.7)	18.7 (262 - 0.2)	0.007 (0.11 - ND)	0.949 (3.66 - ND)	0.086 (0.996 - ND)	18.6 (29.1 - 4.2)	6.1 (151.8 - 0)
2016	25.1 (187 - 6)	45.4 (275 - 0)	5 (75 - 0)	6.5 (14 - 0.2)	7 (9.9 - 6)	16.9 (369 - 0.2)	0.007 (0.15 - ND)	0.976 (3.53 - ND)	0.073 (0.563 - ND)	17.8 (31.7 - 2.2)	4.7 (176 - 0)
2017	26.9 (224 - 3)	48.3 (220 - 0)	5 (72 - 0)	6.5 (13 - 0.4)	7.1 (9.8 - 6)	19.5 (169 - 0.2)	0.021 (0.7 - ND)	0.993 (4.62 - ND)	0.057 (0.205 - ND)	18.9 (28.6 - 2.2)	5.2 (125.2 - 0)
2018	25 (193 - 2)	44.6 (450 - 0)	5 (54 - 1)	6.1 (10.8 - 0.4)	7.1 (9.9 - 4.5)	16.8 (332 - 0.2)	0.009 (0.27 - ND)	0.948 (5.5 - ND)	0.077 (0.396 - ND)	18.3 (29.3 - 2.8)	4.8 (120.2 - 0)
2019	31.4 (207 - 2)	42.6 (200 - 0)	4 (27 - 0)	6.4 (28 - 0.4)	7.1 (10 - 6)	13.5 (105 - 0.2)	0.007 (0.45 - ND)	1.017 (4.14 - ND)	0.065 (0.383 - ND)	18.8 (31.6 - 1.8)	4.6 (165 - 0)
2020	24.9 (62 - 2)	44.5 (330 - 2)	6 (46 - 1)	6 (12 - 0.6)	7.3 (10.2 - 6.2)	17.9 (216 - 0.2)	0.021 (0.26 - ND)	1.09 (5.5 - 0.1)	0.108 (0.662 - ND)	18.6 (35.2 - 2.6)	3.7 (150.8 - 0)
2021	22.4 (60 - 3)	43.4 (290 - 1)	5 (42 - 1)	6.2 (13 - 0.7)	7.3 (10.3 - 6.1)	15.3 (258 - 0.2)	0.043 (0.33 - ND)	1.192 (6.3 - ND)	0.127 (0.86 - ND)	18.1 (34.3 - 1.4)	3.7 (103.6 - 0)
2022	24.1 (105 - 6)	39.7 (204 - 0)	5 (32 - 1)	6.6 (14 - 0.4)	7.3 (10 - 4.9)	15.6 (314 - 0.2)	0.029 (0.24 - ND)	0.603 (2.54 - ND)	0.044 (0.1 - ND)	17.9 (33.5 - 3)	3.9 (105 - 0)
Summer	23.8 (176 - 2)	44.2 (550 - 0)	5 (66 - 0)	5.4 (14 - 0.2)	7.2 (10.3 - 5.7)	16.2 (322 - 0.2)	0.301 (0.7 - ND)	0.593 (2.78 - ND)	0.081 (0.815 - ND)	22.3 (34.8 - 1.1)	4.7 (165 - 0)
Fall	28.6 (207 - 2)	42.8 (450 - 0)	5 (54 - 0)	6.8 (28 - 0.2)	7.1 (9.9 - 5.7)	14.5 (322 - 0.2)	0.007 (0.29 - ND)	0.939 (4.9 - ND)	0.083 (0.996 - ND)	15.7 (31 - 1.4)	4.7 (150.8 - 0)
Winter	20.2 (224 - 3)	54.6 (220 - 0)	4 (55 - 0)	7.6 (13 - 0.6)	7 (9.6 - 4.9)	19.4 (369 - 0.2)	0.026 (0.45 - ND)	1.322 (6.3 - ND)	0.094 (0.86 - ND)	14.8 (29.2 - 1.4)	4.4 (133.6 - 0)
Spring	26 (207 - 2)	51.4 (290 - 0)	5 (75 - 0)	6 (16 - 0.4)	7.1 (10.2 - 4.5)	16.6 (329 - 0.2)	0.006 (0.26 - ND)	0.95 (5.5 - ND)	0.073 (0.662 - ND)	20.5 (35.2 - 7.1)	5.1 (238 - 0)

Table 2

	Predictor	AIC	Δ AIC	ω	Predictor relative importance (%)
CE	OM, DO, pH, Turb, TP	1003.38	-	0.03	21.6, 20.9, 36.3, 7.2, 13.9
	OM, DO, pH, Turb, NO ₃ , TP	1003.48	0.1	0.03	22.6, 20, 30, 6.6, 10.3, 10.4
	OM, DO, pH, TP	1003.73	0.35	0.02	23.3, 20, 41.2, 15.4
	OM, DO, pH, NO ₃ , TP	1003.81	0.43	0.02	24.3, 19.2, 34, 11.3, 11.2
	Alk, OM, DO, pH, TP	1004.19	0.81	0.02	22.2, 19.9, 37.6, 14.6, 5.7
	OM, DO, pH, Turb, NO ₃	1004.37	0.99	0.02	14.3, 22.8, 21.8, 33.4, 7.7
	OM, DO, pH, NO ₂ , NO ₃ , TP	1004.5	1.12	0.02	23.9, 18.9, 33, 1, 11.6, 11.4
	Alk, OM, DO, pH, Turb, TP	1004.51	1.13	0.02	20.6, 20.8, 32.7, 7, 5.4, 13.3
	Alk, OM, DO, pH, NO ₃ , TP	1004.65	1.27	0.01	23.1, 19, 31.1, 10.6, 5.1, 10.9
	OM, DO, pH, Turb, NO ₂ , NO ₃ , TP	1004.68	1.3	0.01	22.5, 19.9, 29.5, 6.2, 0.7, 10.7, 10.4
MC	DO, pH	686.26	-	0.03	41.2, 58.8
	Alk, DO, pH	687.21	0.95	0.02	10.2, 42, 47.7
	DO, pH, Turb	687.88	1.62	0.01	37.1, 54.9, 7.9
	Color, DO, pH	688.02	1.76	0.01	1, 40.1, 58.8
	DO, pH, TP	688.12	1.85	0.01	41.1, 58.8, 0
	DO, pH, TE	688.14	1.88	0.01	40.9, 59.1, 0
	DO, pH, PR	688.17	1.91	0.01	41.1, 59, -0.1
	OM, DO, pH	688.24	1.98	0.01	3.4, 40, 56.5
	DO, pH, NO ₂	688.26	2	0.01	41, 57.9, 1
	DO, pH, NO ₃	688.26	2	0.01	39.5, 56.4, 4

Final Considerations

The spread of *C. furcoides* has accelerated in recent years in South America in general and in Brazilian environments in particular, having been recorded in many states (Matsumura-Tundisi et al. 2010; Crossetti et al. 2019; Severiano et al. 2022), indicating an ongoing expansion process (Meichtry-de-Zaburlin et al. 2016). The dinoflagellate benefited from climate shifts, entering the Rio Grande do Sul region at the end of a La Niña event (the drought in 2011–2012) and forming blooms while the state was affected by expressive amounts of rain caused by the extreme El Niño of 2015 (Silva et al. 2022; NOAA 2023).

These events also ruled interaction between both dinoflagellate and *Microcystis* spp., as *C. furcoides* was often related to disturbances of El Niño, while the stability provided by La Niña usually benefited the cyanobacteria.

In all scales, the results here presented suggest high degree of segregation, where the dinoflagellate bloomed and maintained its abundance throughout the sampling period, in contrast with *Microcystis* spp., that sporadically had high abundances. Considering that shifts in precipitation and temperature are expected to increase (Huntington, 2010), the habitual dominance by cyanobacteria bloom-forming species will change in *Ceratium*'s favor, and subtropical regions may be strongly affected.

The Guaíba hydrographic region showed the largest number of municipalities with the occurrence of the organisms as well as the highest densities, making this an area of interest for water management bodies, as their blooms can have a variety of impacts including health concern due to toxins (Komárek et al., 2002), could cause significant increase in pH (Almeida et al., 2016), death of animals (Pitcher et al., 2011), oxygen depletion (Matsumura-Tundisi et al., 2010; Pacheco et al., 2021).

The results of both works represent an addition of information to the growing issue of the invasion of *Ceratium furcoides* in South America. The results presented show how important a long-term monitoring program can be in detecting patterns relating planktonic organism, being a relative straight-forward method, as is an automatic process. Its applicability is also very high and can be adapted to a variety of cases, as was demonstrated in both studies.

Furthermore, the results from the first chapter have been presented during the *IV Congreso Iberoamericano de Limnología* and *X Congreso Argentino de Limnología (CILCAL)*, that occurred in Buenos Aires – Argentina (31st July to 4th August 2023) and enabled a partnership between our group and researchers from Uruguay and Argentina, to study the invasion of *C. furcoides* in the MERCOSUL, contemplated by CAPES (Edital 003/2023 PROPG/UFRGS – PRINT/CAPES). A study in an international level, focusing on its dispersion patterns, could prove to be essential to mitigate the species consequences in freshwaters environments, as the South American region presents high abundances and high occurrences. This would be especially important for Brazilian environments, that recorded *C. furcoides* the most, usually associated with the highest blooms for the region (Rio Grande do Sul, in particular).