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POTENTIAL DISTRIBUTION OF THE INVASIVE FRESHWATER DINOFLAGELLATE *CERATIUM FURCOIDES* (LEVANDER) LANGHANS (DINOPHYTA) IN SOUTH AMERICA[1]

Norma Meichtry de Zaburlín

Departamento de Biología, Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Rivadavia 2370, Posadas N3300LDX, Argentina

Roberto E. Vogler[2]

Departamento de Biología, Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Rivadavia 2370, Posadas N3300LDX, Argentina
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

María J. Molina, and Víctor M. Llano

Departamento de Biología, Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Rivadavia 2370, Posadas N3300LDX, Argentina

Dinoflagellates of the genus *Ceratium* are predominantly found in marine environments, with a few species in inland waters. Over the last decades, the freshwater species *Ceratium hirundinella* and *Ceratium furcoides* have colonized and invaded several South American basins. The purpose of this study was to create a distribution model for the invasive dinoflagellate *C. furcoides* in South America in order to further investigate the basins at potential risk, as well as the environmental conditions that influence its expansion. This species is known to develop blooms due to its mobility, resistance to sedimentation, and optimized use of resources. Although nontoxic, blooms of the species cause many problems to both the natural ecosystems and water users. Potential distribution was predicted by using a maximum entropy algorithm (MaxEnt). Model was run with 101 occurrences obtained from the scientific literature, and climatic, hydrological and topographic variables. The developed model had a very good performance for the study area. The most susceptible areas identified were mainly concentrated in the basins between southeastern Brazil and northeastern Argentina. Besides already affected regions, new potentially suitable areas were identified in temperate regions of South America. The information generated here will be useful for authorities responsible for water and watershed management to monitor the spread of this species and address problems related to its establishment in new environments.

Key index words: **aquatic invasions; freshwater algae; MaxEnt; phytoplankton, species distribution modeling; South American basins**

Abbreviations**: AUC, area under the curve**

Biological invasions along with climate change and environmental fragmentation constitute serious threats to the maintenance of global diversity (Vitousek et al. 1996, Nentwig 2007). The introduction of exotic species may have significant impacts on natural environments and represent one of the major challenges faced by communities and endemic species, given that invasions may irreversibly alter the ecological functioning of ecosystems, leading to changes in the diversity, local species composition, dominance and primary productivity (Simberloff 1996, Mack et al. 2000, Gozlan et al. 2010, Strayer 2010, Silva et al. 2012). Local extinction of native species caused by strong competition and predation can be considered the most serious consequence of an invasion, although the long-term effects will depend on the particular response of each community (Baskin 1994, Delariva and Agostinho 1999). Freshwater habitats are particularly susceptible to the invasion by microorganisms, since their dispersal is usually unnoticed and also favored by water flow. In general, such invasions are poorly understood and their impacts on the environment are currently underestimated (Strayer 2010, Silva et al. 2012, Padisák et al. 2016).

Ceratium Schrank, 1793 is a genus of planktonic dinoflagellates, subcosmopolitan, with few representatives in inland waters. Some of its species are known to produce blooms due to their mobility, resistance to sedimentation, and the optimized use of resources such as light and nutrients. They are also tolerant to stress due to: (i) the ability to swim

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[2] Author for correspondence: e-mail robertovogler@fceqyn.unam.edu.ar.

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and to perform vertical migrations in the water column in search of more favorable microhabitats, (ii) temporary cyst formation, and (iii) low grazing pressure by zooplankton (Pollingher 1988, Olrik 1994). Freshwater species of this genus are known to occur in many temperate and subtropical areas of the world, including Africa (e.g., South Africa), Asia (e.g., Japan, Taiwan, Turkey), America (e.g., Canada, United States), Europe (e.g., Greece, Hungary, Italy, Poland, Portugal, Spain, United Kingdom), and Oceania (e.g., Australia, New Zealand) (Cassie 1978, Nicholls et al. 1980, Heaney et al. 1983, 1988, Padisák 1985, Echevarría and Rodríguez 1994, Danielidis et al. 1996, Wu and Chou 1998, Whittington et al. 2000, Pérez-Martínez and Sánchez-Castillo 2001, Van Ginkel et al. 2001, 2007, Baldwin et al. 2003, Carty 2003, Grigorszky et al. 2003, Çelekli et al. 2007, Hansen and Flaim 2007, Hart 2007, Hart and Wragg 2009, Pandeirada et al. 2013, Napiórkowska-Krzebietke 2014). Particularly in South America, the species *Ceratium hirundinella* (O. F. Müller) Schrank and *Ceratium furcoides* (Levander) Langhans have been recorded over the past two decades showing an invasive behavior and a rapid colonization of the southern environments (Cavalcante et al. 2013, Meichtry de Zaburlín et al. 2014). Since 1991, *C. hirundinella* began to colonize inland water bodies of Argentina, Chile, Bolivia, Brazil, in a northward direction, extending over ~2,000 km in 10 years (Guerrero and Echenique 1997, Boltovskoy et al. 2003, 2013, Mac Donagh et al. 2005, Silverio et al. 2009). By contrast, the invasion of *C. furcoides* is more recent and appears to have occurred in the opposite direction; first through the colonization of those areas not occupied by the genus and subsequently invading environments inhabited by *C. hirundinella*, where a species replacement was observed in many cases (Boltovskoy et al. 2013, Salusso and Moraña 2014).

Ceratium furcoides was recorded for the first time in South America at the beginning of this century in Colombia, where blooms at high densities were found in reservoirs (Ramírez et al. 2005, Restano et al. 2011, Bustamante Gil et al. 2012, Villabona-González et al. 2014). In Brazil, the species was recorded for the first time in the state of Minas Gerais in 2007, and its occurrence was considered to be rare (Santos-Wisniewski et al. 2007, Oliveira et al. 2011). However, *C. furcoides* has been recorded in rivers and reservoirs across several Brazilian basins in at least eight of the 26 states of this country, which indicates an ongoing expansion process (Matsumura-Tundisi et al. 2010, Oliveira et al. 2011, Amazonas et al. 2012, Müller et al. 2012, Nishimura 2012, Bressane et al. 2013, Cavalcante et al. 2013, Cortez 2013, Cassol et al. 2014, Jati et al. 2014, Moreira et al. 2015). Similarly, the occurrence of this dinoflagellate was first reported in Argentina and Paraguay for the High Paraná River in 2014 (Meichtry de Zaburlín et al. 2014), and now it is known to occur in at least five of the 23 Argentinean provinces (i.e., Corrientes, Entre Ríos, Misiones, Salta, Santa Fe; Barreda 2014, Meichtry de Zaburlín et al. 2014, Salusso and Moraña 2014).

Ceratium furcoides is currently considered an invasive species in South America, which is in an expansion stage. The species can develop blooms in tropical and subtropical reservoirs which, the same as *C. hirundinella*, may produce harmful effects such as unpleasant taste and odor of water, as well as depletion of dissolved oxygen that leads to the death of other organisms. Subsequently, this situation causes a serious impact on local communities, particularly in those countries with problems in water supply (Pollingher 1988, Van Ginkel et al. 2001, Bazán et al. 2007, Pierotto et al. 2007, Hart and Wragg 2009, Matsumura-Tundisi et al. 2010, Meichtry de Zaburlín et al. 2014). In this context, the potential distribution of *C. furcoides* in South America was modeled in order to further investigate the basins susceptible to be invaded, as well as the environmental conditions that influence its expansion.

MATERIALS AND METHODS

Study area and species records. The study area included all South American countries: Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Peru, Suriname, Uruguay and Venezuela. Presence data ($n = 101$) for *C. furcoides* were obtained from the scientific literature (Table 1). For those localities without coordinates, a georeferenced position was derived secondarily following Wieczorek et al. (2004).

Environmental variables. A total of 23 variables were used as predictors, including 19 climatic, three hydrological and one topographical variable (Table 2). Environmental variables

TABLE 1. Sources of *Ceratium furcoides* occurrences in South America used in the distribution model.

Country	Consulted sources
Argentina	Barreda (2014); Meichtry de Zaburlín et al. (2013, 2014); Salusso and Moraña (2014); Bordet F. (2015), pers. comm.
Brazil	Santos-Wisniewski et al. (2007); Matsumura-Tundisi et al. (2010); Oliveira et al. (2011); Amazonas et al. (2012); Silva et al. (2012); Bressane et al. (2013); Cavalcante et al. (2013); Cassol (2014); Cassol et al. (2014); Jati et al. (2014); Moschini et al. (2014); Moreira et al. (2015); Nishimura et al. (2015)
Colombia	Ramírez et al. (2005); Restano et al. (2011); Bustamante Gil et al. (2012); Villabona-González et al. (2014)
Paraguay	Meichtry de Zaburlín et al. (2014)
Uruguay	Bordet F. (2015), pers. comm.

TABLE 2. Variables used in model development. Temperatures are expressed in °C *10, precipitations in mm, elevation in m, and flow accumulation in number of cells.

Variable	Description
alt	Altitude
bio1	Annual mean temperature
bio2	Mean diurnal range (monthly mean, T° max-T° min)
bio3	Isothermality (bio2/bio7) × 100
bio4	Temperature seasonality (standard deviation × 100)
bio5	Maximum temperature of warmest month
bio6	Minimum temperature of coldest month
bio7	Temperature annual range (bio5-bio6)
bio8	Mean temperature of wettest quarter
bio9	Mean temperature of driest quarter
bio10	Mean temperature of the warmest quarter
bio11	Mean temperature of coldest quarter
bio12	Annual precipitation
bio13	Precipitation of wettest month
bio14	Precipitation of driest month
bio15	Precipitation seasonality (coefficient of variation)
bio16	Precipitation of wettest quarter
bio17	Precipitation of driest quarter
bio18	Precipitation of the warmest quarter
bio19	Precipitation of the coldest quarter
acc	Flow accumulation
dir	Flow direction
con	Hydrologically conditioned elevation

were obtained from WorldClim (http://www.worldclim.org) and HydroSHEDS (http://hydrosheds.cr.usgs.gov) at a spatial resolution of 30 arc seconds (~1 km^2). WorldClim provides climatic information derived from weather stations spanning 1950–2000 (Hijmans et al. 2005), and HydroSHEDS provides hydrographic data derived from a SRTM digital elevation model (Lehner et al. 2008). These variables were chosen because it has been reported to provide good results for distribution models in aquatic species (e.g., Kumar et al. 2009, Scholte et al. 2012, Byers et al. 2013, Montecino et al. 2014). All environmental layers were clipped to the extent of the study area.

Modeling of susceptible areas. Model of the potential distribution of *C. furcoides* was estimated by using a maximum entropy algorithm in the MaxEnt software v. 3.3.3k (Phillips et al. 2006, Phillips and Dudík 2008). This algorithm models the species' ecological niche (a set of ecological conditions habitable for a species) by examining the relationship between the locations of known species' presence and the environmental characteristics of that region and then extrapolating from this the regions where similar conditions take place in the study area (Vogler et al. 2013, Beltramino et al. 2015). Seventy-five percent of occurrences were randomly selected and employed in the model training, while the remaining 25% were employed in the model testing. The model output was computed as *logistic*, which returns a map with an estimated probability ranging between 0 (no probability of the species presence) and 1 (high probability of presence). Increased presence probability areas for *C. furcoides* were considered to be more susceptible to invasion by the species (Vogler et al. 2013). The resulting model was evaluated using the area under the curve (AUC) of the receiver operating characteristic curve (ROC curves analyses; Fielding and Bell 1997). The AUC is a threshold independent measure commonly used to assess prediction maps that range from 0.5 (no predictability) to 1 (perfect prediction; Vogler et al. 2013). According to Loo et al. (2007), values above 0.8 indicate a strong prediction. The relative contribution of variables to the development of the model was assessed by means of a jackknife test, and through the response curves obtained in the MaxEnt program as in Vogler et al. (2013) and Montecino et al. (2014).

RESULTS

The model generated had very good performance, with AUC values of 0.975 for training data and 0.912 for test data, with a standard deviation of 0.034. The areas most susceptible to invasion by *C. furcoides* were located in central-east South America (Fig. 1) between 17° and 31° of south latitude mainly linked to the Del Plata basin (Paraná, Paraguay and Uruguay Rivers), the South Atlantic basin (Jacuí River), and comprising northeastern Argentina, eastern Paraguay, southeastern Brazil and northwestern Uruguay. In addition, regions with moderate to high susceptibility were predicted for Colombia, Ecuador, Peru and Bolivia. The areas of lower susceptibility, which would not be suitable for *C. furcoides*, were located in Chile, French Guiana, Guyana, Suriname, Venezuela, and a large portion of Brazil that includes the Amazonas basin (Fig. 1).

The jackknife test of variable importance showed that mean temperature of coldest quarter (bio11), minimum temperature of coldest month (bio6) and annual mean temperature (bio1) were the predictors that most influenced the development of the model when these variables were used alone (Fig. 2). Flow accumulation (acc) exhibited important reduction in training gain when it was removed from the model, thus indicating that contain information necessary for the model. The remaining variables contributed less to model development (Fig. 2). The response curves for the temperatures with the highest training gain (i.e., bio11, 6, 1) were unimodal and are shown in Figure 3. When used in isolation, the higher probability of presence of *C. furcoides* was found ~17°C for bio11 (Fig. 3a), ~10°C for bio6 (Fig. 3b), and between 18°C and 22°C, with optimal ~21°C for bio1 (Fig. 3c). In addition, the probability of *C. furcoides* occurrence was higher at lower levels of flow accumulation and declined gradually with an increase in this predictor (Fig. 3d).

DISCUSSION

In recent years, species distribution models have become a fundamental tool for predicting the potential distribution of invasive species (Peterson 2003, Jeschke and Strayer 2008, Elith and Leathwick 2009, Guillera-Arroita et al. 2015). However, few modeling studies have addressed invasions by freshwater algae species (e.g., Kumar et al. 2009, Montecino et al. 2014). To our knowledge, studies using modeling approaches for predicting areas susceptible to phytoplankton invasions are virtually nonexistent as most

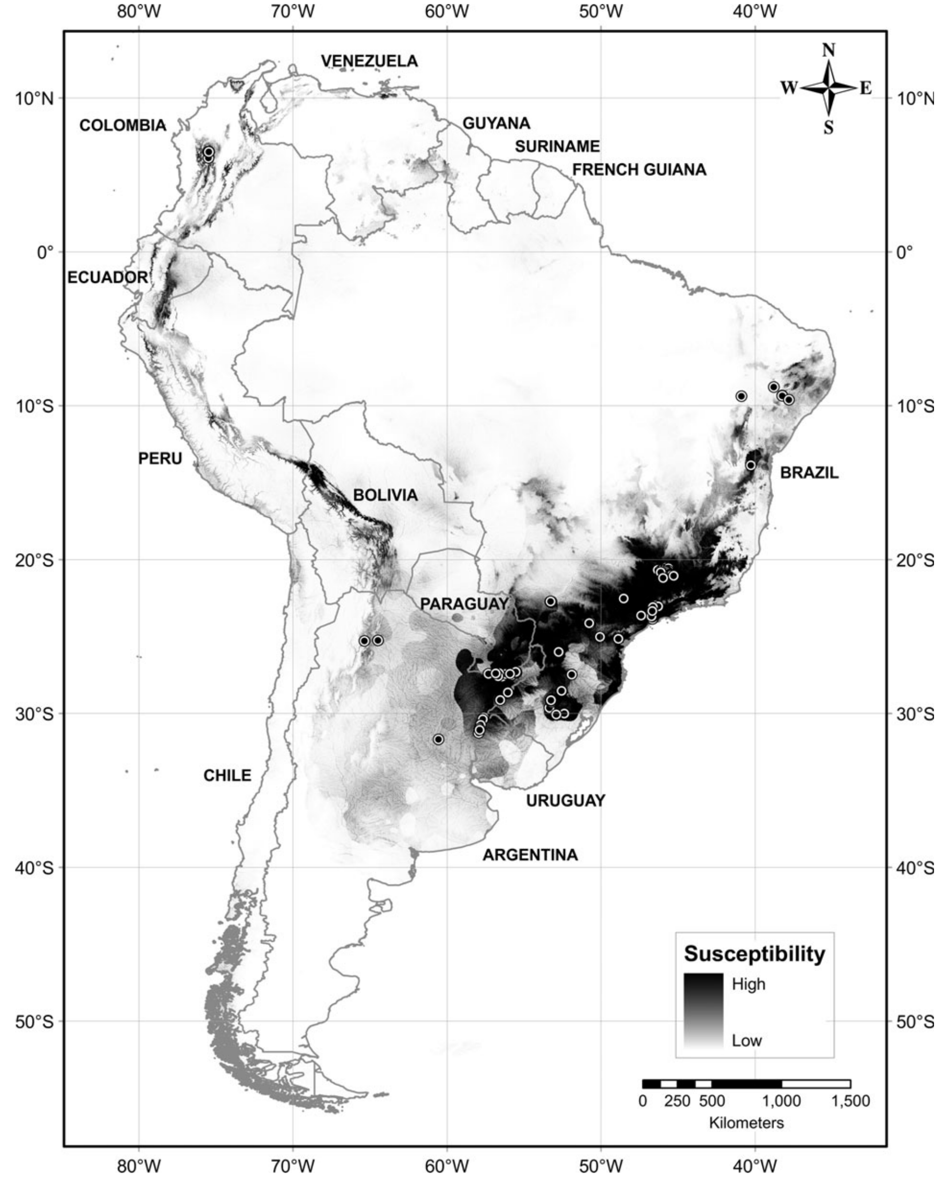

Fig. 1. Potential distribution of *Ceratium furcoides* in South America. Lighter areas indicate low susceptibility regions and darker areas indicate high susceptible regions. Points indicate occurrences records used in study.

of the studies in this field are descriptive, although with good predictions (e.g., *Cylindrospermopsis raciborskii*, *Prymnesium parvum*, *Skeletonema potamos*; Padisák 1997, Duleba et al. 2014, Roelke et al. 2016).

The potential distribution model developed here for *C. furcoides* in South America had a very good performance for the study area, with predictions that indicate that most of the rivers in the Del Plata basin and the South Atlantic basin sensu Agostinho et al. (2007) contain suitable habitats for the species. The flow accumulation was a good predictor of the potential distribution for *C. furcoides*. The model predicted that habitat suitability increase at lower levels of flow accumulation. This variable makes sense in view of the species preference for a high stability of the water column, which may explain its preferential occurrence in reservoirs where higher densities were recorded with low and intermediate flow rates and increased water residence time, as mixing periods inhibit the growth of dinoflagellates populations (Pollingher and Zemel 1981, Reynolds et al. 1983, 2002, Heaney et al. 1988, Strayer 2010, Padisák et al. 2016). Heaney and Butterwick (1985) considered the stability of the water column as a regulatory factor in the size of *Ceratium* spp. populations, and Cassol (2014) also emphasized the importance of the stability of the water column, the thermal stratification and the temperature for the development of *C. furcoides*. According to the obtained results, mean temperature of coldest quarter, minimum temperature of coldest month and annual mean temperature were the variables that have the most significant effect on the potential distribution of *C. furcoides*. Thus, the environments most susceptible to invasion would be those with an

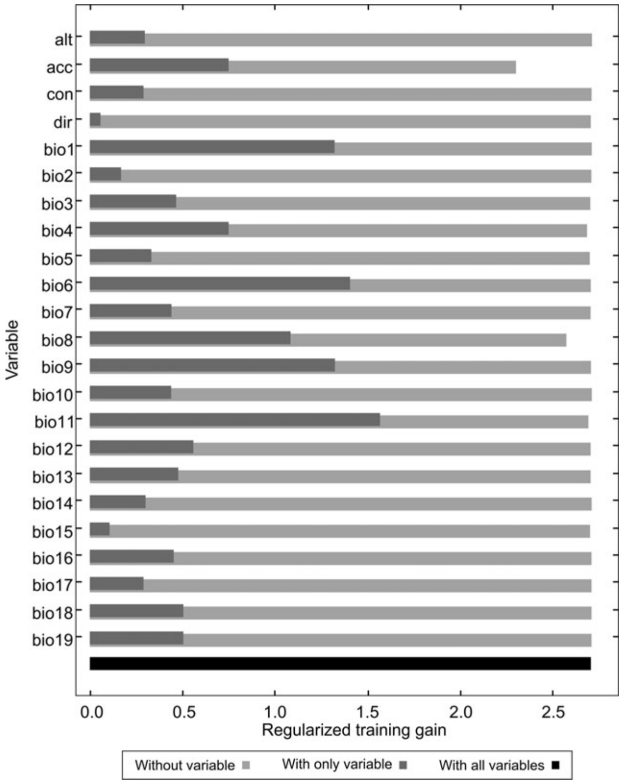

FIG. 2. Relative importance of the environmental variables for the potential distribution of *Ceratium furcoides* in South America based on the jackknife test. For abbreviations, see Table 2.

annual mean temperature between 18°C and 22°C. In addition, the higher probability of the presence of *C. furcoides* was close to 17°C and 10°C when the mean temperature of coldest quarter and the minimum temperature of coldest month were considered in isolation, respectively. Taking into account what is known about the thermal tolerance ranges for the species, this information is consistent with the cell division of *C. furcoides*, which is limited by high and low temperatures. A temperature of 10°C was found by Heaney et al. (1983) as the threshold for vegetative growth. Butterwick et al. (2005) pointed out that the species show no growth at temperatures below 10°C and above 25°C, with a maximum growth observed at 20°C. In addition, Cassol (2014) determined a temperature of 20°C as the most propitious for its development.

The results suggest that the most suitable conditions for the species are mainly located in the subtropical and temperate regions of South America. According to the model, those basins located in Guyana, French Guiana, Suriname, Venezuela and Chile would be the least susceptible to invasion. In Brazil, a large area that covers most of the Amazon, Tocantins and part of the North Atlantic *sensu* Agostinho et al. (2007) basins were found to have low susceptibility; the highest mean temperature values recorded for these environments possibly make them less suitable for the invasion of *C. furcoides*. In addition, the São Francisco River basin would be in an intermediate situation, and the Paraná, Uruguay and South Atlantic basins would have a much greater risk of invasion, a fact that might account for the species spread toward the temperate regions of central and southern Argentina and Uruguay. In Paraguay, despite the fact that the majority of the eastern portion of the country can be considered as a highly susceptible area, *C. furcoides* has only been reported in the Yacyretá Reservoir in the High Paraná River (Meichtry de Zaburlín et al. 2014). The absence of reports from any other regions of this country may reflect the lack of sampling in freshwater environments. Due to the number of occurrences of *C. furcoides* in Argentina along the Paraguay border, it can be assumed that the species may occur in other locations of Paraguay but its presence has not yet been reported. In Argentina, the northeast region shows varying degrees of susceptibility but the overall trend is toward a medium-high susceptibility level. Even the south central area could be recognized as susceptible, although with a low probability. For Bolivia and Peru, model indicates that the area of highest susceptibility involves Lake Titicaca; the presence of genus was reported in this lake although the species implicated was not determined (Fontúrbel et al. 2006). In Ecuador, much of the country contains areas of high susceptibility. Also regions of medium–high susceptibility were identified for Colombia, mainly linked to the Magdalena River where the species has already been registered (Ramírez et al. 2005, Restano et al. 2011, Bustamante Gil et al. 2012, Villabona-González et al. 2014).

Based on the potential distribution pattern, the species would not occur either in the southernmost region of South America characterized by strong seasonality and low temperatures, or in the north of the subcontinent where mean temperatures are high. However, large areas of temperate southern South America would contain minimal conditions for the establishment of the species, similar to those reported in temperate areas of Europe where *C. furcoides* is considered a summer species (Heaney et al. 1988, Hickel 1988, Pollingher 1988, Reynolds 1996, Hansen and Flaim 2007, Pandeirada et al. 2013). By contrast, *C. furcoides* blooms in South America are recorded mostly during winter and spring months (Matsumura-Tundisi et al. 2010, Nishimura 2012, Serico et al. 2012, Silva et al. 2012, Cortez 2013, Cassol 2014). Blooms of this species produce direct impacts on the ecosystems, such as: (i) fish and invertebrates mortalities through deoxygenation of the water column, (ii) changes in the structure of planktonic communities (e.g., zooplankton composition), and (iii) unpleasant taste, odors or objectionable appearance of water for human use, as well as filter clogging in water purification processes (Hart and Wragg 2009, Matsumura-Tundisi et al. 2010).

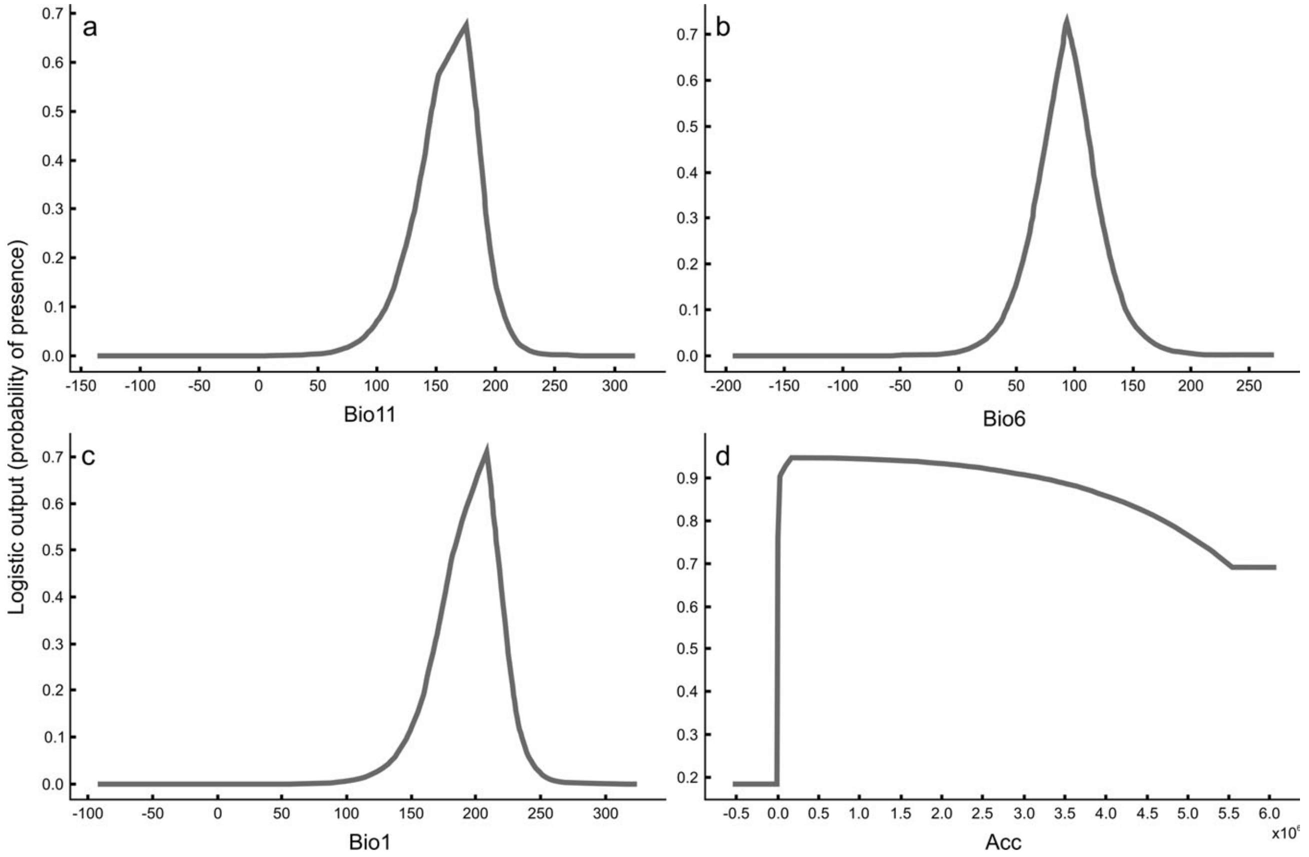

Fig. 3. Marginal response curves for the four strongest environmental predictors. (a) Mean temperature of coldest quarter (bio11); (b) Minimum temperature of coldest month (bio6); (c) Annual mean temperature (bio1); (d) Flow accumulation (acc).

Current presence records of *C. furcoides* in South America encompass a wide diversity of environments in terms of geomorphology, hydrology, sediment transport, and water chemistry, suggesting a high degree of ecophysiological adaptability of this dinoflagellate, as it has been observed in other invasive phytoplankton species (e.g., Padisák 1997). This is in agreement with the statement that temperature may not necessarily be the only designer of distribution patterns in phytoplankton species (Padisák et al. 2016). Thus, while climatically suitable areas for *C. furcoides* were identified for different aquatic systems in South America, it is worthy to mention that the influence of limnological variables on each system (e.g., pH, conductivity, trophic status) may limit or even exclude the presence of *C. furcoides*. However, delineating the climatically suitable areas that might be excluded by the limnological variables is a difficult task in light of the current knowledge. This issue clearly requires further and specific investigation.

At this point, when interpreting the areas susceptible to invasion it is important to consider the eventual coexistence between *C. furcoides* and *C. hirundinella* and the difficulty to distinguish them from each other, since they are morphologically and ecologically similar and exhibit a great variety of morphotypes (Heaney et al. 1988, Santos-Wisniewski et al. 2007, Matsumura-Tundisi et al. 2010, Bustamante Gil et al. 2012). A high percentage of dubious determinations found in literature suggest that *C. furcoides* might be present in several areas indicated by the model as suitable but not yet reported. In this sense, due to the difficulty of specific identification by nonspecialists, it seems probable that the current range of *C. furcoides* in South America is certainly underestimated. Moreover, it has been suggested that the formation of cysts represents a major factor promoting dispersal in *Ceratium* (Mac Donagh et al. 2005). Regarding to the ongoing invasion of this genus in South America, Padisák et al. (2016) pointed out the need to investigate the dormancy period. According to the present knowledge, *Ceratium* cysts need an obligated dormant stage (Heaney et al. 1983, Rengefors and Anderson 1998, Rengefors et al. 1998, Padisák et al. 2016), although also a perennial behavior has been reported mostly from Spain (Pérez-Martínez and Sánchez-Castillo 2001). In the context of this study, we agree with the need to deepen the knowledge about dormancy period, as it could have significant implications in the spread of *C. furcoides* in South

American basins. Other main factor underlying the dispersal of species of this genus includes human activities usually considered as vectors of invasive species in freshwater ecosystems, e.g., navigation, commercial and sport fishing, ornamental trade, ecotourism, recreational activities (Incagnone et al. 2015). Although the arrival of cells or cysts is a prerequisite for an establishment to be successful, it is also necessary that freshwater habitats provide adequate conditions for cell survival, growth and the formation of blooms.

We identified that a large area of South America is susceptible to be invaded by *C. furcoides.* The rapid expansion and establishment of this species in this region of the world might be associated with changes in the hydrological regime and water quality of rivers following the construction of numerous reservoirs in the main South American basins (Padisák et al. 2016). In addition, it could be expected an increase in blooms of this harmful dinoflagellate as a consequence of climate change. An increase in water temperature and changes in pH, patterns of vertical mixing and stratification of the water column, precipitation and evaporation have been predicted as results of global warming. This would involve major changes in the composition of phytoplankton, and highly motile organisms such as dinoflagellates that are capable to optimize floating in the water column will be better adapted to the novel conditions (Moore et al. 2008, Winder and Hunter 2008).

Finally, it is expected that the model developed here will be useful for efforts from the responsible authorities of water resource management to assess risk, define surveillance areas and mitigate the potential impacts of *C. furcoides* in countries where the invasion has been recently confirmed or has not yet been reported.

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