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Species distribution models as a tool for early detection of the invasive *Raphidiopsis raciborskii* in European lakes

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ABSTRACT

In freshwater habitats, invasive species and the increase of cyanobacterial blooms have been identified as a major cause of biodiversity loss. The invasive cyanobacteria *Raphidiopsis raciborskii* a toxin-producing and bloom-forming species affecting local biodiversity and ecosystem services is currently expanding its range across Europe. We used species distribution models (SDMs) and regional bioclimatic environmental variables, such as temperature and precipitation, to identify suitable areas for the colonization and survival of *R. raciborskii*, with special focus on the geographic extent of potential habitats in Northern Europe. SDMs predictions uncovered areas of high occurrence probability of *R. raciborskii* in locations where it has not been recorded yet, e.g. some areas in Central and Northern Europe. In the southeastern part of Sweden, areas of suitable climate for *R. raciborskii* corresponded with lakes of high concentrations of total phosphorus, increasing the risk of the species to thrive. To our knowledge, this is the first attempt to predict areas at high risk of *R. raciborskii* colonization in Europe. The results from this study suggest several areas across Europe that would need monitoring programs to determine if the species is present or not, to be able to prevent its potential colonization and population growth. Regarding an undesirable microorganism like *R. raciborskii*, authorities may need to start information campaigns to avoid or minimize the spread.

1. Introduction

Climate change is a catalyst for the global expansion of harmful invasive bloom-forming algae in aquatic environments (Paerl and Huisman, 2009). Outside their native range, invasive species pose a threat to biodiversity, ecosystem functioning, economy and human health (Litchman, 2010). In recent decades, the number of species that have spread into new freshwater habitats has increased, mainly due to dispersal through natural pathways such as active or passive movement through connected waterways, wind and, migrating birds as well as human-mediated mechanisms such as commercial and recreational activities (Incagnone et al., 2015). In freshwaters, bloom-forming cyanobacteria can be problematic, resulting in impaired water quality and security (Richardson et al., 2019). The impacts of cyanobacterial blooms are extensive, ranging from environmental asphyxiation due to excessive consumption of oxygen (causing the deaths of fish and benthic invertebrates, among others) to problems in leisure areas, when blooms forms colorful and often smelly scum on the water surface (Benayache et al., 2019). Additionally, some species of cyanobacteria produce secondary metabolites (cyanotoxins) leading to neurological, hepatic and digestive diseases, which cause water quality problems for fisheries, aquaculture, farming, and sanitary threats to human and animal health (Benayache et al., 2019).

Detecting an invasive species at an early stage is crucial to ameliorate or mitigate potentially harmful effects in a cost-effective way (Morisette et al., 2020; Reaser et al., 2020). However, the early detection of aquatic invasive species, particularly microorganisms, is challenging (Bolius et al., 2019; Litchman, 2010). For example, if their biomass is low, many cyanobacteria are able to survive undetected in freshwater habitats, allowing them to continue dispersing unobserved (Sukenik et al., 2012),

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hence the term "invisible invader" (Litchman, 2010). This might create a significant risk to freshwater habitats and native species that will be exposed to the microorganism's harmful effects (Figueredo and Giani, 2009). For example, one of the main threats of non-native cyanobacteria is the production of secondary metabolites, functioning as allelochemicals that could inhibit the growth of other phytoplankton species and grazers, affecting the whole food web (Ger et al., 2014; Paerl and Paul, 2012).

A suitable tool to forecast where a species may find suitable conditions to establish are species distribution models (SDMs), statistical procedures that link occurrence records of a species to environmental variables to estimate spatial distribution patterns using a correlative approach (Escobar et al., 2018; Leidenberger et al., 2015). In invasion biology, SDMs are increasingly used to forecast invasion risk and to improve approaches to control their expansion (Barbet-Massin et al., 2018; Bradley et al., 2010; Tingley et al., 2018). However, two central assumptions of SDMs do not hold when modeling invasive species, (i) they are not in equilibrium with their environment and, therefore, (ii) niche quantification and transferability in space and time are limited (Gallien et al., 2012). The violation of the climatic equilibrium assumption has some repercussions on the potential climatic niche of the species, which could potentially underestimate the geographical area the species can occupy (Barbet-Massin et al., 2018; Václavík and Meentemeyer, 2012). Even though SDMs cannot predict the complete potential invasion range of an invasive species that has recently established, they are still valuable for invasive species management and can be a powerful tool to predict where invasive species are more likely to disperse and establish next (Barbet-Massin et al., 2018; Václavík and Meentemeyer, 2012; Warren and Seifert, 2011). Identifying areas where a species is more likely to occur can also be used to guide sampling protocols and prioritize areas of study (Guimarães et al., 2020).

The invasive cyanobacteria *Raphidiopsis raciborskii* (former name *Cylindrospermopsis raciborskii*), a toxin-producing and bloom-forming species known to impact local biodiversity (Svirčev et al., 2016; Svirčev et al., 2014) and ecosystem services (Hawkins et al., 1985), is currently expanding its range across Europe (Wilk-Woźniak et al., 2016). As a cosmopolitan species of tropical origin, *R. raciborskii* thrives in reservoirs, lakes, and rivers worldwide (Sinha et al., 2012; Yang et al., 2018); in Europe this species has been shown to proliferate in shallow, turbid, and eutrophic/hyper-eutrophic lakes (Kokociński et al., 2009; Kokociński and Soininen, 2012). Dispersing from the tropics to northern temperate regions, *R. raciborskii* is now found on almost all continents in many climatic zones (Wilk-Woźniak et al., 2016). In the last few decades, *R. raciborskii* has migrated towards the northern regions of Europe, reaching lakes in countries such as Poland and Lithuania (Kokociński et al., 2017), with the most northern point recorded being Lake Nero, in Russia (57°09′26.0″N, 39°25′35.5″E; Babanazarova et al., 2015). Prediction of the geographic areas that meet the climatic conditions required by *R. raciborskii* can be used to estimate areas where *R. raciborskii* is present but currently undetected. This is especially important in lake rich countries like Sweden, where the phytoplankton composition is known in only a small proportion (1500 lakes in the National monitoring database, https://miljodata.slu.se/MVM/Search) of the over 100 000 lakes, to focus monitoring efforts of this species.

In this paper, we used SDMs to visualize and predict the potential distributional patterns of *R. raciborskii* across Europe to 1) identify potential habitats for *R. raciborskii*; 2) identify important climatic variables underpinning establishment; and 3) ultimately predict lakes in northern parts of Europe that are at risk of invasion. We based the SDMs on published observations of *R. raciborskii* and environmental predictors obtained from climatic models. The resulting probability of occurrence map can be used in risk assessments by authorities and to design monitoring programs and information campaigns to protect the health of both citizens, domestic animals and the aquatic environment.

2. Materials and methods

2.1. Occurrence data

Raphidiopsis raciborskii records were retrieved from published studies and reports found in Scopus, Google scholar and Google using the search terms "*Raphidiopsis raciborskii*", "*Cylindrospermopsis raciborskii*" or "*Amoeba raciborskii*" (i.e. including former names of the species), and delimiting the search to European countries (Table S1, Supplementary materials). When an exact location (latitude and longitude) was not included, but there was a map showing the sampling sites, Google Earth was used to extract the points to match with the locations shown on the maps. When information regarding a country was not retrievable via literature due to scarcity of complete datasets or ambiguity, the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/) or direct contact with the author of the paper were used. All records with positional uncertainty and duplicates with same coordinates were removed to increase accuracy and reduce risk of overfitting. Occurrences were grouped to obtain one observation per 2.5 arc-minute grid cell (~4.5 km^2) to match the Worldclim (Fick and Hijmans, 2017) environmental predictors' resolution. These steps resulted in a European dataset of lakes comprising 209 unique data points, with records of *R. raciborskii* (Fig. 1) distributed across 17 countries (Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Italy, Lithuania, Montenegro, the Netherlands, Poland, Portugal, Serbia, Slovenia and Spain; Table S1).

2.2. Environmental variables

High spatial resolution climatic data were used in the model: bioclimatic variables related to temperature, precipitation, average altitude, and yearly solar radiation (Table S2, from WorldClim 2.1, http://worldclim.org/version2; Fick and Hijmans, 2017). These 21 environmental variables have previously been used to predict cyanobacterial blooms as well as the invasive potential of selected phytoplankton, phytobenthic and aquatic plants species (Guimarães et al., 2020; Meichtry de Zaburlín et al., 2016; Montecino et al., 2014; Wittmann et al., 2017). Air-temperature was used as a proxy for water-temperature as they are highly correlated (Montecino et al., 2014) and temperature is known to be a strong predictor of cyanobacteria growth and metabolism (Guimarães et al., 2020). Precipitation is considered as one of the most important carriers of nutrients to freshwater habitats due to runoff (Guimarães et al., 2020). Solar radiation is the basic energy input for autotrophic organisms like cyanobacteria (Khanipour Roshan et al., 2015). Altitude, besides being related to temperature, often indicates exposure to human activities and eutrophication (De Oliveira et al., 2019; Guimarães et al., 2020; Teittinen et al., 2016). Only non-collinear predictors were used in the final model (Feng et al., 2019).

2.3. Species distribution models (SDMs)

We built ensemble SDMs prediction using the Biomod2 package for R version 3.6.1 (Thuiller et al., 2009; R Core Team, 2020). Together with *R. raciborskii* presence data and the environmental variables, we included a random set of pseudo-absences at a minimum distance of 0 km to presence records (1000 pseudo-absences) as recommended for reliable models (Barbet-Massin et al., 2012). We used four different algorithms, Generalized Linear Model (GLM), Generalized Boosted Models (GBM), Maximum Entropy (Maxent; Phillips et al., 2004) and Generalized Additive Models (GAM). As independent data were not available, 70% of the data were used for model calibration, whilst the remaining 30% of the data were used for model validation. Each model algorithm was run four times. Model performance was evaluated with the true skill statistic (TSS; Allouche et al., 2006; Ruete & Leynaud, 2015), defined as sensitivity + specificity -1. For the final ensemble model, we used a

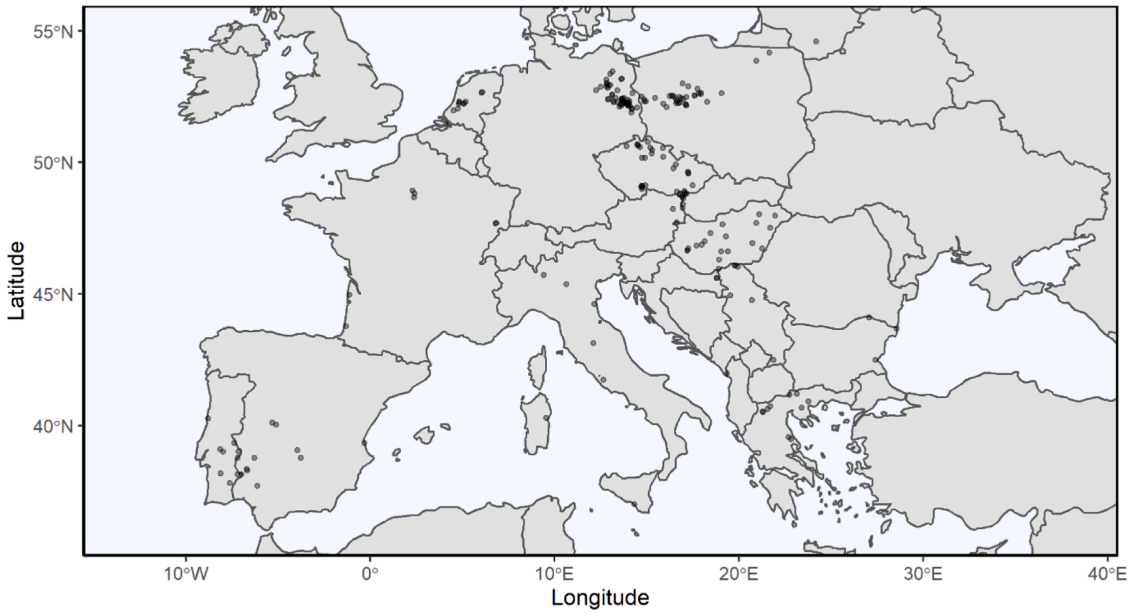

Fig. 1. *Raphidiopsis raciborskii* occurrences in European lakes based on published data in the scientific literature, GBIF or direct contact with the author of the paper.

threshold of TSS $\geq$ 0.6 to guarantee that only accurate models were included.

2.4. *Targeting results to eutrophic lakes*

Cyanobacteria blooms in Scandinavian lakes and elsewhere are correlated with high total phosphorus (TP) concentrations (Vuorio et al., 2020). However, published data on the occurrence of *R. raciborskii* did not include adequate information of nutrient levels to be included as an environmental predictor variable in the SDMs. We included data from a number of nutrient-rich Swedish lakes to more accurately predict areas at risk of *R. raciborskii* invasion, to compare with the probability of occurrence map. Total phosphorus data for 4800 lakes, sampled between mid-September and mid-November (once during a six-year reporting cycle) and analyzed by a certified lab (Fölster et al., 2014), were retrieved from the Swedish environmental monitoring database (https://miljodata.slu.se/MVM/Search). Three nutrient groups were used: 0 - 20 µg/L, 20 - 50 µg/L and > 50 µg/L, representing TP concentrations that characterize risk of low to high levels of cyanobacterial blooms (Vuorio et al., 2020).

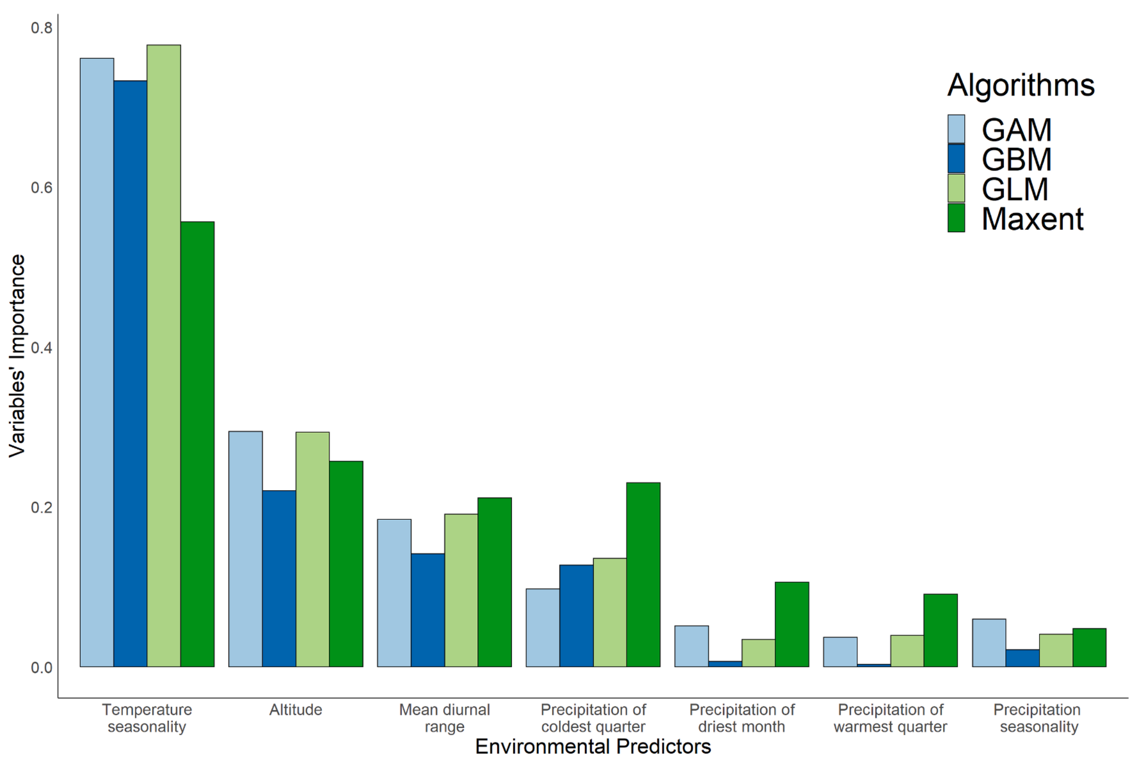

Fig. 2. Variables Importance, for each algorithm, influencing the probability of occurrence of the cyanobacterium *Raphidiopsis raciborskii* in Europe.

3. Results

In model calibration, only non-collinear predictors were retained (Variance of Inflation Factor, VIF < 4) resulting in 7 of the 21 available environmental variables included in the final model: mean diurnal temperature range; temperature seasonality; precipitation of driest month; precipitation seasonality; precipitation of the warmest quarter; precipitation of coldest quarter; and altitude.

SDMs accurately predicted approximately 85% of *R. raciborskii* presences in Europe (sensitivity) and 89% of the pseudo-absences (specificity) with an ensemble TSS value of 0.747 (Table S3). Variable importance estimates showed that temperature seasonality and altitude were the two most relevant environmental predictors in all four algorithms (Fig. 2; Table S4). Temperature seasonality between 4–8 °C resulted in a high probability of occurrence of *R. raciborskii*, whereas at higher values probabilities decreased (Fig. S1). For altitude, the probability of occurrence was lower at altitudes > 500 m a.s.l., suggesting a preference for lowland lakes (Fig. S2).

The ensemble probability of occurrence map shows suitable habitats for the occurrence of *R. raciborskii* in many areas of Europe (Fig. 3). The map also highlighted areas with zero or low occurrence probability (<0.5), e.g. in the mountainous regions of continental Europe and the Nordic countries (Norway, Finland, and northern Sweden). Areas with occurrence probabilities > 0.5 were concentrated in areas where *R. raciborskii* has been recorded, particularly in central Europe. Interestingly, the southern and central regions of Sweden showed areas with high occurrence probability (> 0.5), indicating areas where *R. raciborskii* may have already colonized or where future invasions may occur (Fig. 3). In addition, the probability of occurrence map identified several areas of high suitability in the southern and central regions of Europe, where occurrences of *R. raciborskii* have not been recorded. Thus, the results from this study suggest several areas across Europe that need further study to determine if this problematic species is present or not.

The area of suitable climate (Fig. 3) for *R. raciborskii* corresponded to areas with lakes of medium and high concentrations of TP in the southeast of Sweden (Fig. 4). Accordingly, lakes in this area with moderate to high TP concentrations are recommended to be targeted for increased monitoring for early detection and to possibly implement management interventions.

4. Discussion

4.1. Climatic conditions influencing potential occurrences of Raphidiopsis raciborskii

This study showed that low temperature seasonality was the main factor determining the high probability of occurrence of *R. raciborskii* in Europe. Based on results, we interpreted that with low temperature seasonality the number of days with warmer weather are prolonged, as there is less variation between seasons, resulting in a longer growth season for *R. raciborskii* to thrive. This conjecture is supported by a recent study of eutrophic lakes in Poland. Lenard et al. (2019) showed that concentrations of chlorophyll-a, total biomass of phytoplankton and cyanobacteria were considerably higher after milder winters. Hence, as the seasons become milder and there is less extreme or pronounced seasonal variability, the presence and duration of cyanobacterial bloom events might increase. Although *R. raciborskii* has not yet been recorded in Sweden, our modeling indicates that favorable conditions exist in the southern and central regions. Consequently, there is a high probability that the species may increase its geographical distribution into this area in the near future. Altitude was the second-best predictor determining the probability of occurrence of *R. raciborskii*. Our model results show that above 500 m a.s.l. the probability of *R. raciborskii* decreases markedly. This finding is not surprising as lowland areas generally have milder climates. Furthermore, lowland lakes are often situated in catchments that are affected by land use such as agricultural and urbanization, resulting in elevated nutrients that favor cyanobacterial blooms (Cordeiro et al., 2020). By complementing climatic variables with information on the nutrient status of Swedish lakes, we were able to identify areas of high risk for invasion success. These findings indicate that if/when dispersal occurs it is highly probable that *R. raciborskii* will become established and possibly result in problematic cyanobacterial

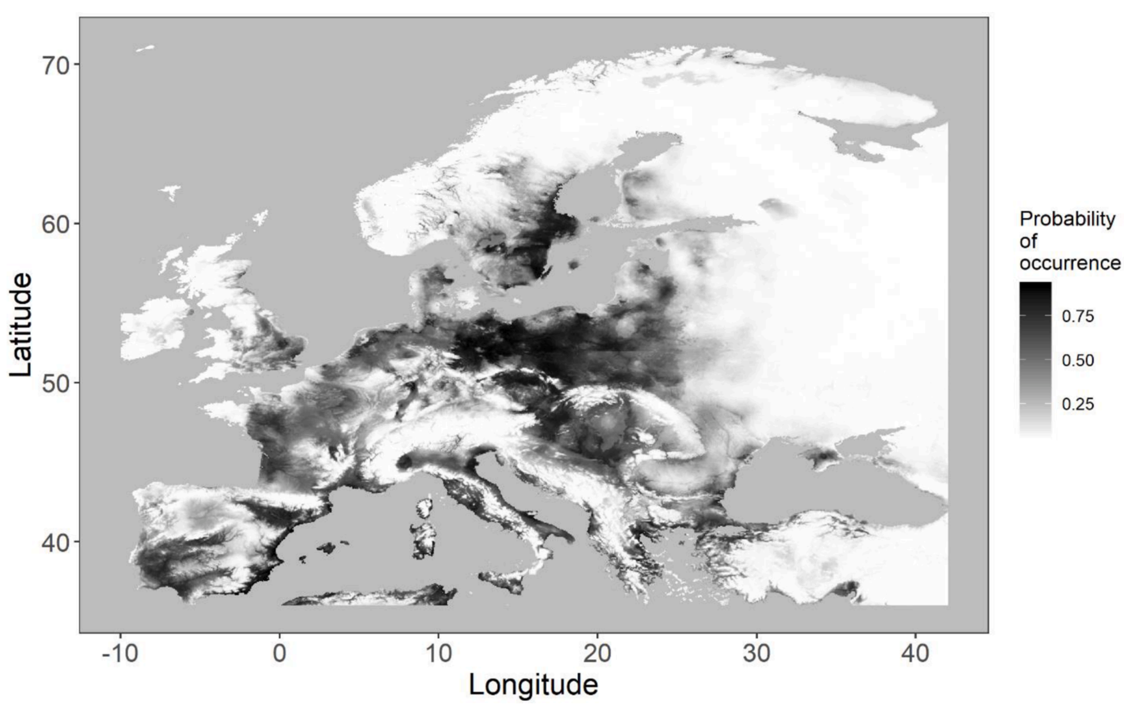

Fig. 3. *Raphidiopsis raciborskii* (Cyanobacteria) SDMs ensemble probability of occurence map for Europe based on presence data from 209 sites and climatic grid based variables. Black color show high probability of occurrence if standing water is present, while lighter shades of black show intermediate probability of occurrence, and white color shows a probability of occurrence close to zero.

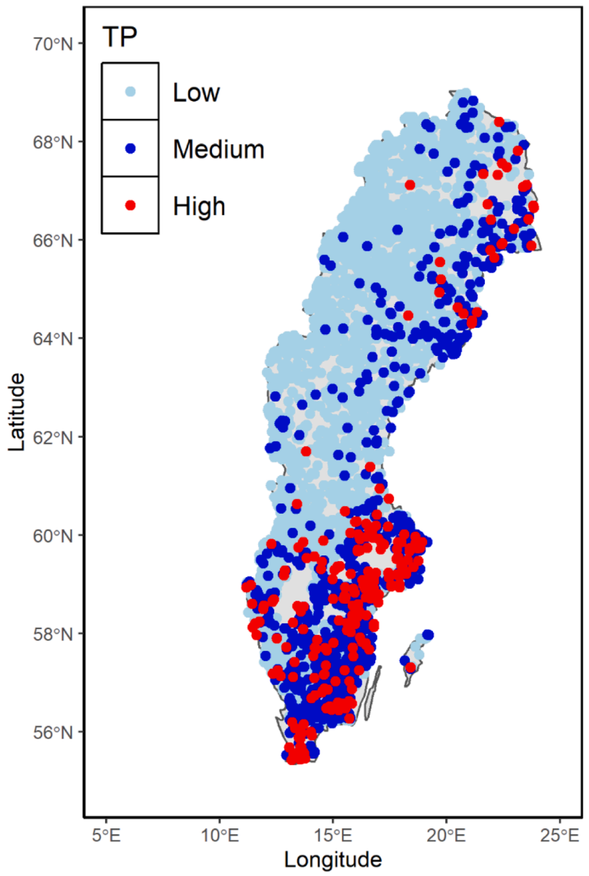

Fig. 4. TP concentrations of 4800 Swedish lakes. Light blue dots, represent lakes with low concentrations of TP (< 20 μg/l), blue dots represents lakes with moderate concentrations of TP (between 20 and 50 μg/l) and red dots represent high concentrations of TP (> 50 μg/l). Eutrophic and hypereutrophic lakes are mainly located in central/south of Sweden, where the large cities and agricultural areas are situated.

blooms. This result narrow down the number of lakes for specific monitoring efforts in search for this invasive cyanobacterium.

4.2. Non-climatic factors helping with microorganism's dispersal

Dispersal limitation is one of the main factors regulating the distribution and range expansion of a species. For an invasive microorganism like *R. raciborskii*, dispersal limitation is often overcome by the presence of a resting stage (e.g. akinetes), as these are easily transported by both physical and/or biological vectors (Padisák, 1997). Migratory water birds are considered as an important long-distance vector for the dispersal of resting stages between freshwater habitats (Bauer and Hoye, 2014; Incagnone et al., 2015). Indeed this is likely a very important vector in Europe as birds migrate between southern and northern areas for nesting and overwintering (Incagnone et al., 2015). Moreover, there is a high probability that resting stages of certain cyanobacteria are continuously being transported into new areas, but viable populations are unable to establish until favorable environmental conditions are reached (Cellamare et al., 2010; Kaštovský et al., 2010). On smaller spatial scales, humans may facilitate dispersal by using lakes for recreation. Although it is unknown if *R. raciborskii* is currently occupying new freshwater habitats predicted by our models, it is important to closely monitor its ongoing range of expansion in Europe and, in particular, in Northern Europe.

4.3. How to improve the model

Species distribution models are useful to predict habitats suitable for colonization by an invasive species outside the endemic range, in particular when knowledge of a species geographic distribution is incomplete (Guimarães et al., 2020). This information is critical to evaluate if colonization of a region is climatically feasible, to predict potential dispersal pathways, and for selecting high-risk sites for regular monitoring (Guimarães et al., 2020; Marcelino and Verbruggen, 2015). The invasive cyanobacterium *R. raciborskii* has been expanding its range relatively unobserved for the past few decades, although interest in understanding the factors underpinning its dispersal, colonization and population growths has recently increased (Falfushynska et al., 2019; Svirčev et al., 2016; Supplementary material S1). In our study, we predicted geographic areas that meet the environmental conditions of *R. raciborskii*, and accordingly we have identified areas that are suitable for successful invasions.

When a species occupies a new environment, it will have to cope with not only environmental factors but also potential biotic resistance in the ecosystem, in form of e.g. interspecific interactions, that can act as a species-sorting filter reducing the probability of occurrence (Bombi et al., 2009; Engström-Öst et al., 2015). Biotic interactions may be implemented through mechanistic models and can have large effects on species distributions. However, biotic interactions are difficult to include in the modeling processes as they are less well known; this is particularly true for invasive microorganisms. Our database comprised published scientific data, reports and occurrences recorded in GBIF. The addition of true absences and biotic interactions in the modeling approach would probably increase model accuracy of the actual distribution of the species (Pineda and Lobo, 2009).

The development of cyanobacterial blooms is usually associated with high nutrient levels and weather conditions such as high temperature and precipitation (Deng et al., 2014; Guimarães et al., 2020; Vuorio et al., 2020). Phosphorus is considered the most important nutrient for the development of cyanobacterial blooms in freshwater habitats (Guimarães et al., 2020; Vuorio et al., 2020). However, as discussed, in our study information on lake nutrient levels was not included in the SDMs, as information from the literature was incomplete. Inclusion of total phosphorus as a predictor variable would have likely increased the accuracy of our models in predicting potential blooms of *R. raciborskii* and not simply occurrences in freshwater environments. At a continental level, climate can be considered the dominant factor affecting species distributions, while at local scales factors like substrate (e.g. nutrients), biotic interactions and anthropogenic impacts typically become more important (Marcelino and Verbruggen, 2015). When information in areas with high probability of occurrence is available, local drivers affecting the distribution of *R. raciborskii* can be used to develop a mechanistic model to better understand and ultimately manage range expansions of undesirable organisms.

In addition, to further predict *R. raciborskii* blooms in new invaded areas, we need an understanding of genetic diversity and potential for local adaptation. In fact, the worldwide expansion of *R. raciborskii* could also be explained by the presence of several ecotypes with differences in their physiology, which might explain its tolerance and success in a wide range of different environmental conditions (Piccini et al., 2011). This intraspecific variation is fundamental for *R. raciborskii* success by providing an adaptable population to different environmental pressure and this plasticity, in reaction to different environmental conditions, can increase its realized niche (Baxter et al., 2020; Burford et al., 2016). An explanation for the occurrence of *R. raciborskii* in single lakes both in Lithuania and Russia may be explained by phenotypic plasticity or local adaptation to lower temperatures (Kokociński et al., 2017). However, why the species has not yet expanded to neighboring lakes remains unknown (Kokociński et al., 2017). According to our results, there is a medium-high probability of occurrence of *R. raciborskii* in Lithuanian lakes. This means that based on environmental conditions alone, *R. raciborskii* might be able to establish at those relatively high latitudes. Intraspecific variation should be taken into consideration in experimental designs for predicting and understanding potential success of invasive cyanobacteria. This information could then be used for developing SDMs to predict future *R. raciborskii* blooms in areas where the species has not been observed.

4.4. Management implications

Due to the high cost of monitoring and surveillance programs designed for early detection of invasive species in aquatic habitats, predictive models are often a cost-effective management tool (Barbet-Massin et al., 2018). The benefits of estimating and projecting invasion risk can be very important to assist decision makers and implement sampling effort in areas at high risk of invasion (Srivastava et al., 2019). If the invasive species is already established, managers need to focus more on how to control population growths in the invaded ecosystem to mitigate effects as well as to minimize dispersal and colonization to other ecosystems (Prior et al., 2018). For example, regarding an undesirable microorganism like *R. raciborskii*, authorities may need to start information campaigns to minimize the spread to other lakes via swimwear, diving equipment, fishing gear and boats. In addition, managers may try to control the severity of cyanobacteria blooms through land management and nutrient loading (Stroom and Kardinaal, 2016).

5. Conclusions

The need to model the potential occurrence of this species has been recently highlighted because of its adverse effects in aquatic habitats, human health, and economical loss. To our knowledge, this is the first attempt to predict the suitability of European lakes for the establishment of *R. raciborskii*. Our model predictions showed that the southeastern part of Sweden is an area of concern for potential invasion. Furthermore, our results suggest many suitable habitats across many parts of Europe, signaling that regionally monitoring programs should specifically focus on this invasive and harmful species. In lakes, where *R. raciborskii* is recorded, monitoring programs should include measures of nutrient status to be able to refine predictive models and be able to understand the variables underpinning dispersal and establishment of this unwanted species, as it is the first line of defense.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2022.102202.

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