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USING PLANKTONIC SPECIES AS MODEL ORGANISMS FOR UNDERSTANDING BIOLOGICAL INVASION DYNAMICS IN A CHANGING WORLD

SÃO CARLOS – SP
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Tese apresentada ao Programa de Pós-graduação em Ecologia e Recursos Naturais, do Centro de Ciências Biológicas e da Saúde, da Universidade Federal de São Carlos, como um dos requisitos para a obtenção do título de Doutor em Ciências (Ciências Biológicas), área de concentração em Ecologia e Evolução.

Orientador: Profª. Drª. Odete Rocha

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In dedication to my nuclear family, Sueli M. Lacerda, Jaime da S. Macedo and Jéssica L. M.

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SUMMARY

ABSTRACT

The ability of species to become invasive (ie, species invasiveness) can be investigated through multiple approaches based on ecological and evolutionary characteristics associated with the ability of species to overcome a series of barriers and filters until proper invasion. Until now, formal attempts aiming to define plankton invasions based on niche and whether invasive plankton species reliably respond to environmental parameters are overlooked. Therefore, in this study we analyzed the correlation between the occurrence of invasive and potentially invasive species in plankton and environmental variables, including future climatic alterations, and habitat features. We applied species distribution models for the species and reconstructed the niche spaces occupied using different approaches and algorithms considering their invasion history and invasion processes. We tested the hypothesis of niche conservatism and predicted suitable areas for future invasions of non-native species: *Ceratium furcoides* (dinoflagellate), *Moina macrocopa* and *Cercopagis pengoi* (cladocerans). In addition, we described and modeled the global social-economic costs of planktonic invasive species using the most comprehensible database – the *INVACOST*. Notably, all models reliably supported our hypotheses allowing three main conclusions: (i) Niche shift was detected for one species *C. furcoides*, while niche unfilling was found for the *M. macrocopa* and *C. pengoi*, requiring further investigations on that species regarding evolutionary aspects favoring their expansion; (ii) Future environmental climate allow processes of expansion and colonization in highly disturbed environments such as hydroeletrical reservoirs and temporary ponds. (iii) Impact assessments needs improvement as both taxonomic and geographic gaps exist for the social economic costs of plankton invasions globally. Based on our findings, we strongly believe that these perspectives can contribute to increasing knowledge of the mechanisms that drive plankton invasions, to point the direction for which species and environments need more attention, and to rise novel hypotheses on the invasion processes of fast-evolving planktonic organisms.

Keywords: Non-native cladocerans, invasive dinoflagellate, plankton invasiveness, niche dynamics, economic costs

RESUMO

A capacidade das espécies de se tornarem invasoras (ou seja, invasividade) pode ser investigada através de múltiplas abordagens baseadas em características ecológicas e evolutivas associadas à capacidade das espécies de superar uma série de barreiras e filtros até a concreta invasão. Até agora, tentativas formais de se investigar invasões do plâncton com base no nicho e se espécies invasoras respondem às variáveis ambientais, têm sido negligenciadas. Analisamos a correlação entre a ocorrência de espécies invasoras e potencialmente invasoras no plâncton e as variáveis ambientais, incluindo futuras alterações climáticas, e características do habitat. Aplicamos modelos de distribuição para espécies e reconstruímos espaços de nicho ocupados usando diferentes abordagens e algorítmos, considerando o histórico e o processo de invasão de cada espécie. Testamos a hipótese de conservação de nicho no espaço e construímos mapas de predição de áreas favoráveis para invasões futuras das espécies: *Ceratium furcoides* (dinoflagelados), *Moina macrocopa* e *Cercopagis pengoi* (cladóceros). Além disso, descrevemos e modelamos custos socioeconômicos globais de espécies invasoras planctônicas usando o INVACOST – o mais completo banco de dados acerca do tema. Notavelmente, todos modelos deram suporte de forma confiável nossas às conclusões principais: (i) Expansão de nicho foi detectada para uma espécie *C. furcoides*, enquanto o não preenchimento do nicho nas áreas invadidas (unfilling) foi detectado para *M. macrocopa* e *C. pengoi*, necessitando-se maiores investigações sobre essa espécie quanto aos aspectos evolutivos; (ii) O cenários climáticos futuros permitirão processos de expansão e colonização em ambientes altamente suscetíveis a distúrbios como reservatórios e corpos d'água temporários; (iii) As avaliações de impacto necessitam melhorias, pois existem lacunas taxonômicas e geográficas para os custos socioeconômicos das invasões do plâncton em todo o mundo. Com base em nossas descobertas, acreditamos que estas perspectivas podem contribuir para para aumentar o conhecimento dos mecanismos que impulsionam as invasões de plâncton, apontar a direção para quais espécies e ambientes precisam de mais atenção e levantar novas hipóteses sobre processos de invasão de organismos planctônicos de rápida evolução.

Palavras-chave: Cladóceros não-nativos, Dinoflagelado invasor, invasividade do plâncton, dinâmica de nicho, custos econômicos.

1. INTRODUCTION

1.1 Biodiversity crisis: bioinvasions and other antropogenic pressures

Introduced species are those that, through human action (intentional or not) are transported to systems where they would not originally occur (RICCIARDI et al., 2013). Most introduced species do not establish themselves, while others, due to a series of intrinsic factors (invasive potential), and also by factors of the environment where they were introduced (invasiveness), establish viable and self-sustainable populations. These so-called established species can begin to disperse (without human intervention) to adjacent systems, and cause deleterious effects, which is when the classification of invasive species is incorporated (QUIST et al., 2005; RICCIARDI et al., 2013). Over the past two millennia, hundreds of species have been deliberately translocated from their natural environments by human action, especially for food and recreational purposes (GOLZAN 2008; ESSL et al. 2019). Currently, due to the impacts caused by the action of invasive species, they are considered the second greatest threat to global biodiversity along with climate change, habitat loss and pollution (CUCHEROUSSET & OLDEN, 2011; TILMAN et al., 2017). In this sense, understanding the factors that regulate the distribution and abundance of invasive species is extremely important, considering the high ecological and economic costs of the impacts caused by them (DIAGNE et al., 2020). Among these factors, the characteristics of the invaded environment act as filters during the process of establishment of introduced species through physical and chemical conditions of the system, as well as interactions with the native community, which can limit the occurrence of the species in the new environment (QUIST et al., 2005; RAHEL et al., 2007). However, the increasing anthropic impact, almost omnipresent in ecosystems, can act as a facilitator of the introduction and establishment of new species, by altering environmental filters, destabilizing native communities or increasing the pressure of propagules of these invaders (ESSL et al., 2020). In addition, the effects associated with climate change, caused by the increase in temperature, produce catastrophic responses, as they leave ecosystems more vulnerable to the establishment of introduced species by weakening the resistance of native species, with losses of ecosystem services (MAINKA et al. al 2010; GALLARDO et al 2013).

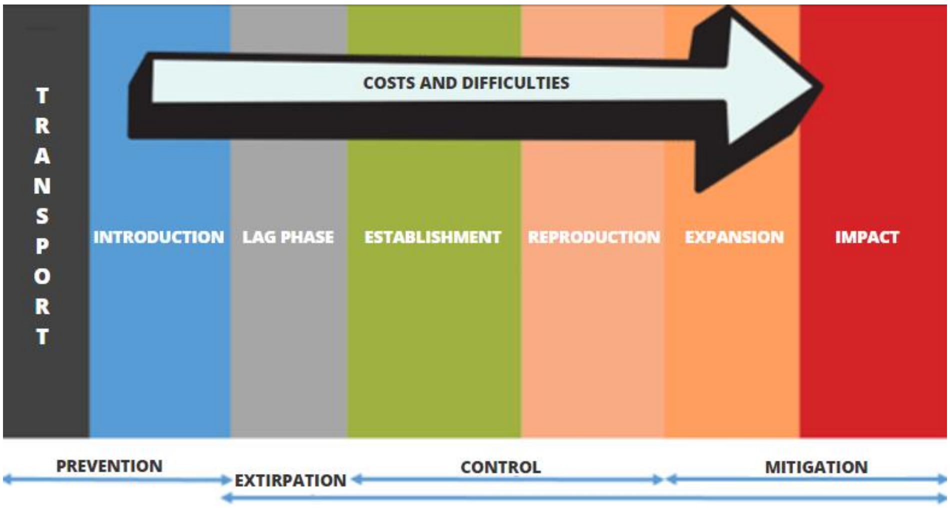

Figure1. Phases and filters of the invasion process. Fonte: Rafael L. Macêdo.

Over the last decades, climate change of anthropogenic origin has been driven by increasing and constant levels of greenhouse gas emissions (eg CO2, CH4 and N2O) combined with the degradation of natural environments which generate an accelerated increase in temperature, leading to several ecological and economic losses (BELLARD et al., 2012). In inland water environments, climate change is expected to promote an increase in water temperature, an increase in the intensity and frequency of rainfall and hydrological changes (RAHEL et al. 2007). Furthermore, although often considered separately, the impacts of climate change and the introduction of invasive species occur simultaneously and can lead to even greater impacts on native communities and ecosystems (WALTHER et al., 2009).

Recent changes in climatic conditions are already altering the composition, dynamics and distribution of native species, as well as ecosystem functioning. This same scenario also operates at all stages of the invasion process and can not only facilitate the transport of propagules (by increasing the frequency of extreme events), but also lead to an increase in the chances of the establishment of invasive species, as well as an expansion of its distribution to regions where there were no conditions for its survival before. These effects can also be perceived at the ecosystem level, which can become more permeable to invasion or more resilient.

1.2 Species distribution models and plankton invasions

The use of species distribution models (SDM) is increasingly popular in the study of biological invasions, e. g. to assess the impact of climate change on invasive species, to prioritize conservation measures, or to study invasive evolutionary biology (PETERSON et al., 2003; 2011). SDM correlates known occurrences of species with environmental variables and predicts the potential distribution of a species in other geographies over space and time. Today, SDMs are widely used to produce invasion risk maps, outlining likely risk areas based on the climatic suitability for a species. These maps can guide early detection and actions towards rapid response. However, applications of SDM in the management of planktonic invasive species are largely overlooked (but see MEICHTRY-DE-ZABURLÍN et al., 2016; SOUSA et al., 2016; JATURAPRUEK et al., 2021).

The use of predictive techniques to evaluate areas prone to the introduction of non-native species has become increasingly important to support immediate action upon detection, and antecipate the potential consequences of species arrival (RICCIARDI et al, 2020). Species distribution models (SDM) are an example of one of the most employed techniques to this end; using the combination of environmental variables and occurrence records aligned to various algorithms, they are able to predict suitable spots within the geographical space in which one species might occur. Ecological niche modeling (ENM) on the other hand, uses the same data of the latter method, but instead of a geographical space prediction, it provides an estimate of the species niche in environmental space. Both methods are based on Hutchinson's duality of niche and biotope, and are especially useful for understanding not only the distribution of non-native species, but also allow us to evaluate environmental niche requirements and potential shifts in species niche between its native and non-native area (GUISAN et al., 2014).

Non-native planktonic taxa are a great concern when it comes to biological invasions due to their silent characteristic (i.e. they can successfully thrive outside of their native regions without being detected) that poses a major threat to conservation of aquatic ecosystems (SPEAR et al., 2021). Most of non-native planktonic species are harmful for the ecosystem and can cause serious damage not only to native biodiversity, but also to economic activities and human welfare (WALSH et al., 2016; AMORIM & MOURA 2020). Additionally, invasive phytoplanktonic species are potentially toxic and frequently form dense blooms, which impairs water resources and consequently human health (MENEZES et al., 2018; AMORIM & MOURA 2020).

Ceratium is a genus of marine and freshwater dinoflagellates that recently have been introduced into various ecosystems and can lead to serious ecological and economic damages. *Ceratium furcoides* is native to temperate and glacial lakes in Europe, and considered invasive in many countries in different regions such as Brazil, Argentina, Australia, China, and the United States (MEICHTRY-DE-ZABURLÍN et al., 2016; SILVA et al., 2018). The presence of this species in non-native areas have already been associated with massive proliferations (i.e., Blooms) that consequently can impair water quality, cause massive fish kills, and trophic disruption (PACHECO et al., 2021). Once in novel ecosystems, this species presents several traits that allow them to thrive and be a highly competitive taxon, such as their cyst forming ability that allows it to resist unfavorable conditions and increase recruitment from sediment, potential mixotrophy, vertical migration, presence of a large apical horn which may prevent herbivory and damage predators, and the capacity to store phosphorus in cysts and cells (CAVALCANTE et al 2013).

The Cladocerans *Cercopagis pengoi* and *Moina macrocopa* are respectively invasive and potentially invasive species in inland and brackish waters. *Moina macrocopa* Straus, 1820 has been reported as native in Europe, Africa, the Middle East, and Asia, mainly in shallow temporary lakes. *M. macrocopa* is claimed to have been introduced in the American continent only more recently (PAGGI, 1997). *M. macrocopa* is a potentially invasive species under ongoing expansion, facilitated by e-commerce propagation and widespread use as food supply for aquaculture and bioessays. On the other hand, the invasive *C. pengoi* have established and spread causing environmental and economic losses, (KATAJISTO et al., 2013; KRYLOV et al., 1999; NAUMENKO et al., 2019). This high invasiveness and severe impacts among other features made *C. pengoi* one of the Worst World Invasive Species (LUQUE et al., 2014).

Here, we analyse the potential distribution in geographical space and the niche dynamics of the aforementioned invasive species using SDM approaches. As each species has different invasion histories and invasion ecology we presented specific aims and hypotheses separatedly in the manuscripts dealing with each one of them (but see general goals in page 9).

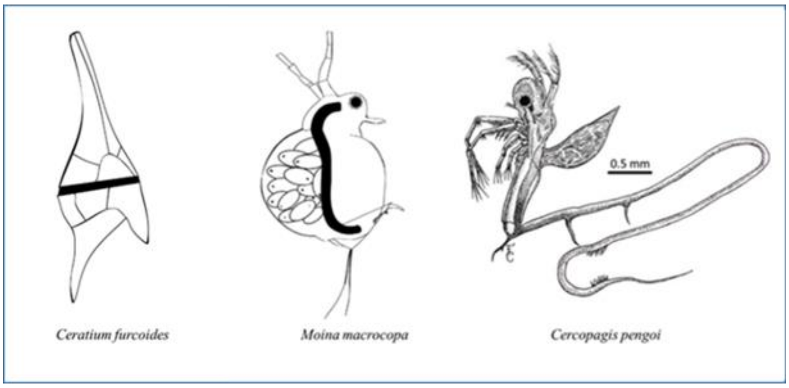

Figure 2. Model Organisms utilized in this study to investigate hipotheses related to bioinvasion. Fonte: Rafael L. Macêdo.

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2 GOALS

- Identify and quantify the invasion mechanisms of planktonic species (potential and/or established and emerging invaders) by modeling species distribution and niche dynamics.
- Identify and relate synergistic factors that enhance invasion success e.g. climate change, changes in basins and landscapes.
- Describe and compare global socio-economic impacts of planktonic invasive species.

3. RESULTS

ARTICLE ONE

PUBLISHED IN HYDROBIOLOGIA DOI: 10.1007/s10750-020-04495-5

The drifting dinoflagellate *Ceratium furcoides* (Levander) Langhans 1925: fundamental niche shift during global invasion

Rafael Lacerda Macêdo, Philip Russo, Raphael F Corrêa, Odete Rocha, Luciano Neves dos Santos, Christina W. C. Branco

Abstract

Ceratium furcoides is a freshwater dinoflagellate originally from cold waters of northern Europe that has been expanding its distribution into new areas worldwide. Species distribution modeling (SDM) based on maximum entropy algorithm (MaxEnt) showed that *C. furcoides* has a much wider potential range than its current distribution and isothermality as the key environmental variable determining its spatial pattern. The model successfully predicts areas of introduction and the climate matching approach has identified mainly tropical and some subtropical regions as most vulnerable areas at risk of introduction and establishment of *C. furcoides*. Furthermore, the observed shift of the climatic niche occurred between native and non-native ranges, providing for the first time, a robust evidence that a dinoflagellate can occupy climatically distinct niche space following its introduction into new areas. This is probably mirroring the lack of adequate management to deal with various impacts on drainage basins, such as ongoing accelerated cultural eutrophication coupled with river impoundments and water diversion. Thus, this framework provides helpful insights on how to optimize our ability to anticipate invasions and to avoid ecosystem services losses, as well as future studies prospects on adaptive mechanisms of this pervasive invader.

Keywords: Aquatic invasion, Dinoflagellate, Invasiveness, Niche shift, Risk assessment

Introduction

Invasive species often progress after the sequential phases of introduction, establishment, and dispersal to novel ranges distribution. The potential distribution issue has become of growing interest in international scientific community as invasive species have been widely acknowledged as threats to social-economic activities and ecosystem services (Lambdon et al., 2008; McGeoch et al., 2010; McDowell & Byers, 2019). The relevance of studying invasive species has increased considerably, especially in Applied Ecology and Conservation fields, in face of high adaptive ability of invaders and magnitude of impacts posed to biodiversity across several multiple purposes ecosystems (D'Antonio & Meyerson, 2002; Arim et al., 2006; Linders et al., 2019). Aquatic invasive species (AIS) are particularly pervasive and may cause food web disruption, water quality deterioration and local species extinctions (Simberloff, 1996; Strayer et al., 1999; Walsh et al., 2016). AIS often have high environmental tolerance and experience broad spatial and temporal demographic fluctuations, which generally contribute to increased success rates of establishment and spread over extended areas (Rahel, 2007). As a consequence, AIS often lead to high levels of hazards and long-term impacts on biodiversity and water quality (Strayer & Dudgeon, 2010; Vandekerkhove et al., 2013; Walsh et al., 2016).

Biogeography of invasive microorganisms is a neglected research field mainly due to difficulties in sampling, inefficient detection strategies and outstanding problems in their taxonomy (Cavalcante et al., 2013; Meichtry-de-Zaburlı´n et al., 2014; Moreira et al., 2015; Padisa´k et al., 2016; Crossetti et al., 2018). These, above mentioned issues can be particularly applied for single-celled protists, as the *Ceratium* species. Many dinoflagellates perform vertical migration and have cyst-forming abilities (Pollingher, 1988), which can hinder their detection by subsurface sampling strategies traditionally used for phytoplankton groups (Pappas & Stoermer, 1996; MatsumuraTundisi et al., 2010; Jati et al., 2014). These strategies may also facilitate multiple introduction events through many types of vectors. Accordingly, the non-resolved geographical distribution status of *Ceratium* species, in both native and invaded areas, make difficult the understanding of relevant autecological and geographical patterns found for this group, challenging conservation plans and policies.

Considered as one of the most invasive species of its genus, *Ceratium furcoides* (Levander) Langhans 1925 was first described as *C. hirundinella* var. *furcoides* Levander, from Finland phytoplankton samples. After Langhans' (1925) revision and classification as separate species, *C. furcoides* has been largely recorded into America, Asia, Oceania and Africa (Cassie 1978; El-Ofity et al., 2003; Haochen et al., 2020). Recent studies have shown the high invasiveness of *Ceratium* across freshwater bodies within South American river basins (Meichtry-deZaburlı´n et al., 2016; Silva et al., 2018) and southwards, since its first appearance in Colombia (Ramı´rez et al., 2005; Cavalcante et al., 2016; Meichtry-deZaburlı´n et al., 2016; Accattatis et al., 2020) what has been even facilitated by water flows and basins interconnectivity (Moreno-Ostos et al., 2008; Nishimura et al., 2015; Macêdo et al., 2021). *C. furcoides* is apparently very adaptable to thrive in different types of habitats, such as rivers, temporary ponds, and altitude lakes (Jati et al., 2014; Moreira et al., 2015; Morales, 2016). Besides that, *C. furcoides* populations are commonly found in lentic tropical freshwaters, especially reservoirs (e.g., Santos-Wisniewski et al., 2007; Matsumura-Tundisi et al., 2010; Meichtry-deZaburlı´n et al., 2014; Morales, 2016; Roriz et al., 2019; Maceˆdo et al., 2021), where impacts on water quality and on native species were already perceived (Santos-Wisniewski et al., 2007; Almeida et al., 2016; Cavalcante et al., 2016; Morales 2016).

Ceratium furcoides is a S-strategist commonly dominant species both in terms of abundance and biomass in many tropical invaded systems. Its flagellated cells are also potentially mixotrophic and therefore highly competitive when challenged by resource variability (Reynolds, 2006). Thus, *C. furcoides* can produce many adverse effects on native resident biota and on natural or artificial aquatic habitats. Further, it produces light-brown water blooms that affect zooplankton filtration, especially of Cladocera species, since its large cell dimensions above which is considered edible by these crustaceans and the mechanical prey avoidance due to the presence of horns, which makes them inedible algae similarly to the case of colonial and filamentous Cyanobacteria. Moreover, episodes of fish mortality by gill clogging, as well as oxygen depletion were attributed to this species large dimensions and high respiration rates during blooms (Nicholls et al., 1980; Santos-Wisniewski et al., 2007; Morales 2016). *C. furcoides* presence and dominance in aquatic systems is thereby of critical concern since water quality impairment and high cost water treatment are predictable (Pollingher, 1988, Van Ginkel et al., 2001; Santos-Wisniewski et al., 2007; Matsumura-Tundisi et al., 2010). Besides the fast expansion of *C. furcoides* worldwide, research investigating its climatic requirements and tolerance levels is necessary to assess its potential spread on freshwaters. Moreover, the distribution patterns, pathways and vectors of *C. furcoides* invasion remains mostly unknown.

Notwithstanding, species fundamental niche determined by its fitness range of tolerance to environmental factors where biotic interactions are absent (Hutchinson, 1957) could draw out some sort of potential areas of distribution for the invasive species (Guisan et al., 2014). Studies on invasive species distribution are also required for using both, the native and the invaded range, in order to avoid underestimated predictions (Mainali et al., 2015) since the prediction based on the invaded range would be the portions of the fundamental niche, non-restricted by biotic interactions, but limited to dispersal ability (Peterson 2003; Peterson et al., 2011). In other words, since fundamental niche can be correlated to geographic distribution, models based on native range solely may underestimate the species fundamental niche due the existence of environmentally suitable but unreachable areas. Moreover, to detect niche shifts, disentangle these changes as likely caused by native niche unfilling or by expansion into novel environments has been considered important for understanding the driving processes of biological invasions (Guisan et al., 2014), as well as for anticipating applied conservation policies (González-Moreno et al., 2017; López et al., 2017). Notwithstanding, only one modeling approach, restricted to South America and calibrated only with non-native distribution data, has so far been developed aiming to understand the current stages of invasion of *C. furcoides* (Meichtry-de-Zaburlı´n et al., 2016). The major objectives of our study were: (i) to generate a probability map in order to identify the regions around the globe most susceptible for the spread of one of the world's most pervasive invasive plankton species: the dinoflagellate *Ceratium furcoides*, (ii) to identify which environmental variables could be the major drivers for its potential worldwide distribution and (iii) to test whether niche conservatism or niche shift has driven the invasive expansion of C. furcoides. In this sense, the hypothesis of our study is that *C. furcoides* has substantially changed its climatic niches during the process of global invasion following significant adaptative changes that have been facilitating its establishment in tropical areas of the world. The major findings of our study in relation to the global invasion risk areas for this species were also discussed, helping mitigation policies toward monitoring programs.

Methods

Geographic distribution overview

Firstly, important taxonomic considerations should be referred on *C. furcoides* (Levander) Langhans (Langhans 1925). Since before 1981, all *Ceratium* cells were identified as *C. hirundinella* (O.F. Miill.) Bergh. (Calado & Larsen, 1997) any data considered taxonomically unreliable or imprecise were excluded from our analysis. As *C. furcoides* was described originally from the temperate region (i.e., European lakes, sensu Levander, 1894;

Langhans, 1925), it is considered as introduced into Americas, Africa and Asia continents (Meichtry-de-Zaburlı´n et al., 2016).

Occurrence data

Occurrence data from native and invasive populations of *C. furcoides* were compiled from scientific literature with precise georeferenced coordinates of all the sites where the species was recorded, except for polar regions. Geographic location of the sites *where C. furcoides* was recorded was checked using Google Earth platform. The 162 occurrence records were split between native or invasive (Jime´nez-Valverde et al., 2011) and plotted in a distribution map separated by the Major Habitat Types of Freshwater Ecoregions of the World (Fig. 1) (Abell et al., 2008).

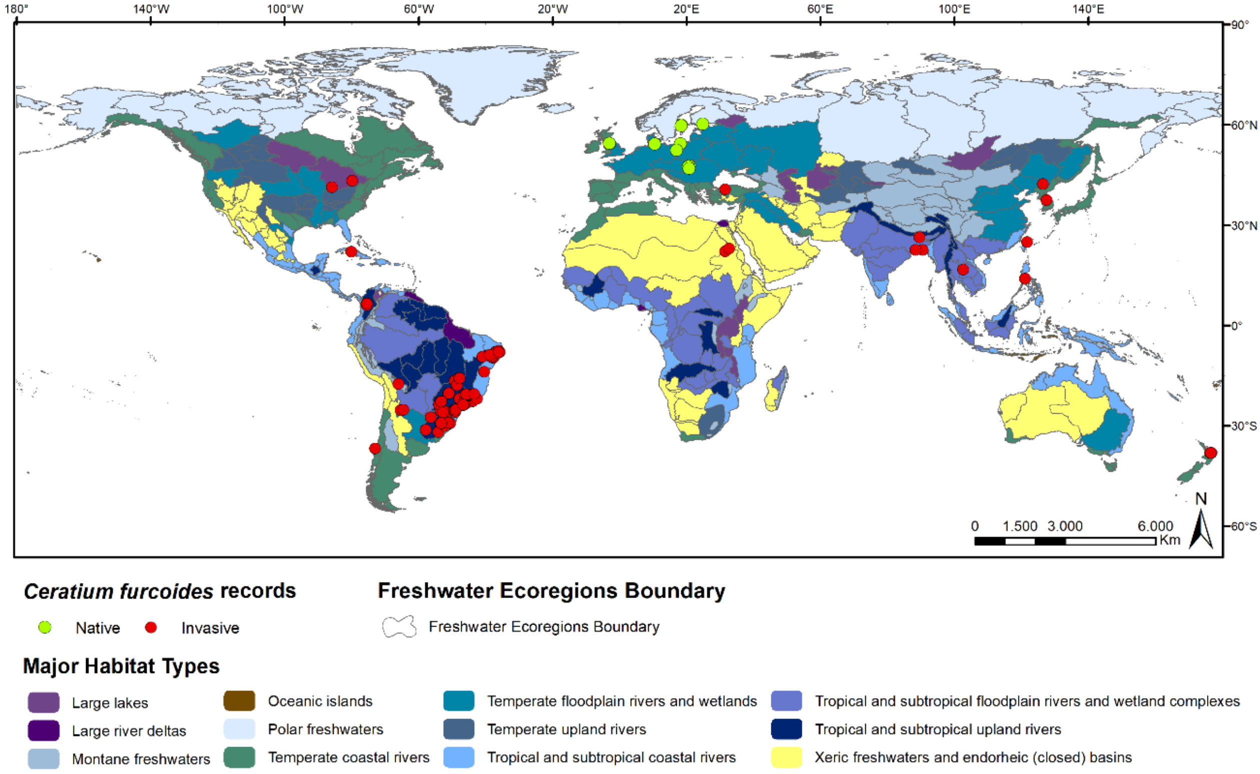

Figure 1. Global distribution of *Ceratium furcoides*. Green and red circles indicate the native and non-native distribution of this species, respectively

Environmental data

Climate information was obtained from 19 bioclimatic variables available in WorldClim (Fick & Hijmans, 2017) and one topographic variable obtained from GTOPO30 (Earth Resources Observation and Science Center, 1997) at a spatial resolution of 30 arc seconds. All environmental layers were clipped to the extent of the study area, resulting in a mask of the world without polar regions. A principal component analysis (PCA) was performed to minimize the spatial autocorrelation between variables and to determine the contribution of each one to the model of susceptible areas. Of the 20 principal component layers resulting from the PCA, the six layers that explained the highest variability ([98%) were selected and used to estimate the potential distribution of *C. furcoides* by using the maximum entropy algorithm in the MaxEnt software version 3.3.3k (Phillips et al., 2004). Species distribution model The model was performed according to the following parameters and procedure. Ten replicates were selected with Bootstrap as Replicated run type and Random seed to each replicate. Twenty-five percent of occurrences were randomly selected to be removed from the model training and applied in the model testing. Model output was computed as logistic format, which returns as a map with probability of suitability between 0 and 1, scaled up in a non-linear way to favor interpretation. The resulting model was evaluated through the option create response curves, which calculate the area under the curve of the receiver operating characteristic curve (AUC-ROC). Finally, the relative contribution of each principal component layer to the model was assessed through a jackknife test and the relative contribution of each variable was by the eigenvalues resulting from the PCA. This approach allowed the identification of the relationships between occurrence data and environmental variables as predictors for *C. furcoides*. For the final visualization the ten resulting models were combined in a consensus using the Weighted Average (WA) consensus method, based on the pre-evaluated AUC of the single models (Marmion et al., 2009). Due to the great difference between the number of records of native and invasive populations, the SDMs were repeated using three datasets (all records; only invasive records; only native records) to infer on the potential distribution of the species and its potential for invasion.

Niche shift

To evaluate if the niche breadth of *C. furcoides* varied between native and invasive distribution, we used the Niche Overlap function of the BioDinamica package, available in the software Dinamica EGO, applying the Schoener's D index to calculate niche overlap (Warren et al., 2008). Results A total of 162 occurrences of *C. furcoides* were retrieved from the search, wherein 13 native records were found in northern Europe, in contrast to 149 invasive records spread across America, Africa, Australia, Asia, and southeast Europe, as shown in Fig. 1. All the models generated had a high performance, and the consensus map using native and invaded distribution (Fig. 2a) showed mean AUC training data of 0.96 and 0.95 for test data with a standard deviation of 0.02. The dataset with only native records (Fig. 2b) had AUC training data of 0.97 and test data of 0.97 ± 0.01. The dataset of only invasive records (Fig. 2c) had mean AUC of 0.97 for training data and 0.96 ± 0.02 for AUC test data. When both native and invasive data were accounted, the most susceptible areas to *C. furcoides* invasion are the Florida State in USA together with Central America, the Caribbean islands, the Peruvian coast, and specific regions of high altitude located in the North of the Andes and in the Central and Southeastern regions of South America, including the Brazilian coast. Outside of Americas, the areas with high susceptibility to invasion are located in Central and in the Southern coast of Africa, in the Eastern Madagascar and Southern Asia, from South India to Vietnam, some Pacific islands in the IndoMalaysian region, and the shorelines of Australia and New Zealand. Our model showed intermediate to low probabilities for the occurrence of *C. furcoides* in its original distribution (northern Europe).

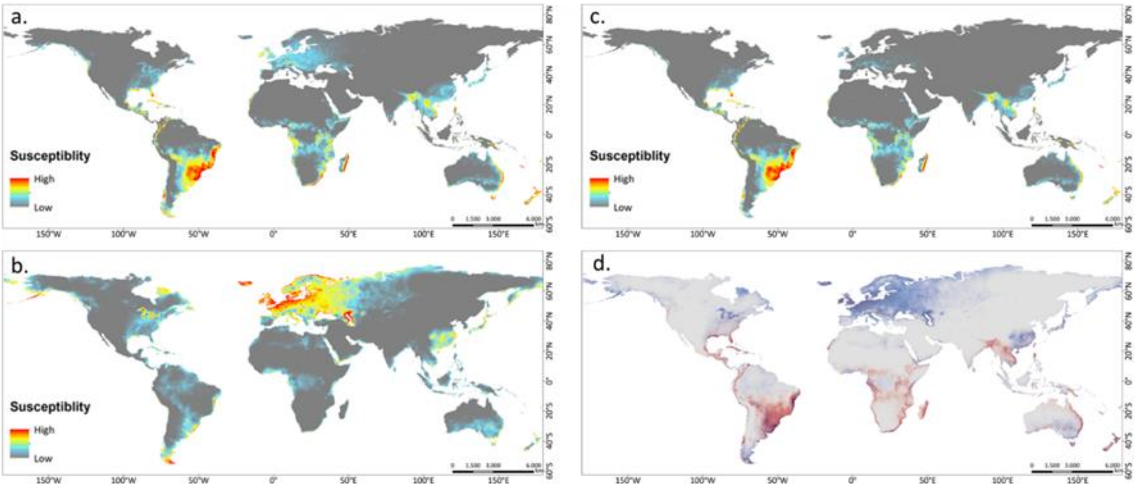

Figure 2. (a.) Consensus model of the potential distribution of *C. furcoides* based on records of native and non-native distribution (n = 162). **(b.)** Consensus model for the potential distribution of *C. furcoides* based on records of native distribution. **(c.)** Consensus model for the potential distribution of C. *furcoides* based on records of non-native distribution. **(d.)** Overlap between the Species Distribution Model (SDM) calculated from native and non-native records. Red scales represent the non-native potential distribution; Blue scales represent the native potential distribution; Purple scales represent the overlap between these two models.

The jackknife test showed that the first PCA axis explained 51.16% of the variance, while axis 2 explained 34.79%. According with the PCA eigenvalues, isothermality (Bio03) was the most important climate variable, followed by mean temperature of the coldest quarter

(Bio11), mean temperature of the driest quarter (Bio09) and minimum temperature of the coldest month (Bio06). These four environmental variables contributed together with 84.52% of the model variation (Table 2), revealing that they play important role to explain the potential distribution of *C. furcoides*. Considering the native distribution alone, the axis 2 of PCA was the one that most contributed to the model explanation. Moreover, mean diurnal range (Bio02), precipitation seasonality (Bio15), temperature annual range (Bio07), and maximum temperature of the warmest month (Bio05) were the best predictors for the SDM using native distribution (Table 2). Thus, this model showed a medium to high susceptibility of *C. furcoides* invasion for the north, east and middle Europe, Northern shoreline of Norway, Iceland, Ireland, and United Kingdom, Italy and northern shoreline of Black Sea. Outside Europe, the probability of occurrence was high in Caspian Sea, west of Russia, east and southeast of China, shorelines of Japan, Tasmania and New Zealand.

Table 2. Main bioclimatic variables of *C. furcoides*' Species Distribution Model (SDMs) using native + invasive (all records), native, and invasive distribution databases. The first four variables are the most significant in the Axis 1 from the PCA, the last four are from the Axis 2. Most significant variables values for each dataset are showed in bold.

	SDM - All records			SDM - Invasive records			SDM - Native records		
Main climate Variable	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
Isothermality (Bio03)	**23.22**	**96.15**	**60.2**	**23.58**	**96.12**	**61.03**	9.02	78.17	29.02
Mean Temp. of Coldest Quarter (Bio11)	**-5.02**	**26.08**	**16.04**	**-1.67**	**24.22**	**16.52**	-25.17	27.45	-1.02
Mean Temp. of Driest Quarter (Bio09)	**-3.52**	**31.13**	**17.47**	**-1.67**	**27.77**	**17.75**	-25.03	35.85	3.49
Min Temp. of Coldest Month (Bio06)	**-10.3**	**22.2**	**10.22**	**-5.6**	**22**	**10.54**	-29.7	24.4	-4.73
Mean Diurnal Range (Bio02)	3.6	14.67	10.36	3.6	14.67	10.54	**1.62**	**12.17**	**7.27**
Precipitation Seasonality (Bio15)	4.96	131.15	47.97	4.91	129.4	48.12	**0**	**101.41**	**9.97**
Temp. Annual Range (Bio07)	7.4	30.9	17.63	7.4	28.5	17.7	**6.2**	**45.8**	**26.4**
Max Temp. of Warmest Month (Bio05)	9.2	38.2	27.85	10.6	36.3	28.24	**1.3**	**42.1**	**21.68**

Correspondingly, the invasion risk was also high on extreme southern parts of South America, shorelines of Uruguay, Buenos Aires province in Argentina and large portions of south, southeast and northeast regions of Brazil. Finally, high invasion probability was related to northeast of Canada and the Southern shoreline of Alaska at the Bering Sea, the big lakes situated in the border between Canada and USA, the south coast of USA at the Gulf of Mexico and from the shoreline of Florida to the Bahamas region. Distribution of *C. furcoides* considering native and invasive records was quite similar to the pattern found when only invasive records were trained (Fig. 2a, c). In the same way, the jackknife and eigenvalues showed similar results, with the same variables contributing to the model explanation (Table 2). Finally, both potential distribution models using native and non-native records of *C. furcoides* showed a low overlap (Schoener index, D = 0.28) (Fig. 2d). These results were supported by the distribution ranges and overlapping level of the variables (Fig. 3a) and SDM values (Fig. 3b) of the models. Additionally, the overlapping degree between the models of native and native? non-native records also showed a low value for the Schoener index, D = 0.38 (Fig. 3c), contrasting, the overlap level found between the non-native and native and non-native records, wherein a high value (D = 0.85) was found for the Schoener index (Fig. 3d).

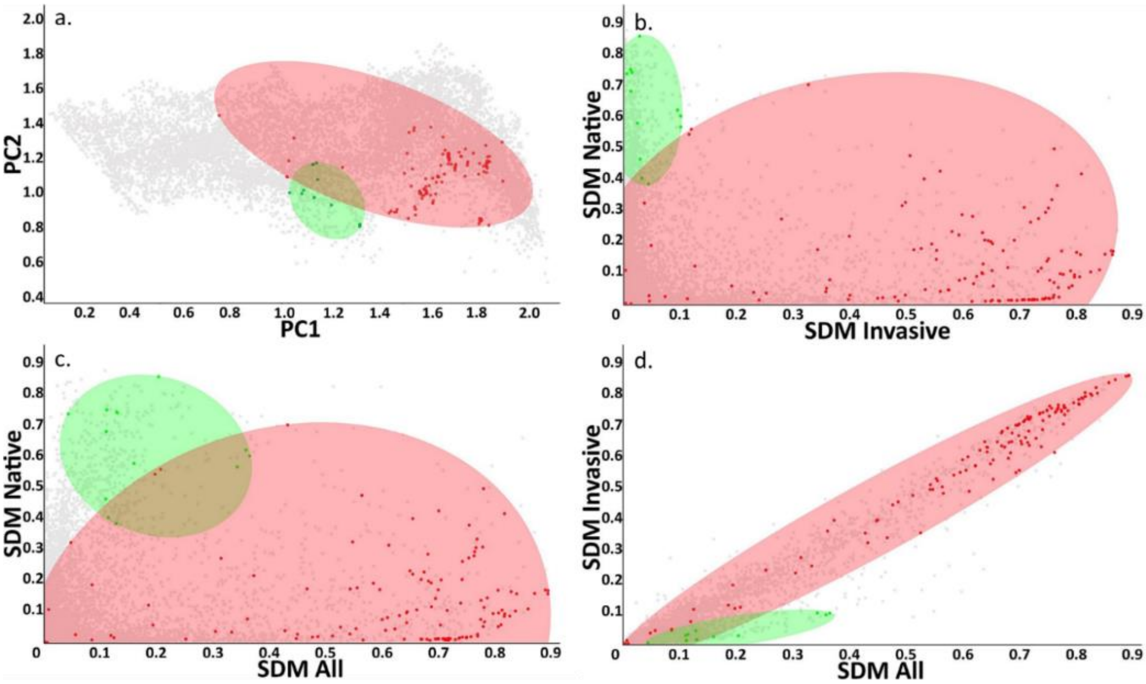

Figure 3. (a.) Diagram ordination of the variable scores used in the models. **(b.)** Diagram ordination of the SDM calculated from native and non-native records. **(c.)** Diagram ordination of the values of the SDM for native and full dataset. **(d.)** Distribution of the values of the SDM of non-native and full dataset. Red dots represent non-native records; green dots represent native records; red ellipse represent the area covered according the distribution of non-native records; green ellipse represent the area covered according the distribution of native records.

Discussion

Distribution pattern Our models were robust enough to properly (i) predict the potential invasive distribution of *Ceratium furcoides* in large portions of tropical areas that have not yet been invaded; (ii) to relate species distributions to warm isothermal environments considering them as main force determining biogeographic patterns and (iii) provide evidence of niche shift through expansion rather than niche conservatism. The tendency for a species to retain its original niche characteristics is useful for understanding the spread of invasive species since it is probably the rule in several of these frameworks (Wiens & Graham, 2005). Numerous studies on invasive species distribution advocated to using distribution data from both the native and the invasive range (Broennimann & Guisan 2008; Mainali et al., 2015). The main reason for this is that whether species climatic niche is conserved from its native to invaded range, distribution data from the native range can be very valuable to characterize the full potential climatic niche of the species and thus the full geographical space it can invade. Although SDM may be sensitive to sampling effort (Anderson, 2012) and thus our findings on the potential distribution may be overrated due to the scarcity of native records, our model sufficiently produced accurate models on the potential distribution of *C. furcoides*. Similarly, using solely non-native records from few places in South America, Meichtryde-Zaburlı´n et al. (2016) also developed accurate models, despite misusing niche conservatism assumptions. Although the new areas suggested by the native data model are already invaded by this dinoflagellate (e.g., Tafas & Economou-Amilli, 1997; Pandeirada et al, 2013), the native model failed to predict the entire region of occurrences of *C. furcoides*, missing highly invaded portions in Neotropical realm. Further, regarding methodological issues, the scarce number of known records to this species in its original range may indicate the need for a greater taxonomic effort on collecting and correctly identifying these organisms in regions where it is considered native. Furthermore, in some cases, using solely invaded ranges data may be efficient to predict potential distribution of species that has the ability to successful adapt to novel conditions over short-to-moderate time scales. Although only climate variables were addressed in our study, other kind of predictors might be added in further working hypothesis since climate variables are also predictors of some water characteristics. In this sense, the possible influence of other abiotic drivers, such as pH, conductivity, and variables related to human interferences (i.e., water residence time of reservoirs) and biological descriptors, such as the density of possible competitors and predators (although not reported until now) or the effects of vectors (i.e., abundance of aquatic birds, fish stocking initiatives), may be useful for advancing the knowledge on the reasons for *C. furcoides* spread. Spatial and temporal variability of *Ceratium* fluctuations is mainly affected by warm temperature and stratification regime (Lindstro¨m 1992; BustamanteGil et al., 2012; Meichtry-de-Zaburlı´n et al., 2014; Meichtry-de-Zaburlı´n et al., 2016; Crosseti et al., 2018). Our model also indicates high occurrence probabilities of *C. furcoides* in mean temperatures higher than 17 ˚C and maximum temperatures higher than 31 ˚C in the driest quarter, matching the results showed in similar but more local-scale studies (Cavalcante et al., 2013, 2016; Meichtry-de-Zaburlı´n et al., 2016; Silva et al., 2018; Macêdo et al., 2021). The occurrence of blooms during warmer periods in European lakes and reservoirs

(Lindstro¨m, 1992; Heaney et al., 1988; Hickel, 1988; Cavalcante et al., 2016; Silva et al., 2018) also agree with our predictions of potential for expansion of *C. furcoides* across tropical and some subtropical areas.

Climatic niche shift. This framework provides strong evidence of shifts on *C. furcoides* niche delimitation toward consistent niche expansion into isothermal and warmer areas in the global invaded ranges. Niche-based models trained in the native range relies on the assumption that invasive species conserve their climatic niche in the invaded ranges and thus are commonly used tools to predict the potential spatial range of invasive species. Although rare among many groups of animals and plants (e.g., Medley, 2010; Webber et al., 2012), niche shifts during invasions highlights an inconsistent pattern of niche conservatism during invasions, potentially hampering predictions in the new range (Broennimann et al., 2007). This apparent niche expansion of *C. furcoides* by comparing its native and non-native distribution overlaps, suggested that climatic fundamental niche in its native range has expanded or could still be expanding in the non-native distribution range (Broennimann et al., 2007; Lauzeral et al., 2010), probably mirroring its high invasiveness over different environmental conditions and suggest that this species might have significant plasticity not expressed in the native range of its fundamental niche. In other words, plasticity may confer invasiveness, since a broad and flexible niche might be able to perform well in a greater number of new habitats (Alpert et al., 2000; Pettitt-Wade et al., 2015). Range expansions may be related to rapid evolutionary changes after invasion processes (Colautti & Barrett, 2013; Li et al., 2015) or a result of differential realized niche space in native and exotic ranges (Gallagher et al. 2010; Tingley et al., 2015). Nonetheless, detailed genetic or autecological features of the majority of plankton species is poorly investigated, this hindering our ability to infer the drivers of observed spatial niche dynamics. Although our models showed almost no niche space overlap between native and invaded ranges and speciation process during invasion of *Ceratium furcoides* is a possibility, some studies found also niche expansion despite evolutionary constrains (Broennimann et al., 2007; Dellinger et al., 2016). Moreover, the first phylogenetic characterization of non-native populations of *C. furcoides* in South America provided by Accattatis et al. (2020), showed identical sequences when compared to Asian populations, thus providing an important step to allow us to understand the processes accounting for the invasion success of this dinoflagellate. Since fundamental niche corresponds solely to the physiological tolerance limiting species distribution (Hutchinson, 1957; Peterson et al., 2011) a detailed understanding of the constraints imposed by biotic factors such as competition, predation and dispersal limitations in a given geographic area is also needed to understanding invasion processes regionally and locally. Other plankton community residents such as the cosmopolitan predatory rotifers Asplanchna spp, are known to predate on *Ceratium* cells at both native (Pociecha & Wilk-Woz´niak, 2008) and invaded ranges (Kappes et al., 2000), including habitats where *C. furcoides* was found at very low cells density (Christina W. C. Branco, unpublished) suggesting that this interaction may not be exclusively determined by the abundance of potential prey organisms. Thus, it is important to closely investigate potential adaptive changes of the fundamental niche at different organization levels.

Conclusions and future prospects

Attempts to predict present and future distributions of invasive plankton species are rare (e.g., Padisa´k, 1997; Meichtry-de-Zaburlı´n et al., 2016; Sousa et al., 2017). However, species distribution modeling is demonstrated here to accurately detect the broad range of areas that are suitable to be invaded by the freshwater dinoflagellate *Ceratium furcoides* at a global scale throughout its invasion history. Herein and in other few studies, using solely non-native records seems to similarly generate equally precise models (Meichtryde-Zaburlı´n et al., 2016; Barbet-Massin et al., 2018). In this regard, there is yet a bias toward higher sampling intensity in South America, especially in Brazil. This was supposed to generate a disproportionate probability of occurrence within intensively studied areas and lower probabilities in other lessstudied regions. Although further studies covering other cases of biological invasion are needed to extrapolate this approach to other plankton species and groups, our findings validate the use of SDMs to track the invasion process and predict the spatial distribution of small but rather pervasive invader.

Our models have also revealed how rapidly this species may shift its climatic ranges, significantly expanding its fundamental niche. Although most predictive studies consider often environmental variables, additional factors such as reduced biological pressure, habitat type, and natural and anthropogenic disturbances should be added since they might affect species invasiveness in novel non-native areas. In this sense, we would likely suggest i) to build SDMs that incorporate quantitative information on cells density or biovolume, ii) to investigate whether the speciesrealized niche is conserved over space (Dietz & Edwards, 2006; Pearman et al., 2008), since *C. furcoides* have already spread and established into habitats in the invaded ranges that are climatically far distinct from those occupied in the native range. This more in-depth knowledge would be helpful to define surveillance areas and mitigate the potential impacts of *C. furcoides* in areas where the invasion could potentially be reported.

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ARTICLE TWO

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Climate and landscape changes enhance the global spread of a bloom-forming dinoflagellate related to fish kills and water quality deterioration

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Global inland water biodiversity is under mounting stress facing future scenarios of climate change, biological invasions, pollution, diversion, damming of rivers, and increase of water abstractions. Apart from having isolated effects, all these stressors threats act synergistically and thus pose additional emerging threats to biodiversity and ecosystem services. Native to Northern Europe, the nuisance and potential toxic dinoflagellate *Ceratium furcoides* (Levander) Langhans 1925 is a silent invader that blooms in freshwater systems; it has one of the most rapid spread rates globally. We propose a framework to determine the worldwide most vulnerable areas for the invasion by *C. furcoides* shortly (2041–2060) by combining future scenarios of climate change (a proxy for invasiveness) derived from ecological niche models with future dam construction data (a proxy for invasibility). The nine models applied in four future scenarios of greenhouse gas emission from Coupled Model Intercomparison Project Phase 6 showed a general increase in areas suitable for the invasion success of *C. furcoides*. High susceptibility overlapped with areas densely occupied by large and medium-size dams and future dam construction projects. Considering that *C. furcoides* can reproduce from a single cell, produces resistant stages, and has several strategies to cope with local environmental constraints, early detection protocols, and mitigation actions are urgently needed to avoid biodiversity declines related to this invader.

Introduction

The proper functioning of ecosystems sustains global biodiversity, human health and economic prosperity, but it is highly dependent on efficient conservation and impact mitigation policies (Dodds et al., 2009; van der Plas, 2019; Maureaud et al., 2020). Inland waters are undergoing rapid changes following both persistent and rising anthropogenic pressures (e.g.

eutrophication, pollution, damming, climate change, and biological invasions; Tundisi et al., 2015), thus threatening biodiversity and the provisioning of nature services to humans (Darwall et al., 2009; Reid et al., 2019; Birk et al., 2020). Although not fully understood, many of these threats are ubiquitous and create cumulative and synergistic impacts that harm global biodiversity and human livelihoods (Darwall et al., 2009; Tundisi et al., 2015). Impact assessment of invasive species and initiatives to mitigate their threats are, however, rare, especially for microorganisms (Rahel & Olden, 2008; Knouft & Ficklin, 2017; Reid et al., 2019), even though they are quite often responsible for disastrous events, such as biotic homogenization, trophic disruption, and water quality deterioration (Vanderploeg et al., 2001; Walsh et al., 2016; Amorim & Moura, 2020). Thus, novel protocols for the early detection of potentially invasive species are needed, as is the identification of areas more prone to invasions. To this end, it is imperative to integrate knowledge on current and future scenarios of climate change and anthropogenic disturbances (Abell et al., 2008; Heino et al., 2020; Ricciardi et al., 2021; Manjarrés-Hernéndez et al., 2021).

Dispersion and establishment of aquatic invasive species in inland waters are especially favored by hydrological alterations and changes in environmental conditions induced by dam constructions (Poff et al., 2007; Johnson et al., 2008; Radinger & García-Berthou, 2020). River damming often connects habitats that were separated by large natural barriers and may also promote artificial connectivity through water diversions (Daga et al., 2020). Impoundments are often regarded as stepping stones for the spread of invasive species throughout watersheds, scaling the impacts up to regional levels as water from different sources is often mixed, which facilitates dispersal and homogenization of biota. In addition, river diversions usually improve the multiple uses of water, increasing the volume of abstractions that summed with rainfall scarcity can cause water stress in drainage basins (Marengo & Alves, 2005; Jeppesen et al., 2015).

Climate-driven hydrological change involves complex interactions of various impacts on water storage and their ecosystem services (Hansen & Cramer, 2015; Hassan et al., 2020), becoming even more deleterious when in synergy with the impacts of biological invasions (Pecl et al., 2017). Climate change is further predicted to exacerbate the environmental changes, through alterations in precipitation and water temperature regimes by increasing the rate of drastic events (e.g. extreme droughts, health challenges) (Cao et al., 2018; Iwamura et al., 2020; Radinger & García-Berthou, 2020; Piano et al. 2020). Both climate change and river damming are likely to affect biological invasions by changing the vectors and pathways of species introduction, altering the invasibility of aquatic systems, and by changing biotic interactions within native resident communities (altering establishment and spread rates) (Hellman et al., 2008; Rahel & Olden, 2008). Moreover, climate change may facilitate the spreading of invasive species and increase the severity of the impacts of invaders worldwide, and climatic stochasticity may also trigger outbreaks of sleeper populations of invaders (e.g., Lennon et al., 2001; Stachowicz et al., 2002; Chapman et al., 2016), namely populations of alien species that persists at low densities in nonnative areas while maintaining the potential to become invasive (Spear et al., 2021). The impact of such climate events seems to be particularly critical in dammed rivers, where the connection among systems may allow for constant re-colonization and multiple introductions (Radinger & García-Berthou, 2020), in particular by small planktonic species favored in lentic systems with high retention time and nutrient accumulation (Bustamante-Gil et al. 2012; Cassol et al., 2014; Branco et al., 2019; Macˆedo et al., 2021a).

The dinoflagellate *Ceratium furcoides* (Levander) Langhans 1925 is a quintessential example of such an invader. This is a highly pervasive, potentially mixotrophic, single-celled chromista, first described from North European waters but currently reffered as an emmerging invader which experienced niche shift expansion during invasion of areas outside of it's native range. Although the species is widely distributed, its introduction routes and pathways are subjected to speculation; often its arrival is ascribed to water diversion and water flows, ballast water, and zoochory, but direct assessments are absent. Recently, a study found no genetic variation between populations from China and Argentina (Accattatis et al., 2020), as otherwise commonly found for other invasive species (a so-called "invasion paradox"; Frankham, 2005). However, the mechanisms behind the wide invasion success of *C. furcoides* are unresolved, and often generically explained by its adaptive strategies and phenotypical plasticity in response to environmental changes (Cassol et al., 2014; Kruk et al. 2021). Low precipitation, decreased water level, and, consequently, increased turbidity, favors mixotrophic algae due to light limitation and implications for productivity (Wilken et al., 2013; Jeppesen et al., 2015; Costa et al., 2019). In addition to the development of improved competitive skills for food uptake, *C. furcoides* has high mobility through the water column due to its motile flagella (allowing it to reach more favorable conditions by depth adjustment) and distinctive morphological characteristics, such as the presence of horns and relatively large body size, favoring predation avoidance. Ultimately, its high invasiveness from clear water reservoirs to highly eutrophic systems and sewage discharges, and its occurrence from glacial to tropical warm waters, means that this flagellate is one of the most pervasive phytoplanktonic species globally. This bloom-forming dinoflagellate *Ceratium furcoides* Levander 1984 already had severe impacts on Neotropical biodiversity and human activities. These impacts encompass massive fish kills

(Pacheco et al., 2021), phytoplankton homogenization (Amorim & Moura, 2020) up to socio-economic hazards, for instance by affecting the water quality of domestic supplies and storage reservoirs facilities (Matsumura-Tundisis et al., 2010; IMA, 2015; Amorim & Moura, 2020; Macêdo et al., 2021a,c). Consequently, there has been increasing interest in identifying the main predictors shaping its distribution pattern and invasion success (Accattatis et al., 2020; Macêdo et al., 2021b; Kruk et al., 2021). Yet, despite some recent advances in the knowledge about *Ceratium*, its dynamics in invaded systems are still not elucidated, and predicting its invasion success under environmental change is urgent.

Accordingly, policy and management decisions require predictive tools to better assess the likelihood of *C. furcoides* spread and establishment in aquatic ecosystems to initiate effective mitigation actions where possible. Biogeography and biodiversity informatics have successfully filled knowledge gaps in invasion biology since ecological niche models (ENMs) approaches can be used to forecast the effects of changes in environmental conditions on species distributions (Srivastava, 2019; Liu et al., 2020). These models combine geographical occurrence data with bioclimatic variables allowing to predict the potential distribution of a given species (Anderson et al., 2003) and even to understand species adaptations to different environmental ranges (Sax et al., 2013; Sexton et al., 2017; Mammola et al., 2019). Regarding invasive species, ENMs have been widely used to predict susceptible areas for non-native and invasive species to foresee where these species will and will not be able to establish (Peterson & Vieglais, 2001; Broennimann et al., 2007; Zhang et al., 2020). Understanding niche dynamics is pivotal to the development of effective conservation strategies (Jim´enez-Valverde & Lobo, 2007; Guisan et al., 2014; Dinis et al., 2020). Therefore, the invasion process of *C. furcoides* represents an intriguing opportunity to investigate how a small planktonic species will respond to changing environments since niche expansion was detected in its invasion process despite no relevant genetic changes (Accattatis et al., 2020; Macêdo et al., 2020b).

Prevention of the establishment and spread of *C. furcoides* largely depends upon the early detection of invasion (such as alarm lists of priority areas) and the frameworks for prompt and effective guidance of decisions on eradication or management of new and ongoing invasions and impacts. Since the species can interfere with multiple uses of water from disturbing water treatment systems (Almeida et al., 2016) to potentially causing fish kills (Pacheco et al., 2021), predictions of its occurrence in aquatic systems are urgently needed. Following the global boom in hydropower dam construction aligned with the future scenarios of global climate change in the Coupled Model Intercomparison Project Phase 6 (CMIP-6), we describe a priority-setting framework for detection, monitoring, and further controlling the spread of *C. furcoides* in the invaded range worldwide. We detect priority areas for monitoring and conservation in the near future (2041–2060) by combining the future scenarios of climate change using the MaxEnt algorithm as an indicator of *C. furcoides* invasiveness (i.e. the propensity to invade a given ecosystem); with future dam construction data as a proxy for invasibility (i.e. the susceptibility of a recipient ecosystem to be invaded).

Here, we investigate the future distribution of the most prominent invasive plankton species across Neotropical helm, *Ceratium furcoides*, by integrating for the first time at a global scale the combined threat posed by climate change and biological invasions to existing and projected dams and the riskiest areas for this species invasion. We hypothesize that *future climate scenarios will result in an expansion of the potential range suitable for C. furcoides* as it moves towards the occupation of its fundamental niche following its current expansion through niche shift (Macêdo et al., 2021b). Further, we aim to investigate whether this pattern of niche expansion will show an overlap between highly suitable areas and dense occupation by dam constructions, especially in South America where many countries rely on hydroelectric reservoirs for power generation and multiple domestic uses and also shows the highest invasion rates, globally (Corrêa et al., 2022). We further expect that seasonal variables are relevant factors regulating the future expansion of *C. furcoides* since this species is highly influenced by water column stability and run-offs (Cavalcante et al., 2013; Cassol et al., 2014; Kruk et al., 2021; Pacheco et al., 2021). Combined use of the outputs of future projections of suitable areas and distribution of prone environments to *C. furcoides'* invasion will robustly underpin global and regional conservation of inland water ecosystems through the selection of priority areas for its early detection in recently invaded areas.

Methods

Global occurrence records

We gathered occurrence records of *C. furcoides* in the scientific literature from the early description in 1894 until 2020. As *C. furcoides* is undergoing fast expansion, new records on its distribution have become available (e.g. Honti et al., 2020; Amorim & Moura, 2020; Çelekli and Lekesiz, 2021) supporting the predictions of the currently suitable areas (see Macêdo et al., 2021b). We thus included these new records in our analysis of ENM. After removing duplicated records to reduce the sampling bias effect, 168 georeferenced records were retained and double-checked using Google Earth (Google Inc. 2015) to obtain proxy coordinates for records lacking precise geographical coordinates. The final dataset used for the analysis is provided in Supplementary Material Table S1. To predict areas at higher risk of invasion by *C. furcoides*, combinations of localities from native and invaded areas were used (Loo et al., 2007; Peterson

& Vieglais, 2001; Sobek-Swant et al., 2012) to extrapolate to areas similar to their current niche and thus their full potential distribution.

Bioclimatic variables

We obtained the standard set of 19 bioclimatic variables and one topographic variable (elevation) available in the WorldClim 2 database (Fick & Hijmans, 2017) at a spatial resolution of 30 arc-seconds for present projections and of 2.5 arc-minutes for the future projections (2041–2060) (same as found in Macêdo et al., 2021a). To model future scenarios, we used all nine available general-circulation models (BCCCSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, GFDL-ESM4, IPSLCM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0), namely multimodel future climate projections based on alternative scenarios of future CO2 and aerosol emission rates (https://www.worldclim. org/data/cmip6/cmip6climate.html). Nine bioclimatic future models were generated for SSP126 and SSP370 scenarios of CO2 emission, and eight for SSP245 and SSP585, yielding 340 predictions outputs from the MaxEnt. Further, consensus maps were generated for each of the four green gas emission scenarios and also one final consensus map based on the average result across all scenarios.

All environmental layers were clipped to the extent of the study area, resulting in a mask of the world without polar regions. A principal component analysis (PCA) was performed for each CMIP6 variables subsets, to minimize the spatial autocorrelation between variables and to determine their contributions to the model of susceptible areas. Of the 20 Principal component layers resulting from the PCA of each CMIP6 variables subsets, the first six components cumulatively explained > 98% of the variance and were therefore selected to model the potential distribution of *C. furcoides*.

Ecological niche modeling

We used the maximum entropy algorithm in the MaxEnt software version 3.3.3 k (Phillips et al. 2004) to predict the species distribution. This method is comparable to previous studies regarding *C. furcoides* (Macêdo et al., 2021a). MaxEnt background points (n = 10,000) were generated by random selection of background pixels across the study area. Given that the number of occurrence records was above 100, we generated MaxEnt models with the default setting for the regularization multiplier and feature classes (Morales et al., 2017).

We performed the models' projections for future scenarios according to the following parameters and procedures stated in the previous publication for the current distribution model (see Macêdo et al., 2021b). Ten replicates were selected with Bootstrap as Replicated run type and Random seed to each replicate. Twenty-five percent of occurrences were randomly selected to be removed from the model training and applied in the model testing. Model output was computed as logistic format, which returns a map of probability of suitability (between 0 and 1), scaled up in a non-linear way to facilitate interpretation. The resulting model was evaluated through the option create response curves, which calculate the area under the curve of the receiver operating characteristic curve (AUC-ROC) Manel et al., 2001. Finally, the relative contribution of each principal component layer to the model was assessed through a jackknife test and the relative contribution of each bioclimatic variable was given by the eigenvalues resulting from the PCA. This approach allowed the identification of the relationships between occurrence data and environmental variables as predictors for *C. furcoides*. For the final visualization, the ten resulting models were combined in a consensus using the Weighted Average (WA) consensus method, based on the pre-evaluated AUC of the single models (Marmion et al., 2009). Furthermore, we assessed the absolute performance of species predictions using the Boyce index, which is meant to be more appropriate for evaluating presence-background algorithms (Boyce et al., 2002; Hirzel et al., 2006). Boyce index measures how much model predictions differ from a random distribution of observed presence across the prediction gradient, and varies continuously between − 1 and + 1. Positive values indicate that model predictions are consistent with the distribution of actual presence data (observed presence), values around zero indicate that the model is no better than a random model, and negative values indicate counter predictions (e.g. predicting no occurrence in areas where actual presence is recorded).

Invasion risk and conservation priority

We propose a unified framework for identifying priority areas for mitigation of the impacts of *C. furcoides* based on the initial stages of the invasion process: i) the transport/introduction into inland waters facilitated by reservoirs (Daga et al., 2020; Macêdo et al., 2021a, c), and ii) environmental barriers, the main filter for invasion success (Gallien et al., 2015). To identify areas for successful invasion of *C. furcoides*, the consensus ENM projection generated for its global potential invasion was superimposed on the “Global Reservoir and Dam Database” (GRanD database; Zarfl et al., 2015) map of the current and future distribution of large dam constructions (“Future Hydropower Reservoirs and Dams” – FHReD; Zarfl et al., 2015), here used as a proxy of the global landscape and environmental change, thus acting as a logical framework for large-scale conservation strategies. Ultimately, reservoirs enhance the susceptibility to biological invasions due to the conversion of free-flowing rivers to standing waters and the associated water diversions (Havel et al., 2005; Havel and Medley, 2006; Emerson et al., 2015; Xiong et al., 2018).

Results

Projected future scenarios

Ceratium furcoides' probability of occurrence predicted using the MaxEnt for each of the four shared socio-economic pathways (SSP126, SSP245, SSP370, and SSP585) was generally high in most invaded areas. The performance of the global climate change model which included all GCMs and emission scenarios for 2041–2060 tended to be excellent in representing the future potential distribution of *C. furcoides* (Training AUC = 0.952; AUC Test = 0.943; SD = ±0.017). Also, the high value of the Boyce index (mean ± S.D. = 0.61 ± 0.216) indicated that the model's output is positively correlated with the observed presence, thus resulting in a well-performed model. South America is predicted to have the largest potential susceptibility to further spread of *C. furcoides*, especially Brazil, Uruguay, the southwest coast of Chile, and the northern region of the Andes. Also, the Caribbean and Central America, the United Kingdom, intertropical portions of the African continent, the east coast of Madagascar, southern portions of the Indo-Malaysia realm, the middle of New Guinea Island. The eastern coast of Australia, and New Zealand showed high predicted susceptibility values.

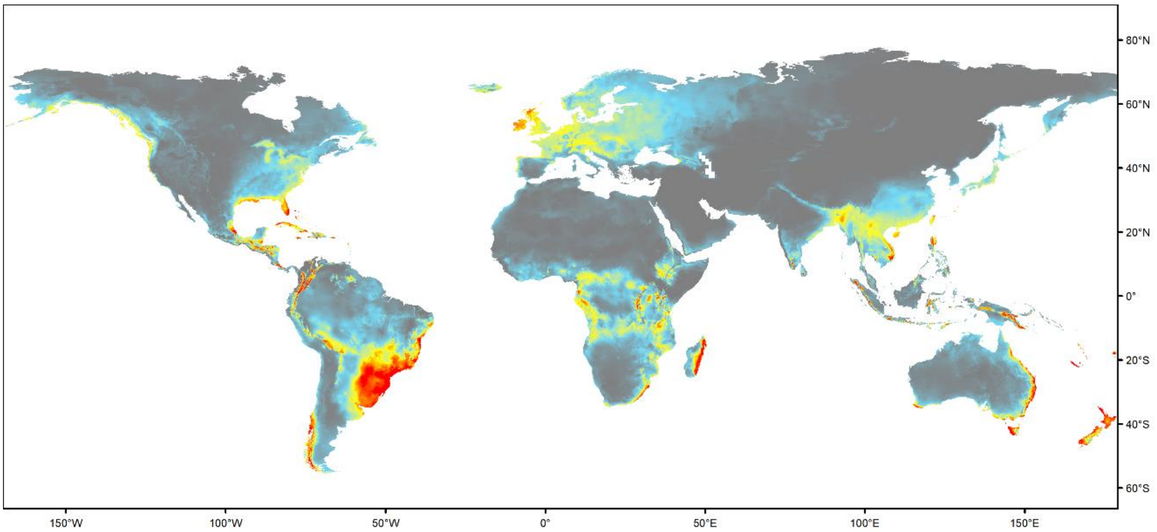

Figure 1. Consensus map of estimated climate suitability based on the average of all the predicted future scenarios of climate change.

Range expansion

The probability of *C. furcoides* occurrence at a given location (each point is a pixel/location on the map) tends to increase in the future than in the present. This trend is seen mainly at the native range. In contrast, a few locations showed a decrease in the predicted susceptibility value, both in the background and for invasive records, suggesting that a few areas may become less favorable for the establishment of the species in the future (Fig. 2). The present values of the ENM Consensus are presented are presented in the previous work by Macêdo et al. (2021b). For the future, the models showed a considerable expansion of suitable areas of *C. furcoides* in all scenarios. In the second half of the 21st century, mainly in South America and across tropical and subtropical latitudes in the Southern Hemisphere (~30 to 50 ◦S, Fig. 3A and B). However, the distribution expanded also in other parts of all five continents (Fig. 4).

Response variables

The jackknife test illustrated the significant percent contribution of the first two axes for the predictive models. The first axis of the PCA contributed with 71.4%, while the second axis contributed with 12.1% to the multivariate variability and eigenvalue retrieved the contribution of each variable of these axes thus showing the most effective environmental variables. Temperature seasonality (bio4) was the most important variable for explaining the suitability of an area for *C. furcoides* occurrence in all four models. In addition, Mean Temperature of Coldest Quarter (bio11) and Mean Temperature of Driest Quarter (bio9) showed high contributions along the first axis. Mean diurnal range (bio2), Precipitation seasonality (bio15), and Temperature annual range (bio7) were the most important for the second axis.

The role of impoundments

The superimposition of the consensus model for the future distribution of *C. furcoides* in climate change scenarios, including the world's distribution of large dams and future projections, highlighted the hotspots for the occurrence of this silent invader (Fig. 5). South America, the Caribbean, Central Africa, and China are priority areas for detection and control of *C. furcoides* since they harbor massive amounts of dammed systems that are projected to spread even further in the future.

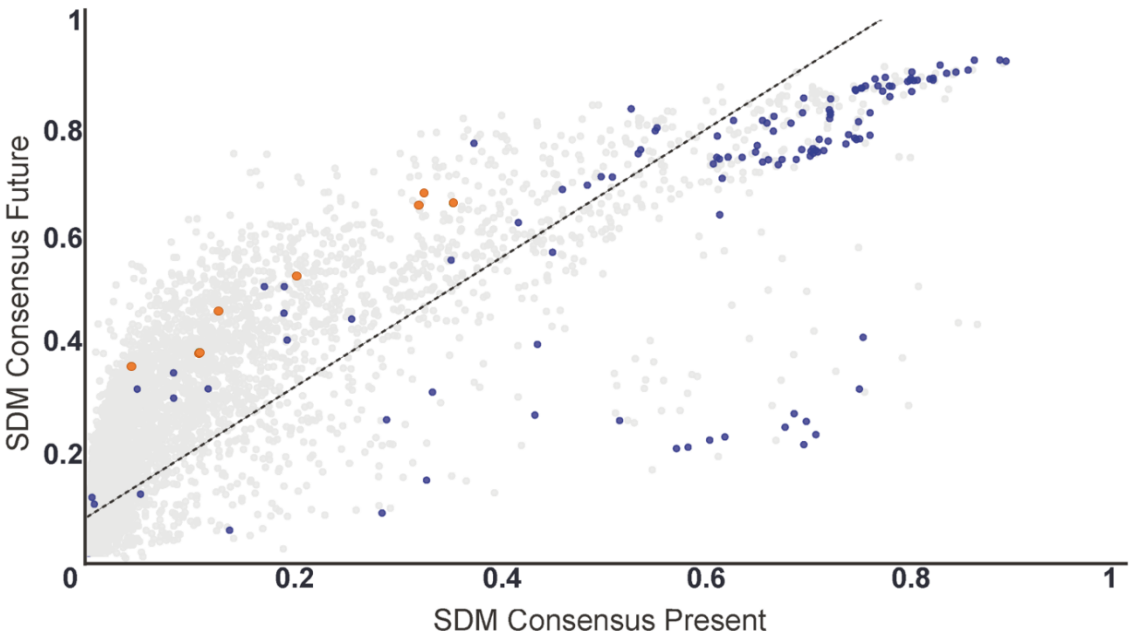

Figure 2. Probability values of both present and future scenarios. Native records are in orange and non-native records in blue. Background data (or pseudo-absence) are represented by gray circles.

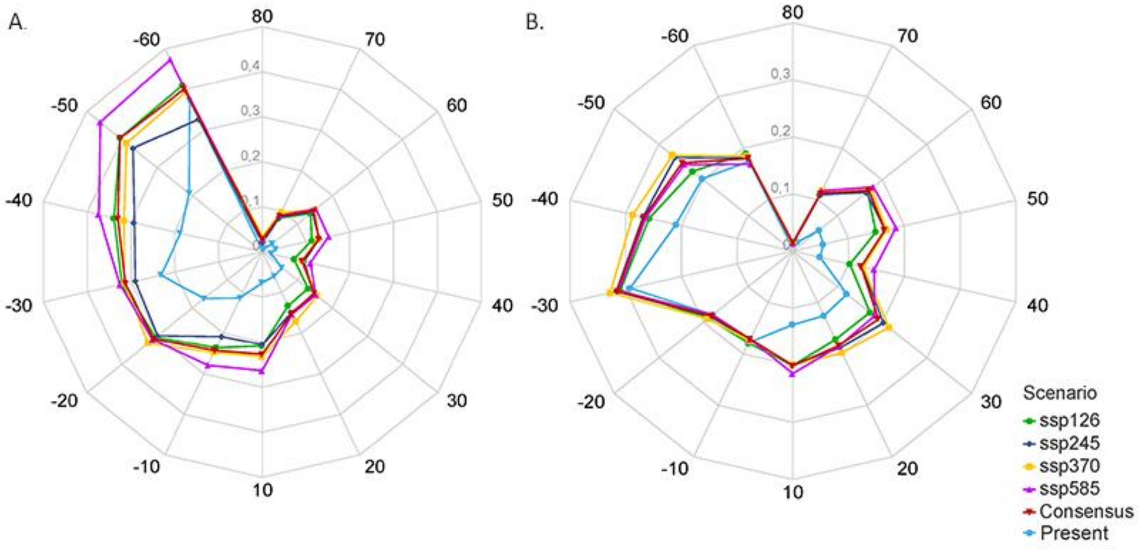

Figure 3. Radar graphs showing the A) average, and B) standard deviation of suitability values in the geographical space (sorted by latitudinal bands). Colors represent the different projected scenarios (four future scenarios of climate change, the consensus of these four scenarios and the present model.

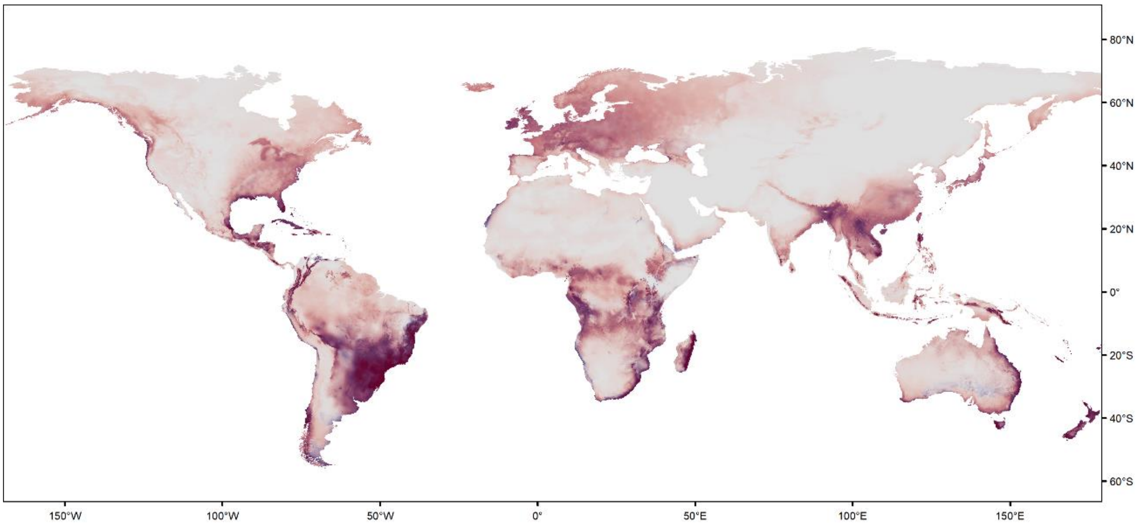

Figure 4. Map showing the geographical range expansion of *Ceratium furcoides* (Levander) Langhans 1925. Future (red) and present (blue) distribution are shown. The purple shades indicate an overlap between the present and the future projections.

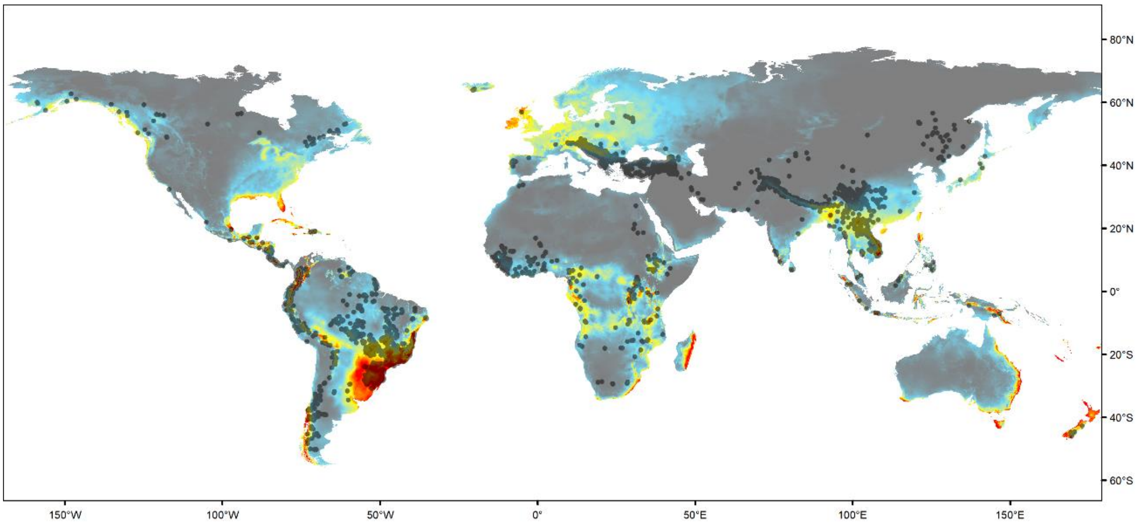

Figure 5. Future dam constructions predicted until 2030 overlapping the consensus map of fundamental niche in future scenarios (2041–2060).

Discussion

Climate change and land transformations have been conclusively related to invasive species (Smith et al., 2012; Bellard et al., 2012; Radinger & García-Berthou, 2020) and reservoirs are advocated as stepping stones for several invasive species (Havel et al., 2005; Turak et al., 2016; Xiong et al., 2028; Franco et al., 2020), thereby escalating the extent and impacts of invaders (Essl et al., 2020). However, little is known about their synergetic potential to recruit invasive species under climate change scenarios. Our framework combines ENMs, considering near-future scenarios of climate change (2041–2060), and the spatial data on future dam constructions, in order to map global areas at risk of invasion by the harmful *Ceratium furcoides*. By coupling suitable areas (i. e invasiveness) with ecosystems that are more prone to be invaded (i.e. invasibility) our results suggest general range expansion of *C. furcoides*, reflecting both a global trend of increasing suitable areas for this species until the year 2060, the high habit-relatedness in reservoirs (Macêdo et al., 2021c) and its rapid adaptation to adverse local climates (Macêdo et al., 2021b; Kruk et al., 2021). Moreover, the expected high number of future dam constructions addressed for water shortages may escalate as water crisis aggravates, and this, as well as indirect effects posed by future scenarios (i.e. weakening capacity of the invaded ecosystems to detain its establishment and proliferation, droughts favoring mixotrophy), will likely favor its expansion.

Our models indicated that *C. furcoides* will expectedly thrive in inland waters of South America, the Caribbean, Central Africa, and China, encompassing some of the most populated areas in the world, and this will probably result in social and economic crises by deteriorating the water supplied for millions of people. Complex and interrelated socioeconomic factors drive the synergetic threats imposed on biodiversity in the Anthropocene. Climate change and biodiversity loss are interacting crises that should be handled together, as short- to middle term climate modifications have the potential to exacerbate many other impacts at multiple scales of the biological organization (from organismal to ecosystems; Bellard et al., 2012; Reid et al., 2019; Weiskopf et al., 2020). Combined with increased nutrient loads, this scenario may be beneficial for certain harmful algal species with vertical migration ability (advantageous for resource acquisition across different strata), leading to more frequent algal blooms episodes. These blooms potentially disrupt trophic links (zooplankton - phytoplankton interactions) due to the inedibility of large-celled phytoplankton which zooplankton can scarcely ingest (Xie et al., 1998; Hart & Wragg, 2009; Howeth et al., 2013).

The higher and increasing suitability of invasion ranges in future climate scenarios likely indicates that the previously detected niche shifts for the species in current scenarios (Macêdo et al., 2021b) may favor invasion success also in a future climate. Accordingly, the geographical distribution of the predicting model agreed well with the current distribution. Environmental disturbance, landscape alteration, and high resource availability as facilitators of successful establishment and the spread of non-native species are common patterns observed in invasion science (Daga et al., 2020; Robinson et al., 2020). Considering the realistic eutrophication scenarios, coastal areas are of particular concern given the higher values of future climatic suitability and the expected population growth by the 2080 s (Rabalais et al., 2008). Therefore, *C. furcoides* will encounter increased levels of urbanization and agricultural land use, and thus higher eutrophication in a world exploiting controversial energy sources based on hydroelectricity and dams. *Ceratium* species will be favored by the eutrophication, i.e. nutrient enrichment (mainly nitrate and phosphorus), and less turbulent conditions of the water column. In all the model projections, the temperature played a key role in determining the future distribution of the species.

Global warming and the changes in the hydrological regime are considered the major stressors triggered by climate change (Woodward et al., 2010; Reid et al., 2019; Rogers et al., 2020). Consequently, the evaporative demand will accelerate the drought condition mainly in South Asia and South America (Zhai et al., 2020; Moon & Ha, 2020). Droughts are predicted to favor facultative mixotrophic organisms (Costa et al., 2016; Costa et al., 2019) by decreasing the water volume, and the light propagation to photosynthesis through the reduction of water transparency (Jones, 2000). Low water availability can also cause catastrophic impacts on the availability and sustainability of water for domestic supplies, human health, and ecosystem functioning (Walsh et al., 2016; IPCC, 2021), with much of these impacts manifested at archipelagos, mountains, tropics, and Northern polar areas (Breslin et al., 2020; Browne et al., 2021; Zanowski et al., 2021), as well as in groundwater systems (S´ anchezFernandez ´ et al.,2021; Jasechko & Perrone, 2021). Other consequences of water level decrease are eutrophication followed by increases in nutrient concentrations and salinity, which constitute a serious threat to aquatic biodiversity in the 21eth century (Reid et al., 2019), and which may have severe implications for native phytoplankton communities and native consumers by diminishing the productivity (Jeppesen et al., 2015). However, *C. furcoides* seems not to be affected by the constraints imposed by climate change due to its broad distribution in temperate, subtropical, and semi-arid regions, (Silva et al., 2018; Amorim & Moura, 2020; Macˆedo et al., 2021a). Therefore, the impacts expected in the climate change scenarios will decrease biotic resistance, which may further contribute to the invasion success of pervasive and harmful species such as *Ceratium* spp.

The patterns of *C. furcoides* distribution seem to be limited by aridification since low suitability was predicted for the arid regions of Australia, North Africa, and large portions of northeast Brazil. However, the habitat relatedness of *C. furcoides* to artificial systems, such as reservoirs (Macˆedo et al., 2021c), may enhance its distribution, even in less suitable areas as in semi-arid regions (Costa et al., 2016, 2019; Amorim & Moura, 2020). This is also the case for water diversion projects (Zhang et al., 2020; Daga et al., 2015; Macêdo et al., 2021a) undertaken to improve water security in these regions. The megaproject of inter-basin water diversion of the São Francisco River in semi-arid northeast Brazil is an example of great concern regarding the spread of *C. furcoides* (Silva et al., 2018). Passive dispersion of this species due to water diversion was already reported in south-south-east Brazil where *C. furcoides* was transported in pumping water between two reservoirs in the Parana ´ River basin (Nishimura et al. 2015) as well as in waters from the Paraíba do Sul River basin diverted to another (Guandu River basin; Macêdo et al. 2021a). On the other hand, dams can also facilitate the establishment of the congeneric, and also harmful dinoflagellate, *Ceratium hirundinella* (O.F.Müller) Dujardin 1841 in areas climatically unsuitable for *C. furcoides*. This hypothesis may be sustained by some different environmental requirements of *C. hirundinella* which is frequently found at high densities in dams of arid and semi-arid areas e.g.: in the Argentinian Patagonia (Casco and Mac Donagh, 2014; Casco et al., 2014), Turkey (Varol, 2016), and Iran (Darki & Krakhmalnyi, 2019). Moreover, the more arid climate would be not a barrier for *C. furcoides* spread and its associated effects in basins impacted by impoundments as this invasive species is showing fast expansion through several public supply reservoirs in northeastern Brazil (Severiano et al., 2021).

A warmer climate will also impact precipitation as indicated by the CMIP6 models, which will affect both biodiversity patterns and human well-being worldwide at various spatial and temporal scales (Hirabayashi et al., 2021). Following these predictions, the increase of primary productivity and phytoplankton biomass dominated by harmful algae (Finni et al., 2001; Paerl & Huisman, 2008; Gobler, 2020) are the most ubiquitous consequences of elevated nutrient concentrations. Increased surface water temperatures, salinization, reduced wind in several parts of the world, and less warm summers linked to climate change could lead to stronger stratification of the water column in deep lakes and permanent or temporary stratification in some of the shallow lakes, thus preventing oxygenation of the colder bottom waters and possibly leading to anoxic conditions (Deng et al., 2018), favoring dinoflagellate, such as *C. furcoides*. (Tundisi et al., 2010; Cassol et al., 2014; Amorim & Moura, 2020; Pacheco et al., 2021).

C. furcoides relies on a silent invasion strategy through mechanisms that hinder early detection such as cyst-forming and vertical migration. Furthermore, molecular analysis of different invasive populations showing higher genetic similarities is of particular importance since they reveal a suite of ecological traits that act as barriers to and drivers of its invasion success (Crossetti et al., 2019; Kruk et al., 2021). Additionally, *C. furcoides* has a broad feeding strategy, which makes it less constrained by changes in turbidity and transparency of the water column, while its ability to form cysts increases its spatial or temporal resilience to abrupt environmental changes. With these invasiveness features documented for *Ceratium* sp. combined with a higher ecosystem vulnerability, considering both optimistic and pessimistic scenarios, *C. furcoides* is likely to establish and proliferate to an even higher extent than expected.

Changing wind patterns, linked to climate change, could influence circulation and biogeography by affecting existing patterns of airborne dispersion (Hamilton & Lenton, 1998; Hughes-Martiny et al., 2006; Kling & Ackerly, 2020), an alternative pathway for water flow and zoochory regarding aquatic species (Kristiansen, 1996), especially microorganisms (Sharma et al., 2007; Naselli-Flores & Padisak, ´ 2016). Recently, Kling & Ackerly (2020) have predicted winds to shape future climate vulnerability patterns by altering dispersal and range expansion of wind-dispersed species, leading to profound ecological consequences for indirectly reducing biological and ecosystem resilience and biotic resistance to invasive species. From the ecological and evolutionary perspective, it raises an interesting debate on how invasive populations of *C. furcoides*, which has shown no genetic variation throughout its expansion through niche shifting (Accattatis et al., 2020; Macˆedo et al., 2021b), may be favored by the genetic weakness of the native biota.

Overall, our study supports the idea that the widespread species *C. furcoides*, with strong invasiveness features, is likely to cope with the ongoing changes of the Anthropocene – the accelerated global warming in a world caverd with stepping-stone reservoirs. Consequently, in rising global temperature scenarios, *C. furcoides* is expected to maintain its fitness throughout a much greater temperature range, enhancing its invasion success into inland waters worldwide. However, great superimposition between dams and suitable areas was found, and the future of this dinoflagellate, and whether it will continue to expand its range into low suitability areas with the predicted boom of reservoirs remains uncertain. Precipitation dynamics may also be a confounding factor regulating abrupt population shifts, giving rise to concern about its silent feature until sudden bloom formations. Furthermore, we also anticipate even more drastic scenarios, especially in the neotropics, Central Africa, and China as these regions combine habitat relatedness with high probability values. Higher future invasion risks may therefore require effective management intervention and policies relying on interdisciplinary tools to deal with complex and challenging interplays of factors, especially considering microorganisms with detection issues attributable to a microorganism (taxonomy and sampling efficiency). We also expect that our framework can be used for other invasive species development and management has a similar affinity to dammed systems.

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ARTICLE THREE

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Climate change and niche unflling tend to favor range expansion of *Moina macrocopa* Straus 1820, a potentially invasive cladoceran in temporary waters

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Abstrac

Non-native species' introductions have increased in the last decades primarily due to anthropogenic causes such as climate change and globalization of trade. *Moina macrocopa*, a stress-tolerant cladoceran widely used in bioassays and aquaculture, is spreading in temporary and semi-temporary natural ponds outside its natural range. Here, we characterize the variations in the climatic niche of *M. macrocopa* during its invasions outside the native Palearctic range following introduction into the American continent. Specifcally, we examined to what extent the climatic responses of this species have diverged from those characteristics for its native range. We also made predictions for its potential distribution under current and future scenarios. We found that the environmental space occupied by this species in its native and introduced distribution areas shares more characteristics than randomly expected. However, the introduced niche has a high degree of unflling when displacing its original space towards the extension to drier and hotter conditions. Accordingly, *M. macrocopa* can invade new areas where it has not yet been recorded in response to warming temperatures and decreasing winter precipitation. In particular, temporary ponds are more vulnerable environments where climatic and environmental stresses may also lower biotic resistance.

Keywords: Climate change · Ensemble · Invasiveness · Moinidae · SDM

Introduction

The Anthropocene has been a challenge for biodiversity management and conservation of freshwater resources (Reid et al., 2018; Dudgeon, 2019). This "age of mankind" is characterized by widespread environmental disturbances undertaken by several human activities, e.g., climate change, degradation of natural habitats, and biological invasions. The above threats can also enhance biological invasions, which may synergistically threaten biodiversity from species to ecosystems level, thus requiring substantial conservation and management efforts. Therefore, because species distributions are expected to shift with future climates and global trades (Parmesan, 2006; Olden et al., 2021; Wang et al., 2021), more than generating discussions on new paradigms of biogeography concepts and novel ecological hypotheses (Capinha et al., 2015; Hill & Hadly, 2018; Pyšek et al., 2020), we need to forecast the distribution and environmental relatedness of invasive species to then implement adequate monitoring policies.

Assessing species niches and their dynamics can help elucidate alien invasive species distributions and species adaptations to diferent environmental conditions (Wiens et al., 2009; Tingley et al., 2014). As species distribution models use the ecological characteristics of its known occurrences to estimate suitable areas for the species in its potential distribution area (Peterson & Vieglais, 2001; Cordier et al., 2020), we can theoretically investigate its invasion success and spreading into new areas based on species data and spatial constraints. The assessment of niche conservatism—whether a species may overcome historical constraints and invade previously inaccessible areas (Peterson et al., 1999; Peterson, 2003; Wiens et al., 2010) or niche shifts of invasive populations—whether its success depends on the ability of individuals to undergo new local adaptations not shown in its ancestral niche (Müller-Schärer et al., 2004) is a central question in biological invasions. Explaining the underlying reasons for these individualistic responses requires comparing multiple clades and environmental change types. Accordingly, niche tests complement fundamental assumptions for applying SDMs assuming that the species occupy similar environmental conditions in new geographical ranges or periods (Pearman et al., 2008).

Currently, some taxonomic groups are adequately investigated in terms of invasion mechanisms involving niche evolution (e.g., plants Broennimann et al., 2007), as for freshwater fshes (Lauzeral et al., 2011), dinofagellates (Macêdo et al., 2021), and aquatic invertebrates (Torres et al., 2018). However, few studies have combined niche dynamic analysis to changes in species redistribution, making it hard to obtain a general pattern of climate-induced shifts across broad taxonomic spectra (Taheri et al., 2021) making hard to obtain a general pattern of niche dynamics across broad taxonomic spectra. Thus, understanding niche dynamics and mapping the potential distribution of a new invader may provide valuable tools for management actions, particularly if the potential invader (i) has life histories that facilitate colonization (e.g., asexual reproduction; resting stages) (Ruiz et al., 2000), and (ii) if the risk of adverse environmental impacts is high based on taxonomically related species information, especially in the initial stages of invasion (Sousa et al., 2017; Dexter & Bollens, 2019).

Although there is strong literature bias for the environmental efects on invasive microfauna, invasive zooplankton taxa have shown potentialities for exerting moderate to high adverse efects on biodiversity. Specifcally, cladocerans are a group of invertebrate animals potentially threatening aquatic biodiversity when acting as invasive species. For example, the invasive *Daphnia lumholtzi* Sars, 1885 which has a negative impact on other native zooplankton populations (Dzialowski et al., 2000; Soeken-Gittinger et al., 2009). Also, the two invasive predatory cladocerans Bythotrephes longimanus Leydig, 1860 and Cercopagis pengoi Ostroumov, 1891 recognized as major drivers of biodiversity and economic losses (Jacobs & MacIsaac, 2007; Walsh et al., 2016). Among cladocerans, *Moina* has been intensively studied (Neretina et al., 2020) regarding taxonomy (Alonso et al., 2019), cryptic diversity (Petrusek et al., 2004; Bekker et al., 2016; Montoliu-Elena et al., 2019), and biogeography (Elmoor-Loureiro et al., 2010; Farias et al., 2017). Moinids have also shown morphological similarities with daphniids (Goulden, 1968). However, moinids' invasion processes are understudied compared to other cladoceran species such as daphniids, despite their relative importance in the Neotropical and Palearctic regions (Forró et al., 2008).

Moina macrocopa Straus, 1820 has been reported as a potential invader of inland waters (Paggi, 1997; Okolodkov et al., 2007). Reported to be native in water bodies of Europe, Africa, the Middle East, and Asia, mainly in shallow temporary lakes, *M. macrocopa* is claimed to have been introduced in the American continent only more recently due to anthropogenic vectors (Paggi, 1997). However, its invasion pathway and vectors remain largely unknown. In this respect, we set up the framework for evaluating the potentialities of *M. macrocopa* (Cladocera) as an emerging invasive species and the eventual role of niche evolution to explain its expansion success, while invading new ranges following the transoceanic introductions from the Palearctic region. We tested whether niche conservatism or shift has driven the geographical expansion of *M. macrocopa* using multivariate analyses, mapping areas suitable for *M. macrocopa* under current and future climate scenarios (2041–2060) at a global scale. Specifcally, as a stressadapted cladoceran and considering its initial widespread in tropical ponds (an essential detail of its known invasion history), we hypothesized that *M. macrocopa* would expand its distribution as climate change progresses. We also evaluated environmental predictors of its expected range expansion in the face of the predicted warmer and drier future climate. In doing so, we aim to advance discussion on biogeography and invasion biology of inland water zooplankton and contribute to making policies managers better informed.

Material and methods

Species' distribution data and curation

We gathered occurrence records from the Global Biodiversity Information Facility (GBIF) (https:// doi.org/10.15468/dl.4u4kmf) and a literature review in SCOPUS using the following keywords: "*Moina macrocopa*" OR "*Moina macrocopa*." We performed a broad search based on title, abstract, and keywords, with no additional filter on language or document type. Here, we considered as *M. macrocopa* s.l., excluding the American clade *Moina macrocopa americana* Goulden, 1968 as recent research has indicated that these clades are different species (Montoliu-Elena et al., 2019).

We compiled a dataset for further curation using R studio. First, we converted the original data frame into a spatial polygon object, which was then restricted by removing all points outside the extent of the inland buffer shapefile since SDMs must ideally restrict model calibration to accessible areas (Peterson & Soberón, 2012). Furthermore, the occurrence data were checked for missing (NA) values in Longitude and Latitude and for the existence of duplicates for each species subset. We then filtered (spatially thinned) the records using the spThin package (Aiello-Lammens et al., 2015), removing all records with a distance of 5 km between occurrences. The final occurrence dataset ("Mmacro.csv"), 95 thinned records (62 invasive and 33 native), and plotted occurrences ("map occur. tif) are present in Supplementary Material. For the plotted occurrences, we used ArcMap v10.8, using a polygon layer obtained from FEOW.org (Fresh Water Ecoregions of the World; Abell et al., 2008).

Niche test analysis

To predict the environmental space of *M. macrocopa*, we used all the 19 climatic variables taken from the WorldClim Project (Fick & Hijmans, 2017; http:// www.wordclim.org) at a spatial resolution of 10 min (of a longitude/latitude degree).

With those variables, we used Broennimann et al. (2012) approach to measure niche conservatism between the native (Palearctic) and the invasive ranges in America. This approach calculates an observed measure of niche overlap and compares it to randomized niche overlap measures. This method calculates the available environmental space, defined by the first two axes from the PCA-env, for each study area (Broennimann et al., 2012). Later, it measures the niche overlap between native and exotic ranges using Schoener's D metric (Schoener, 1970). This metric varies from 0 to 1, representing totally diferent or completely overlapping niches, respectively (Broennimann et al., 2012). Then, for the niche overlap, we calculate the D metric and its significance, using a similarity test (based on the 95% confidence interval) which compares the niches in their native and introduced regions (Warren et al. 2008; Broennimann et al., 2012). We repeated each randomization process 100 times, producing a null distribution of overlap values to which the observed score was compared. An observed overlap score that is significantly smaller than one obtained with the null distribution of overlap scores suggests that the species is occupying diferent environmental spaces in the considered ranges. By doing this, we can investigate the invasion pattern through the niche dynamics and interpret the current knowledge of its genetic comparisons between these areas (Montoliu-Elena et al., 2019).

Modeling fundamental niche

Predictor variables

We used the 19 WorldClim variables at a spatial resolution of 10 min (of a longitude/latitude degree). All environmental layers were clipped to the extent of the study area, resulting in a mask of the world without polar regions. Before processing the models, we carried a multicollinearity test by using the variance inflation factor (VIF) (Marquardt, 1970), a widely used approach to avoid instability in parameter estimation and bias in inference statistics (Dormann et al. 2012). The selected variables (bio02/Mean diurnal range (monthly mean, T◦ max − T◦ min), bio08/Mean temperature of wettest quarter, bio09/Mean temperature of driest quarter, bio13/Precipitation of wettest month, bio14/Precipitation of driest month, bio15/ Precipitation seasonality (coefficient of variation), bio18/Precipitation of the warmest quarter, bio19/ Precipitation of the coldest quarter) that were not highly correlated (Pearson's R <|0.80|) were considered biologically relevant, or had already been used in other studies and their efficiency demonstrated (Jiménez-Valverde et al., 2011; Palaoro et al., 2013; Sousa et al. 2017).

For future estimations (2041–2060), we used the MIROC6 model from CMIP6 (Coupled Model Intercomparison Project Phase 6), characterized by CO2 and aerosol emission rates (https://www.worldclim.org/data/cmip6/cmip6climate.html#). We generated two future bioclimatic models for two different scenarios of CO2 emission, the optimistic SSP126 and SSP585 (worst case) shared Socio-economic Pathways. We further generated a consensus map from these scenarios. In other words, WorldClim 2.1 provides Global Climate Models (GCM) of the CMIP6 (Tebaldi et al., 2021) and for the four highpriority scenarios, which cover the range of possible pathways depending on socio-economic choices. Specifically, we chose SSP1-2.6—which assumes a "2°C scenario of the sustainability"; and the SSP5-8.5—which refers to a "high reference scenario" in a high fossil-fuel development world throughout the twenty first century, marking the upper edge of the SSP scenarios (Meinshausen et al., 2020).

Species distribution modeling

We fitted the modeling techniques with species presence data as the response variable and environmental variables as predictors (i.e., explanatory variables). We used algorithms implemented in the SDM R package version 1.0-67 (Naimi & Araújo, 2016): random forests (RF; Breiman, 2001) and maximum entropy (Maxent; Phillips et al., 2006). Maxent is a correlative model based on the maximum entropy principle for estimating probability distributions that require presence and background data obtained from the whole accessible area. On the other hand, area, while RF is a high-performing machine learning technique consisting of multiple decision trees (Breiman, 2001; Olden et al., 2008).

For calibration, 70% of the records (training set) were randomly selected for calibration and the remaining 30% for model evaluation. For each algorithm, ten replicates were employed, using the bootstrapping method. Given that the species occurrence data frame included only presence data, an argument for background data of ten thousand (10,000) points per species using the method "gRandom" was employed (in the script; method= "gRandom," n=10,000), with the removal of matching points, to generate pseudo-absence data (Barbet-Massin et al., 2012). Prediction maps were generated from all records without distinction between native and invaded areas

(Broennimann & Guisan, 2008; Sales et al., 2021). Furthermore, the differentiation between native and non-native ranges is not precise since sampling efforts are lacking globally. The usual method to overcome these issues includes both the native and invaded ranges because such models have better performance than models using only the native range (Broennimann & Guisan, 2008). We evaluated the models using multiple approaches: (1) area under the curve (AUC), in which AUC>0.9 the predicted model is very good (Swets 1988), (2) Pearson's correlation coefficient (COR), and (3) explained deviance (deviation). The mean performance is presented in Supplementary Table 1.

Models were summarized in Ensemble maps, using weighted averaging over all predictions from the fitted models (method= "weighted"). In other words, the ensemble combines the prediction of different algorithms and replications to develop a single output. Finally, we visually assessed projected ensemble-based distribution maps (Araújo & New, 2007).

By applying a threshold (i.e., the mean model TSS criteria of model evaluation, "max (se+sp)," the respective maps of binomial probability of occurrence (0 or 1) were obtained. By using the "predict" function (Naimi & Araújo, 2016), the fitted models were used to generate future predictions with the future data layers (per time frame, per SSP scenario). Further, future and present distributions were compared in terms of overall mean probabilities and changes in suitability by mapping areas of decrease, stability, and increase. We performed our analysis in R 4.0.1 (R Core Team, 2021), the extensible R platform for species distribution modeling (Naimi & Araújo, 2016).

Results

According to the multivariate niche analyses, the two niches are more similar than expected randomly (similarity test=0.02); therefore, we did not reject the niche conservatism hypothesis, although both niches were not identical, showing low observed Schoener's D=0.05. We detected high portions of niche unfilling (74%). In other words, more than 70% of the original niche is not filled in the invaded range. The niche expansion was 2.7%, following also high values of stability 97%. The centroid of the introduced niche (green) was slightly shifted towards higher precipitation and lower temperatures than that of the native area (orange) (Fig. 1B). The first two principal components of the nineteen bioclimatic variables for the native and introduced areas explained about 73% of the total variation (Fig. 1A).

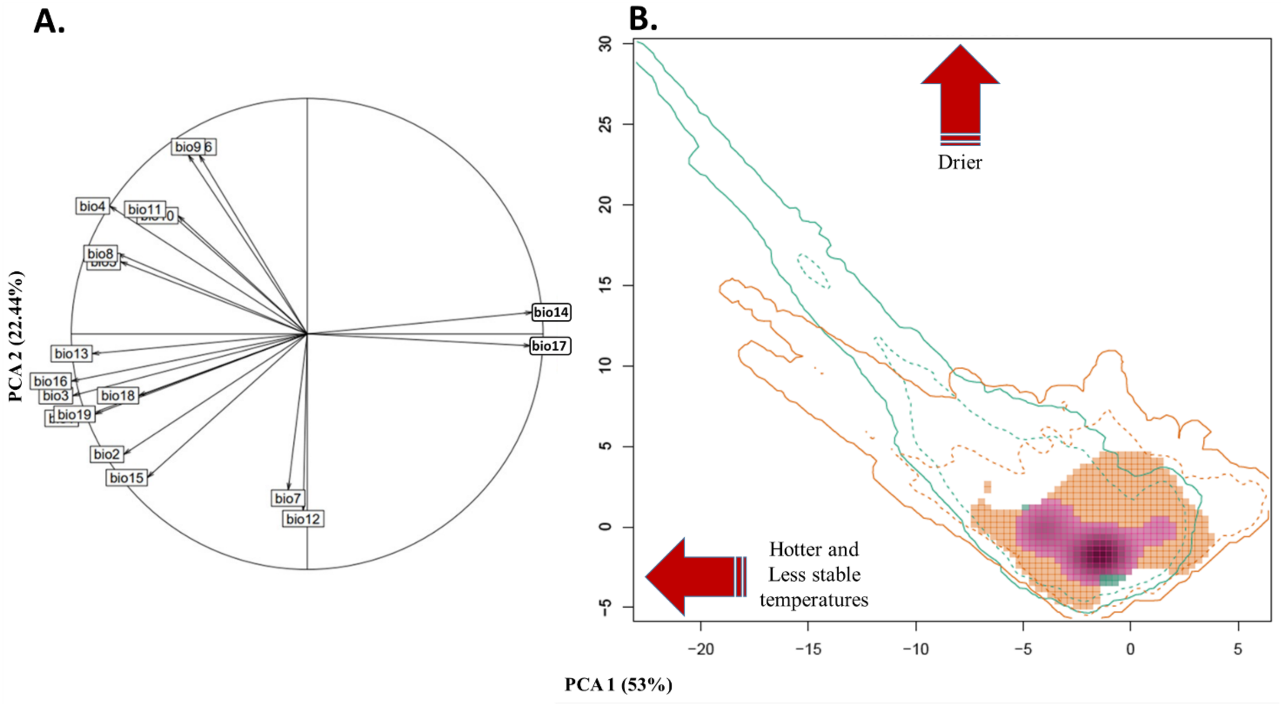

Figure 1. A. The resulting PCA with variables available for *Moina macrocopa* used for the PCA-env approach of Broennimann et al. (2012). B. Comparison between the native and exotic ranges of *M. macrocopa*. Niche occupied by *M. macrocopa* in its native range (orange), in its invasive range in America (green) and composed niche overlap of both ranges (purple). The continuous line represents the 100% of available environmental background and the dashed line represents the 50% most common conditions. See Figure S2 for the contribution of each variable to the PCA axes.

The first component (53%) grouped the three precipitation-related variables, whereas the second (approx. 20%) grouped the three temperature related variables. Although the average values of AUC for RF and MaxEnt showed good performance (>0.8), the ensemble model showed maximizing predictive performance (>0.9), showing better ft from the weighted overlap of these algorithms. Furthermore, the potential invasive risk area predicted by ensembles can cover most of the current distribution records of *M. macrocopa* used in this study.

Our distribution modeling revealed that current suitability was considered low in most parts of the Palearctic except for Europe and Southeastern China. Overall low climate suitability was also observed in regions where this cladoceran occurs less frequently in invaded ranges (Fig. 2A). The most important climatic factor limiting the further expansion of *M. macrocopa* was the variable bio09/Mean temperature of the driest quarter (Table 1). Bio19/Precipitation of the coldest quarter and bio02/Mean diurnal temperature range were other infuential variables. Thus, the probability of occurrence of this species is followed by increases in bio09 but declines with the increase in bio19 and bio02. The potential distribution map of *M. macrocopa* in the future is displayed in Fig. 2B.

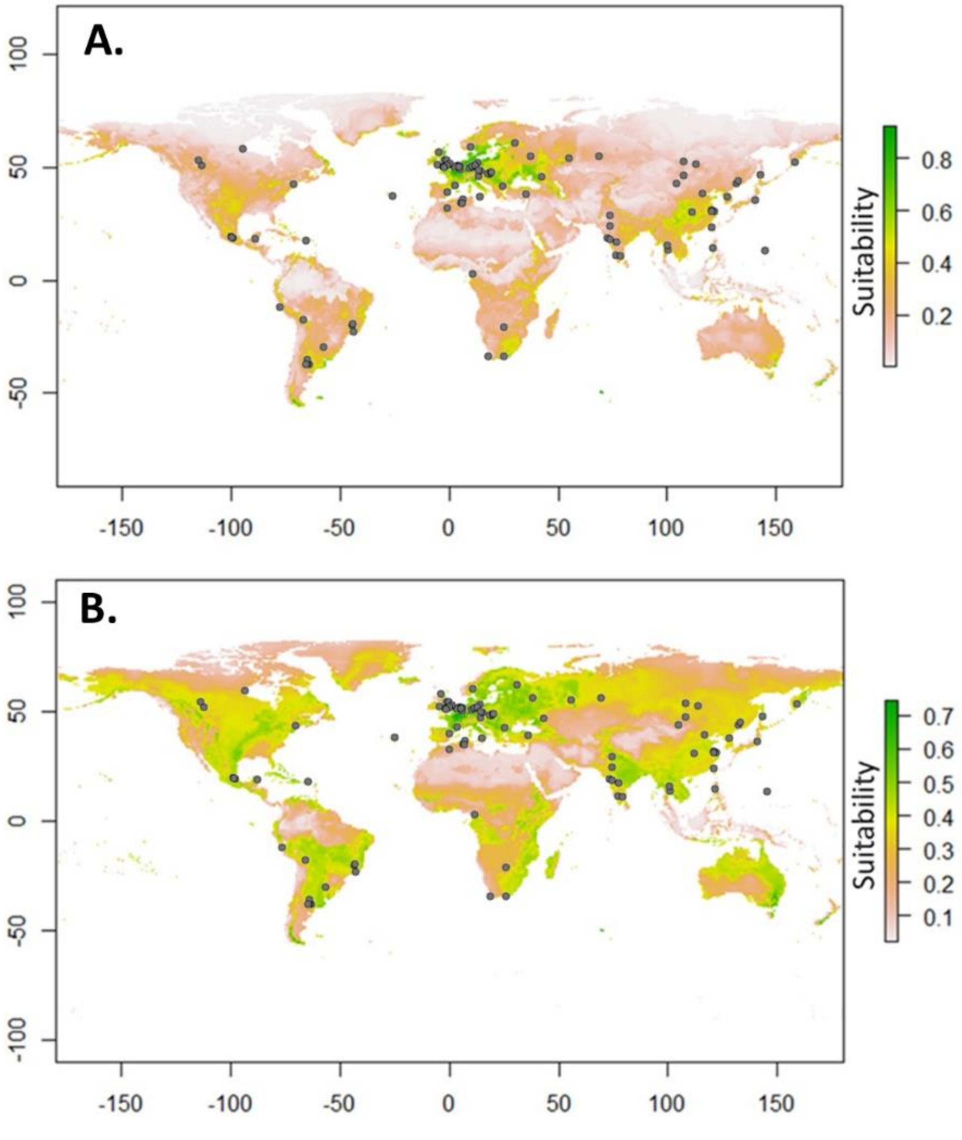

Figure 2. Global projection maps of the ensemble calibrated using thinned records. Green tons for higher environmental suitability. A. Current potential distribution of *Moina macrocopa*: B. Future distribution (2041-2060).

The potential distribution range increased worldwide, with new areas in the American Continent, Asia, Africa, India, and Australia. The suitable areas with suitability≥0.5 for the future climatic conditions were located in the North of Europe, Northeastern Brazil, large portions in the United States, and South Australia. These overall range expansions followed an increase in suitable areas across broad geographic zones except in Europe, which is predicted to decrease in the future scenarios studied (2041–2060) (Fig. 3).

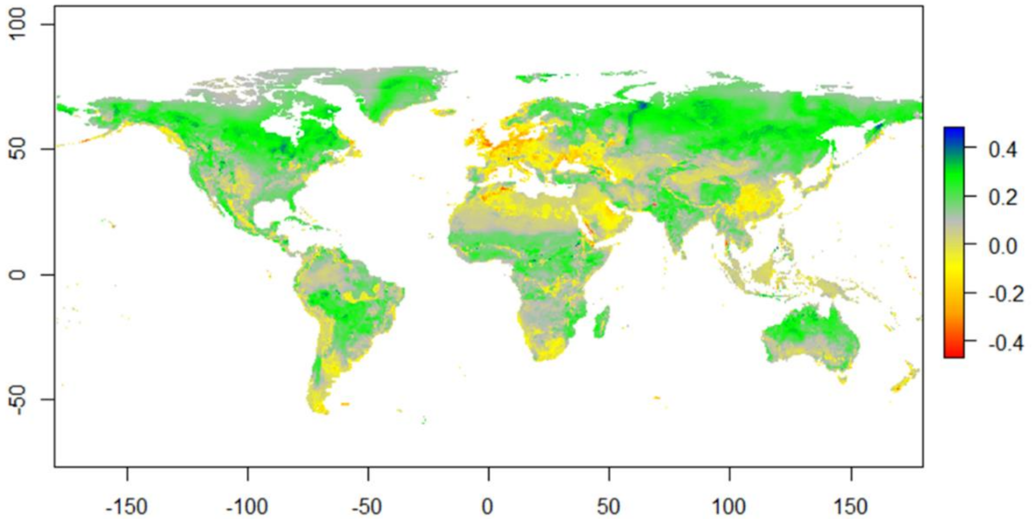

Figure 3. Global suitability loss (below 0.0), gain (above 0.0) and stability (= 0.0) of areas for expansion by the target species *Moina macrocopa* under climate change scenarios.

Discussion

Here, we investigated whether the niches of populations of the stress-tolerant cladoceran *M. macrocopa* remained conserved during the invasion process. We discuss our results focusing on the expansion potential through niche unflling and further mapped areas more susceptible to global invasion. We found that the climatic niche of *M. macrocopa* remained broadly stable. Thus, the investigated native and introduced environmental spaces are more similar than random. Also, we found a low degree of expansion (i.e., a new niche in the non-native range) compared to its native niche. However, given the wide variation in environmental conditions where this species currently occur, the niche overlap between American and Palearctic records was low, refecting their diferent environmental constraints (ElmoorLoureiro et al., 2010; Makino et al., 2020; Bhanushali et al., 2021). Thus, during the invasion of the American continent, *M. macrocopa* retains signatures of its native environmental niche but also indicates diferences in environmental space following the introduction, which can be further ascribed to evolutionary processes, dispersal limitations, or invasion history.

In fact, despite niche shifts observed in some taxa (Torres et al., 2018; Macêdo et al., 2021), most invaders do seem to occupy climates similar to those of their source populations (Martínez-Meyer & Peterson, 2006; Petitpierre et al., 2012; Strubbe et al., 2015; Bates et al., 2020). The low but present expansion in *M. macrocopa* may be due to propagule pressure enhanced by global e-commerce of this species introducing adaptive genetic variation for new areas facilitating colonization of novel environments (Simberloff, 2009). We, therefore, expect propagule pressure to scale the current extent of niche expansion, while decreasing unfilling in the future. On the other hand, hybridization may also impact the evolution of species geographical ranges (Pfennig et al., 2016; Pierce et al., 2017). It is conceivable that hybrids of *M. macrocopa* are more prone to inhabit significant ecological gradients and occupy a different environmental niche, as demonstrated for other cladoceran species (Wolf & Mort, 1986; Petrusek et al., 2008; Liu et al., 2018), further facilitating invasion (Thornton & Murray, 2014). Also, there is morphological evidence of individuals of an intermediate phenotype from different regions in the American continent, e.g., ventral filaments, in the ephippium (Elías-Gutiérrez & Zamuriano-Claros, 1994; ElmoorLoureiro et al., 2010; Vignatti et al., 2013). However, we did not directly investigate the niche differentiation of the species by hybridization. Thus, the development of ecological niche models that include biotic interactions should be considered in the future.

Together, the findings above suggest a close link between these records of *M. macrocopa*, which share environmental niche spaces, corroborating that although closely related, they still may be different taxa. However, apart from the genetic distances between *M. macrocopa macrocopa* and *M. macrocopa* americana (Montoliu-Elena et al., 2019; Bhanushali et al., 2021), the very low overlap also brings cues that might be used to test taxonomic hypothesis regarding *M. macrocopa macrocopa* solely. In addition, the lack of taxonomical identification keys and genetic characterization for many parts of the world (Goulden, 1968) hampers our ability to infer their invasion history accurately.

Currently, there were high portions of the invasive niche of *M. macrocopa* that remained unfilled or were non-occupied in the non-native range despite being present in the original niche (Simberloff, 2009; Soberón & Arroyo-Pena, 2017). This unfilling indicates environmental non-equilibrium, and that the invasion process of *M. macrocopa* is incomplete. Niche unfilling can also occur because dispersal is limited, suitable environments are inaccessible, or the initial bottleneck reduces adaptive genetic variation necessary for broad colonization. Nevertheless, the time since introduction can also be correlated with the magnitude of niche filling (Strubbe et al., 2015), suggesting, in this case, a recent invasion *of M. macrocopa*.

Human activities play an essential role as a vector of new introductions of *M. macrocopa*—one of the most commonly used cladoceran in standardized laboratory bioassays worldwide (Martínez-Tabche et al., 2000; Iannacone & Alvariño, 2002; Nandini et al., 2004). Following its previous introduction in South America, e.g., in Peru (Valdivia-Villar, 1988), Argentina (Paggi, 1997), and Chile (Iannacone & Alvariño, 2002), this vector is a probable source for its late appearance in Brazil (Elmoor-Loureiro et al., 2010; Rietzler et al., 2014; Eskinazi-Sant'Anna et al., 2020). Hence, as dispersal may not limit its spread in invaded areas, bottleneck and/or biotic resistance are more likely to be the most critical factors determining this high unfilling. *M. macrocopa* has intense propagule recruitment through clonal or resting egg production (Vignatti et al., 2013; Sirianni, 2017; Nandini & Sarma, 2019), and bottlenecks are common in organisms that recruit novel populations from a single propagule. Explicitly, in this case of *M. macrocopa*, the selective pressures in cultures intended for aquaculture and live-food production could enhance bottlenecks (Fermin, 1991; Manklinniam et al., 2018). In this case, *M. macrocopa* population must succumb to the many problems associated with a low genetic variation or adapt to the novel environment relying on plasticity. In addition to the bottleneck effect, the enemy release (the absence of natural competitors or predators; Keane & Crawley, 2002) can also play a role in the success of invasive species, which would enable them to grow and reproduce without these regulatory pressures (Allendorf & Lundquist, 2003). *M. macrocopa* can often be found in environments with reduced competitive and predation interactions (e.g., low diverse ponds, subjected to abiotic stress, and known to have no fish or invertebrate predators). However, further studies may hypothesize biotic resistance mediated by native aquatic diversity to act against the colonization of available climatic areas for *M. macrocopa* (Elton, 1958; Levine & D'Antonio, 1999).

Our results also supported the hypothesis of overall geographic expansion following global warming and future predicted hydrological stress, thus forecasting species responses to changing environments in the Anthropocene (Taheri et al., 2021). *Moina macrocopa* is already common in habitats subject to human pressures, viz. (i) eutrophication, dense populations in nutrient-rich waters such as sewage treatment basins (Vignatti et al., 2013; Padhye & Dumont, 2015), (ii) low oxygen (Paggi, 1997; Elmoor-Loureiro et al., 2010; Vignatti et al., 2013), (iii) salinity variation (5.7 g l −1 to 21.8 g l −1; Vanjare et al., 2010; Vignatti et al., 2013), (iv) rapid recover from resting egg bank afected by heavy metals (Oskina et al., 2019), and (vi) the ability to endure signifcant temperature variations (minimum of 9.4 and maximum of 26.9 °C; Vignatti et al., 2013), including thermal tolerance above optimum (Engert et al., 2013) when a trade-of between reduced lifespan and increased reproduction occurs in females (Sarma et al., 2005). Such biological attributes of *M. macrocopa* allow it to establish in many types of waters, including those where extreme environmental conditions limit the presence of zooplankton competitors and where its ftness is reduced, e.g., eutrophic and cyanobacteria dominated (Hansson et al., 2007a, b; Padhye & Dumont, 2015).

The importance of precipitation-related variables would also indicate that this species has essential invasiveness features in unstable environments, e.g., environments subjected to hydrological stress (Alonso, 1996; Vignatti et al., 2013). Accordingly, extreme droughts and rising mean temperature might result in more areas extensively subjected to invasions, at least climatically, by this cladoceran. For example, in some portions of the United States, an increase of 3–9°C in mean annual temperature combined with decreases in precipitation is predicted (Walsh et al., 2014). Also, areas in Australia where high costs with invasive species are reported. Lakes and ponds in Brazilian Pantanal wetlands are currently under severe climate threat. Lakes and ponds in Brazilian Pantanal wetlands that are currently under severe environmental threat. Arid and semi-arid areas in northeastern Brazil, where low precipitation and high-temperature waters tend to expand other planktonic invasive species (Severiano et al., 2022).

Notwithstanding its ability to persist, establish, and expand distribution, *M. macrocopa* can also favor passive dispersal of epibionts, including parasites becoming vectors of novel introductions of harmful organisms (Xu, 1992; Czeczuga et al., 2008; Vanjare et al., 2010). Also, monitoring ballast water should be considered, especially regarding the high resistance and survival of the resting eggs of *M. macrocopa* (Alekseev et al., 2010). Further studies using morphology and DNA barcoding can help to foster hypotheses about the invasion process of this potentially invasive cladoceran.

Overall, our fndings revealed evidence of conservatism in the *M. macrocopa* and a high degree of unflling. Meanwhile, we believe that *M. macrocopa* is expanding its geographical distribution, currently overlooked, following climate change scenarios. However, the mechanisms by which this species could favor the invasion success are unclear. This potentially invasive species can compete with other congeneric native species common in shallow and temporary environments, such as *M. cf. wierzejskii* Richard 1895, *M. dumonti* Kotov, Elías-Gutiérrez & Granado-Ramírez, 2005, and the species complex M. micrura Kurz 1874. We suggest researchers consistently incorporate multivariate analysis of niche into investigations on invasion processes of cladocerans, simultaneously with morphological and molecular information. This integrative approach could more efectively predict future invasions and anticipate detections. In addition, we strongly advocate complete phylogeographical research considering populations in Africa and South America to optimize available information on invasion history and environmental traits in *M. macrocopa*. In doing so, we would be able to recalibrate our models with updated and novel data to better refect concurrent changes in species' realized climatic niche. Ultimately, it could match the proposed interdisciplinarity of Invasion Science.

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ARTICLE FOUR

In preparation for submission to FRESHWATER BIOLOGY

Combining niche analysis and potential distribution to guide conservation actions regarding *Cercopagis pengoi* (Cladocera), a highly invasive pelagic predator

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Abstract

1. Predicting the establishment of an invasive species in new ranges is an emerging conservation and management challenge. Preventing invasions poses a significant challenge because of their taxonomic difficulties, wide physiological tolerances, and the role human activities play as vectors in their spread. The Porto-Caspian cladoceran *Cercopagis pengoi* (Crustacea: Branchiopoda) is a pelagic predator listed among the "100 World's Worst Invasive Alien Species". It has rapidly spread following introductions in Eurasia and North America, where it has been historically impacting fisheries and aquatic native biodiversity.
2. We used species distribution modelling to explore mechanisms that shape the establishment of new ranges. For this, we relied on multivariate niche analysis to quantify niche dynamics and reciprocal species distribution modelling to map suitable areas for the spread of *Cercopagis pengoi*.
3. Although we did not find evidence for niche expansion, we observed a high degree of niche unfilling, suggesting potential niche conservatism in the invasion process of *C. pengoi* in North America. According to our models, *C. pengoi* is suggested to occupy novel brackish and freshwater environments outside the current species distribution, including coastal wetlands, lakes and waterways in Florida, Northeastern Canada, the Mediterrian, Central Europe and Eurasian portions whether movement limitation or monitoring efforts weakens. We identified potential geographic expansion following drier and warmer areas.
4. Our findings are important for managing this invasive species as they are indications that: (i) the potential for future spread is high for this pelagic predator;

and (ii) the vulnerability to invasion may be reduced by management policies. We advocate for improved identification of areas likely to be suitable for this invasive species in areas where monitoring policies are lacking and should, therefore, be prioritised for surveillance focused on early detection and impact mitigation, alleviating potential economic and ecosystem impacts. We also suggest that ballast water regulations may play a key role in limiting spread in North America and Europe.

Keywords: Baltic Sea, bioinvasion management, fishhook waterflea, Great lakes, niche unfilling.

Introduction

Aquatic ecosystems have immense biological value and provide numerous nature’s services to humans, from climate and hydrological regulation to provisioning of goods and life full-filling conditions (Boulton et al., 2016). However, aquatic biodiversity and all the important services it provides to us is being threatened by multiple anthropogenic stressors (Tundisi et al., 2015; Bowler et al., 2020), including the escalating impact posed by invasions of alien species (Ricciardi, 2007; Hulme, 2009; Tundisi et al., 2015). Invasive species can compete with native species, disrupting trophic relationships and altering ecological processes at many levels of the biological organisation (from genes to population to communities and entire ecosystems; Magliozzi et al., 2017; Florian et al., 2016; Bellard et al., 2016). Being multifarious ecological processes, biological invasions should be addressed through diverse approaches and compiling evidence from various studies (Ricciardi et al., 2020). With this, it will be possible to test hypotheses related to the predictors of invasion success and develop risk assessment models (Ricciardi and MacIsaac, 2011; Walsh et al., 2016; Jackson et al., 2017 Cuthbert et al., 2021).

Species distribution modelling (SDM) have emerged as essential tools in invasion biology (Peterson et al., 2003; Herborg et al., 2007; Broennimann et al.; 2012; Torres et al., 2018), allowing to correlate species occurrences from the native and invaded region with environmental data to forecasting environmental suitability and predict invasion potential in space and time. A fundamental assumption of SDM is niche conservatism, namely that the realised niche is conserved between the native and invaded ranges (Peterson, Soberón, & Sánchez-Cordero, 1999; Wiens & Graham, 2005). Yet, a shift in the species realised niche had been reported across a broad range of aquatic taxa such as fish (Parravicini et al., 2015), crustaceans (Zhang et al., 2020) and dinoflagellate (Macêdo et al., 2021) and other freshwater invertebrates and microorganisms (e.g., Capinha, Leung, & Anastácio, 2011; Morehouse & Tobler, 2013; Torres et al., 2018). Therefore, it is critical to detect when niche shifts occur to identify invasive species that are likely to pose problems for management because of their ability to colonise novel environments following evolutionary process at short-time scales (Peterson 2003, Peterson & Vieglais 2001).

Zooplankton invasions have recently emerged as a global conservation concern, threatening native biota and ecosystem services. However, investigations on invasion mechanisms in zooplankton are still largely overlooked, with most of the impacts attributable to few taxa [e.g., microcrustaceans (Cladocera: Cercopagididae) such as *Bythotrephes longimanus* Leydig, 1860 and *Cercopagis pengoi* Ostroumov 1891 (Dexter & Bollens, 2019)]. Specifically, *C. pengoi* is one of the ‘‘World’s Worst Invasive Alien Species’’ (Lowe et al., 2000; Luque et al., 2014; GISD2020). Native to the Caspian and Aral Seas (Mordukhai-Boltovskoi, 1965), *C. pengoi* has recently spread, possibly through ballast water, to the waterways of eastern Europe (Baltic Sea) (Ojaveer and Lumberg, 1995). Subsequently, following transoceanic dispersal to the Great Lakes (MacIsaac et al., 1999; Cristescu et al., 2001), the species has arrived in the Americas. This generalist predator (Pichlová-Ptácníková and Vanderploeg, 2009) competes with native zooplankton and meroplankton, such as *Leptodora kindtii* Focke, 1844 and larval fish (Laxson et al., 2003; Kotta et al., 2006; Pichlová-Ptácníková and Vanderploeg, 2009), with profound negative impacts on native biodiversity and economic activities (Ojaveer and Lumberg, 1995; Maclsaac, 1999; Jacobs and MacIsaac, 2007; Naumenkoa and Telesh, 2019). The invasive *C. pengoi* have established and spread in several locations, yet showing low genetic diversity, but described with high phenotypic variation through cyclomorphosis, the environmental-triggered modifications of cladoceran morphology mostly displayed as changes in tail spine length and shape of the head (Gorokhova et al., 2000; Makarewicz et al., 2001; Litvinchuk & Telesh, 2006). This apparent paradox may be an indication of a more significant influence of adaptive traits on invasion success, regardless of an evolutionary process, commonly found among cladocerans. Also, a recent study relied on analysis where the species are not yet established, aiming to anticipate invasion for a conservation purpose (e.g. *Cercopagis pengoi* in New Zeland;

Torres et al., 2018). For these reasons, we advocate using multiple models within an ensemble forecasting framework and complementary multivariate analysis of niche using a primarily known key species as models for understanding biological invasions by integrating both available biological data and niche modelling and projections.

Decadal of limited geographical distribution and low genetic differentiation in invaded ranges may result from a few introduction events due to non-adaptive mechanisms. This may corroborate the great relevance of specific abiotic conditions for this species, resembling high-stress tolerances from its evolutionary origins in the Ponto-Caspian basin (e.g., high salinity fluctuations; Banarescu1991; Dumont 1998). We hypothesised niche unfilling more than niche expansion from native to invaded ranges and vice-versa. After investigating whether niche conservatism or niche shift has operated during invasions, we tested the hypothesis that higher niche stability between Source (Baltic Sea) and invaded (North America) ranges would reciprocally predict more similar potential areas when compared to native. In doing so, we also assessed the invasive potential of the worst world invasive cladoceran by mapping potential areas where the species is more likely to spread. In agreement with current trends of geographical expansion into Russian waterbodies, we hypothesised higher suitable areas into the Eurasian and North American continents than the current distribution. Possibly, this will serve as evidence that its restricted decadal distribution was due to movement restrictions, currently diminished by human activities.

Materials and Methods

2.1 Occurrence and environmental data

We gathered occurrence records of *C. pengoi* from i) the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.us7urc); ii) The U.S. Geological Survey's Nonindigenous Aquatic Species Database (USGS-NAS; Fuller and Nielson, 2015; USGS, 2021); iii) Ocean Biodiversity Information System (OBIS; https://obis.org/taxon/234025); and iv) a literature search by title, abstract and keywords. We conducted the search with Scopus and the Web of Science online databases with the search string: Cercopagis AND ("Invasive" OR "non-native" OR "non-indigenous" OR "alien" OR "introduced") (Table 1).

We assembled 1,652 records for *C. pengoi* the native range in the Ponto-Aralo-Caspian basin in Southern Europe (NATIVE = 11 records) and two invasive ranges: of Baltic Sea and Russia (INVADED #1 = 1,527 records) and the Laurentian Great Lakes and Finger Lakes in the eastern North American region (INVADED #2 = 114 records). To minimize unevenness in sampling effort and geographical sampling biases, we thinned data with a 10 km buffer around each coordinate using the "spThin" R package (Aiello-Lammens et al. 2014). As a result, we retained a subset of geographically unique occurrences (NATIVE = 11, INVASIVE #1 = 110 and INVASIVE #1 = 63).

We gathered all 19 bioclimatic variables for the current climatic conditions available from the WorldClim database (http://www.worldclim.org; Hijmans et al. 2005) at different resolutions according to the employed analysis. We used the resolution of 10 arc-min in the species distribution modelling. In the niche conservatism test and reciprocal projections, we considered a 4 km resolution (cell size of 0.041° at the equator) and extracted the extent comprising a background based on the occurrence records (Fig1-A, B). These variables are essential to the population dynamics and reproductive patterns of *C. pengoi*, considering that environmental characteristics are significant drivers that may make a region receptive to its invasions (Golubkov et al., 2020; Litvinchuk, 2021). We then cropped both geographic and environmental data according to the three background regions mentioned above (Figure 1), further processed accordingly for the specific analyses. We conducted all the procedures above and followed analyses in R (R Development Core Team 2020).

2.2 Niche conservatism test

We followed Broennimann et al. (2012) to assess the environmental niche similarities among each population from native and invaded ranges. We evaluated the assumption of niche conservatism in biological invasions by quantifying niche metrics, e.g. the amount of niche overlap considering the environmental conditions geographically available for each population. Specifically, we compared the environmental conditions available for the species within the invasive ranges (INVASIVE #1 and INVASIVE #2) to those found within the NATIVE range and between each pair of invaded ranges. To determine the background available conditions for each species, we generated a buffer of ~ 100 km around the occurrence records of each species.

We extracted values for the 19 bioclimatic variables for the model species using the defined backgrounds. After, we applied a PCA for all combined background environmental conditions to generate an environmental space (PCA-env; Broennimann et al. 2012). We divided this environmental space into a grid of 100 × 100 cells. We calculated the occurrence density within each cell of the environmental space grid for the distribution range of the species. Finally, we modeled the occurrence density using a smooth kernel density function that considers the geographical conditions available for each species (Broennimann et al. 2012).

We calculated observed niche overlap scores using Schoener’s D and its significance, using a similarity test (Schoener 1970; Broennimann et al. 2012), which varies from 0 (complete dissimilarity between the compared environmental niches) to 1 (complete overlap). We used a null modelling procedure to test the significance of niche equivalency between the compared ranges. We randomised the occurrence records in both backgrounds and recalculated Schoener’s D 100 times to produce a null distribution of overlap scores ($\alpha = 0.05$), which we then compared to the observed value (Warren et al., 2008). Furthermore, we used the density of occurrences in environmental space to estimate niche expansion (new environmental conditions found in the non-native range), stability (proportion of the native niche conditions found in the non-native one), and unfilling (proportion of the native niche not occupied in the non-native; Guisan et al., 2014) with the “ecospat” package (Silva et al. 2016; Di Cola et al. 2017).

2.3 Projecting potential distribution in current scenarios

We used SDM to predict the potential distribution of the species. In constructing and reporting SDMs, we followed the ODMAP (Overview, Data, Model, Assessment and Prediction) protocol (Zurrell et al., 2020), a tool designed to maximise reproducibility and transparency of distribution modelling exercises. The ODMAP for this study is available as Supplementary material

We performed a principal component analysis (PCA) on the 19 bioclimatic variables to reduce the variables into uncorrelated principal components (PCs). We selected the PCs (~ 95% of the raw climatic variation) as environmental predictors to generate SDMs for the invasive fishhook waterflea. Inv2 → Inv1 + Native (four PCs captured 95% of the total variation). Native → Inv1 + Inv2 and Inv1 → Native + Inv2 (five PCs) (Table 3).

Using few PCs instead of raw variables avoids statistical problems related to the collinearity among predictors (Jiménez-Valverde et al. 2011) and decreases model overfitting (Beaumont et al. 2005). To reduce the effect of geographical sampling bias, we overlaid the species occurrences records on a square grid with the same resolution as our environmental predictors (~ 4 × 4 km) and retained only one random selected point per cell for each species. To cross-validate the SDMs results, we divided occurrences into 50% training-testing subsets. Data for model validation was separated by the block cross-validation method.

To generate reliable predicted ranges for the analyzed species we conduct a spatial restriction of the study extent to be used as the calibration area for the models (VanDerWal et al. 2009; Giovanelli et al. 2010; Acevedo et al. 2017). We obtained an ecoregions shapefile from World Wildlife Fund website (https://www. worldwildlife.org/biomes) and restricted our models to regions where known occurrences of *C. pengoi* were previously recorded in the Nearctic and Paleartic regions.

We also used a spatially structured partition of the occurrences of *C. pengoi* to predict its distribution. For this, the study extent was first gridded in a checkerboard fashion, with an aggregation factor of two. In this partitioning procedure, the occurrences are divided into two data subsets structured in the geographic space, similar to a checkerboard table (Muscarella et a., 2014). Initially, one subset is used to predict the distribution range of the species. Later, in a second modeling run, while the subset first used to evaluate the distribution, the subset used to predict the species range in the first run is now used to evaluate the distribution produced in the second model run.

We constructed SDM comparing three widely used algorithms: Random forest (RF; Breiman, 2001), support vector machine (SVM; Tax and Duin, 2004), and

Maximum Entropy (MaxEnt; Phillips et al., 2006). These algorithms provide greater accuracy models for species with small geographic ranges, which may be appropriately predicted in terms of occurrence (Hernandez et al., 2006; Silva et al., 2014; Zhang et al., 2020).

We used the reciprocal niche modelling technique in which predictions of SDMs between the native and invaded ranges are created. This approach allows identifying which geographic areas share similar climatic conditions between the calibrated and projected ranges combined with multivariate analysis that could reveal potential niche shifts of introduced species (Medley, 2010; Elith et al. 2010; Faleiro et al., 2015). Additionally, results on the potential distribution of the species in introduced locations could be beneficial to infer suitable areas not currently occupied by the species, thus providing indirect information about the magnitude and direction of range expansions. This method has proven robust in predicting suitable areas through environmental and geographical spaces for invasive species (Herrando-Moraira et al., 2019).

As *C. pengoi* is a small invertebrate species (adult body size of 1–3 mm), reliable absence data for this species is lacking and almost impossible to update at a global scale. Therefore, we extracted pseudo-absences in 1:1 ratio (presence:pseudo-absence) to evaluate the predictions into two relatively well sampled and monitored areas. For all methods, the allocation of pseudo-absences was done by first establishing a bioclimatic environmental space and then selecting the pseudo-absences outside this environmental space. Later, we allocated these pseudo-absences into the geographic space for each partition (VanDerWal et al., 2009; Lobo and Tognelli 2011).

We considered the threshold derived from the ROC curve that balances omission and commission errors (ROC-th; Jiménez-Valverde and Lobo 2006, 2007). We were able to produce more conservative (the higher threshold value) predictions of the species' distribution by doing this procedure. We evaluated the goodness-of-fit and predictive capacity of the models using the Jaccard index, whereby values between 0.7 and 0.9 indicate a good model fitting and values above 0.9 as an excellent performance (1908; Leroy et al., 2018). Finally, we constructed the assembles using the weighted mean method from the three algorithms based on the Jaccard threshold.

3. Results

3.1. Current distribution and invasion history

We gathered a total of 1,652 records of *C. pengoi* in its current geographic distribution (see Figure 1A). The lowest number of records was found for the native distribution (N = 11) restricted to the Ponto-Aralo-Caspian basin in South Eastern Europe. On the other hand, the majority of the retained reports referred to non-native populations on the Baltic Sea and Russia (Inv1 = 110), and North America (Inv2 = 63). Although many studies on population dynamics and impacts have been carried on this invasive cladoceran, the number of occurrence records and geographic range kept restricted, for more than two decades, to the background used in the niche analyses (Figure 1B).

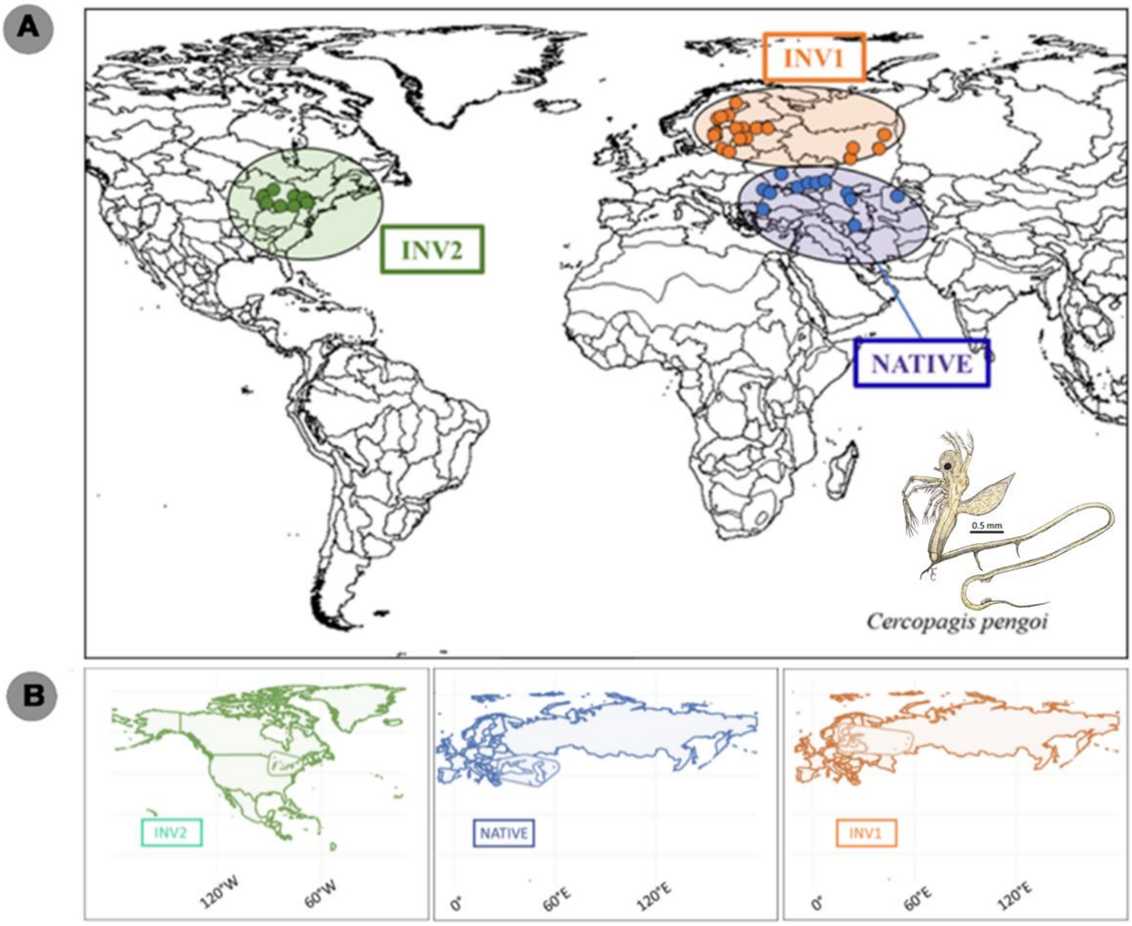

Figure 1. Geographic distribution of the model organism *Cercopagis pengoi* A). Native range corresponding to South-Eastern Europe in Ponto-Aralo-Caspian basin and Black sea (blue, NATIVE). Introduced ranges correspond to the Baltic Sea and Volga rivers in Russia (orange, INVASIVE #1) and Northeastern North America in Great Lakes (INVASIVE #2). Background based on a minimum convex polygon (MCP) made from the occurrence records of Native = 11, Inv1= 110 and Inv2= 63 occurrences B).

3.2 Niche comparison tests

Table 1. Multivariate niche comparisons and related metrics of niche dynamics

	D value	Similarity	Stability	Unfilling	Expansion
Native-Invasive1	0.01	0.02	0.83	0.69	0.17
Native-Invasive2	<0.01	0.28	1	0.92	0.01
Invasive1-Invasive2	0.04	0.08	0.83	0.72	0.17

The first two PCA axes combined explained 68.5% of the environmental variation (41.9% for the first and 26.6% for the second axis; Figure 2E). The variables associated the most with the first axis were annual mean temperature (bio1), mean temperature of the coldest quarter (bio11), and precipitation of the warmest quarter (bio18). The second axis was associated with the mean temperature of the warmest quarter (bio10), the maximum temperature of the warmest period (bio5), and precipitation of the warmest quarter (bio18) (Figure 2B, C). Interestingly, the environmental niche in the INV1 showed some expansion following increasing in bio14 (precipitation of driest month) and bio17 (precipitation of driest quarter).

We found a low overlap between the native range and both invaded regions (Table 1). The similarity test between Native and INV1 is an indication that the observed D value is significantly higher than expected by chance. Observed invaded niches primarily represent a subset of the native niche, with high stability and unfilling, mainly in the INV2 niche (Table 1). Only the INV1 niche had some degree of expansion concerning the native (0.17). The proportion of niche overlap exhibited among all ranges is shown in Figure 3.

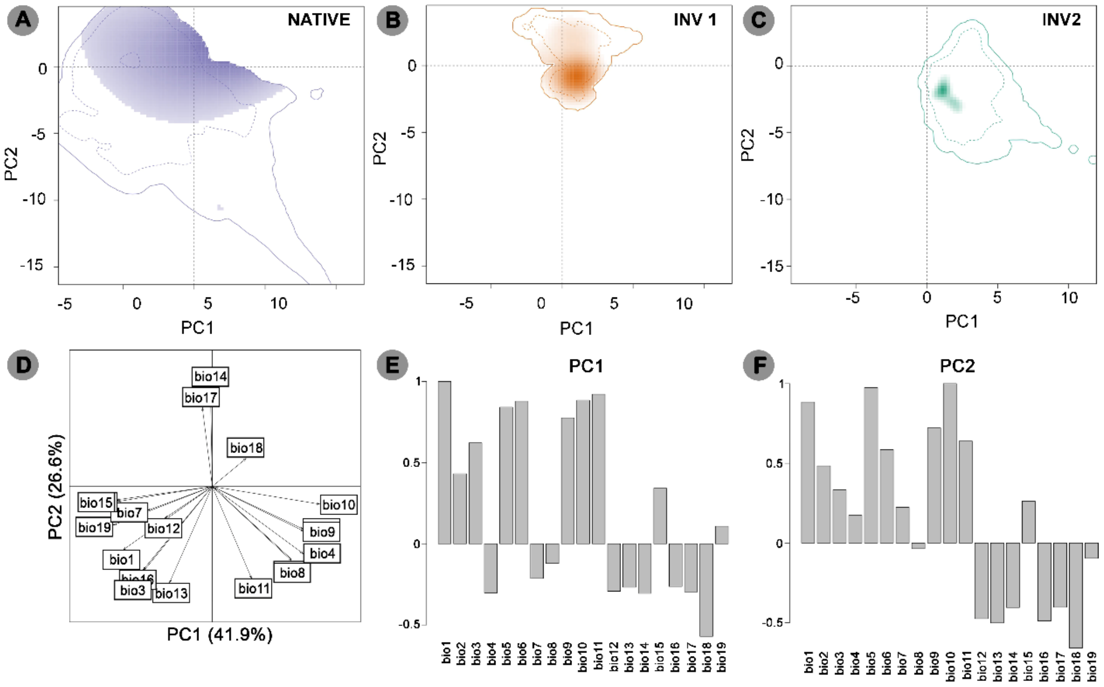

Figure 2. The first two axes of the Principal Component Analysis related to the current distribution in A) native and B, C) invasive ranges of *Cercopagis pengoi*, and its relationship with D) the 19 bioclimatic variables. Variables importance in each PCA axis are given in E) and F). The continuous line represents 100% of the available environmental background, and the dashed line represents the 50% most common conditions.

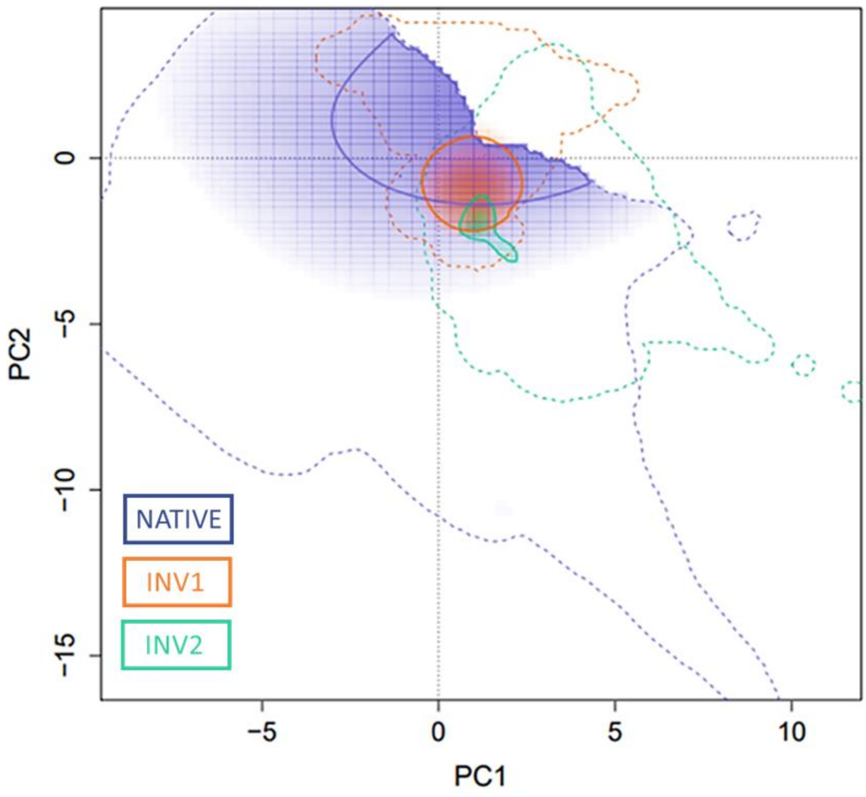

Figure 3. Overlaps in the realised climatic niches of *Cercopagis pengoi* in all considered ranges. Niches are superimposed upon the available climatic background. Native: South-Eastern Europe in blue (Native); North Europe - Baltic Sea in dark orange (Inv1); and North America in green (Inv2). The continuous contours represent the 20% highest values of density, and the dashed thin lines represent 100% of the background available in each region.

3.3 Reciprocal projections of SDM

Table 2. Mean values of Jaccard and standard deviation

	Native	Invasive1	Invasive2
Algorithm	Jaccard (average ± SD)		
MaxEnt	0.50 ± 0.00	0.86 ± 0.01	0.93 ± 0.06
SVM	0.58 ± 0.12	0.85 ± 0.10	0.87 ± 0.10
RF	0.88 ± 0.18	0.89 ± 0.04	0.92 ± 0.11

Ensemble	0.60 ± 0.00	0.85 ± 0.01	0.91 ± 0.08

Considering our results obtained with the Jaccard threshold (NATIVE = 0.38; INV1 = 0.30; INV2 = 0.25), the ensemble models reached values from 0.60 ± 0.01 (mean±standard deviation) trained in native ranges but higher values 0.85 ± 0.01 and 0.91 ± 0.08 when trained in invaded ranges Inv1 and Inv2, respectively. Specific results for each of the modelling algorithms are provided in Table 2.

The potential distribution of *C. pengoi*, obtained with both native records (Fig. 4A) and the invaded ranges (Fig. 4B, C), generally fitted better with its current restricted distribution. Also, training data in the invaded ranges showed more similar extensions of the projected areas in Eurasia. Specifically, the distribution based on INV2 records showed the highest values of Jaccard, considering all methods and the ensemble (Table 2), also predicting a larger suitable area in Eurasia and more restricted and geographically sparse regions in North America (Fig. 4C).

Wider geographic portions were climatically suitable for *C. pengoi* than its current known distribution. A closer examination showed areas at risk in not monitored portions such as North Africa and the Middle East. Nonetheless, such areas also occur in portions that have been already causing harmful effects to national economies, such as South of United States, Hudson Bay, and Gulf of Saint Lawrence in Canada, Central Europe, and the Mediterranean Sea. These areas are hotspots of surveillance resources prioritisation.

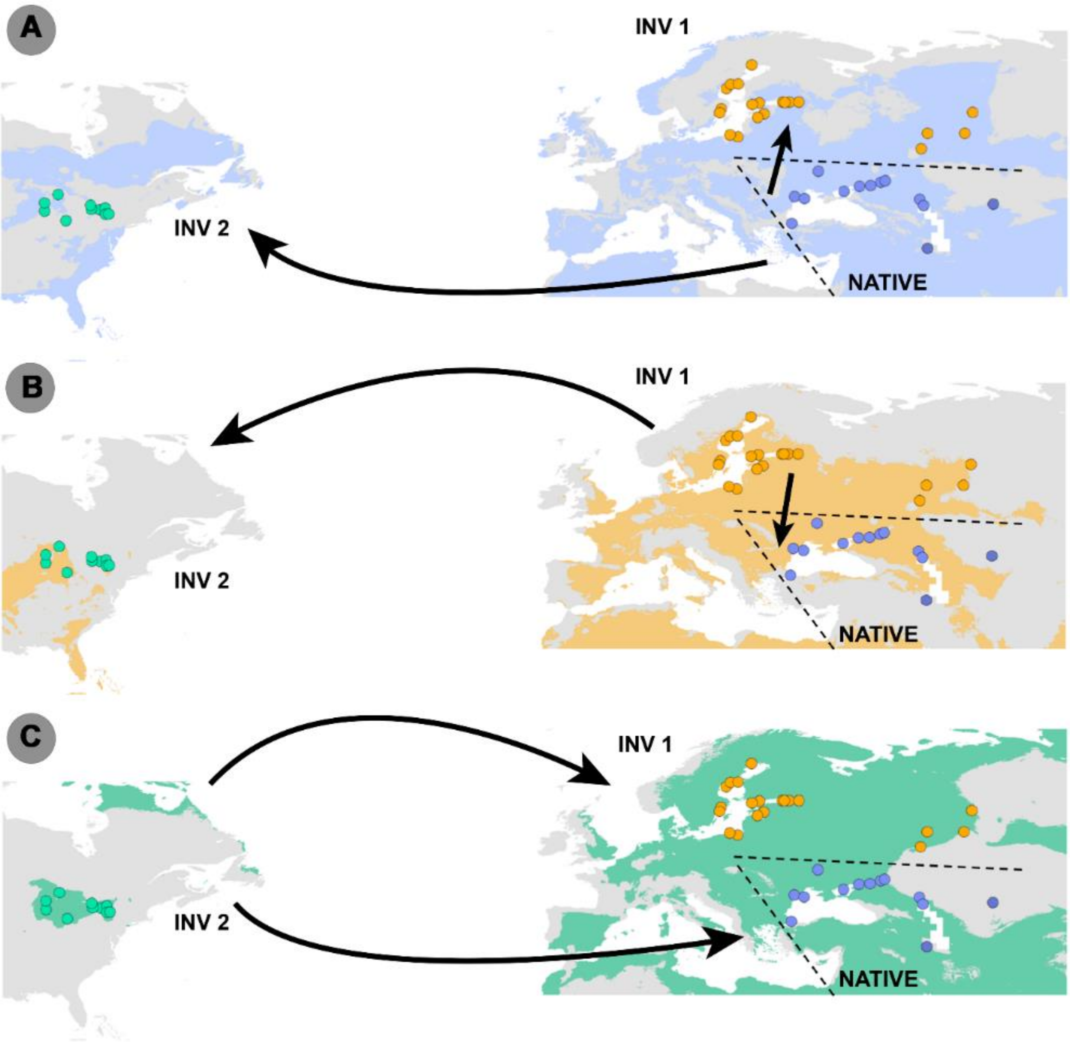

Figure 4. Ensemble predictions obtained for *Cercopagis pengoi* in the current scenario using a weighted mean of the three algorithms MaxEnt, SVM, and RF. The binary suitability maps represent the predicted presence for the species, based on the Jaccard threshold used (see material and methods). Colours (blue, orange, and green) represent suitable areas, whereas unsuitable areas are depicted in grey. A, B, and C for predictions considering training data on Native, Inv1, and Inv2, respectively, following the background shown in Figure 1.

Table 3. Mean variable contribution (%) of each one of the nineteen bioclimatic variables used to predict the potential distribution of *Cercopagis pengoi*. CumVar = cumulative variance in the principal component axes until 95%.

	Coeficients (Native → Invasive)					Coeficients (Invasive → Native)			
Variable	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3	PC4
bio1	0.26	0.22	-0.16	-0.13	-0.12	0.26	0.15	-0.01	0.17
bio2	0.28	-0.02	0.20	-0.12	-0.12	0.17	0.31	-0.50	-0.14
bio3	0.20	0.29	0.04	0.10	0.11	0.26	0.15	0.05	0.08
bio4	-0.01	-0.39	0.09	-0.26	-0.30	-0.24	0.10	-0.27	-0.25
bio5	0.31	0.02	-0.05	-0.25	-0.29	0.24	0.25	-0.23	0.11
bio6	0.17	0.34	-0.20	0.02	0.01	0.26	0.05	0.11	0.25
bio7	0.08	-0.37	0.18	-0.25	-0.27	-0.21	0.17	-0.42	-0.33
bio8	-0.02	-0.10	-0.60	-0.57	0.32	0.12	0.50	-0.05	0.07
bio9	0.26	0.22	0.07	0.05	-0.20	0.25	-0.07	0.04	0.10
bio10	0.30	0.06	-0.13	-0.26	-0.28	0.24	0.23	-0.14	0.12
bio11	0.20	0.32	-0.16	0.01	0.02	0.26	0.07	0.08	0.21
bio12	-0.26	0.22	0.09	-0.18	-0.13	0.26	-0.14	-0.04	-0.22
bio13	-0.23	0.22	0.25	-0.35	0.09	0.24	0.04	0.23	-0.38
bio14	-0.27	0.16	-0.17	0.05	-0.31	0.23	-0.32	-0.19	-0.09
bio15	0.23	0.05	0.38	-0.24	0.47	-0.17	0.36	0.43	-0.14
bio16	-0.23	0.23	0.24	-0.32	0.06	0.23	0.03	0.21	-0.41
bio17	-0.27	0.17	-0.17	0.03	-0.32	0.24	-0.29	-0.17	-0.09
bio18	-0.30	0.03	-0.17	-0.14	0.06	0.21	0.15	0.21	-0.46
bio19	-0.14	0.32	0.28	-0.19	-0.20	0.23	-0.29	-0.11	-0.11

PCVar	0.49	0.30	0.08	0.05	0.03	0.71	0.12	0.06	0.06
CumVar	0.49	0.79	0.87	0.92	0.95	0.71	0.83	0.89	0.95

4. Discussion

If the fundamental niches of invasive populations of a given species are conserved, we expect that only climatically similar regions to the native range would be invaded and that niche modeling of the climatic characteristics of the native range of a species can predict its introduced range (Peterson 2003, Peterson & Vieglais 2001). In this study, we shed light on the importance of niche conservatism to determine which regions may be invaded by *Cercopagis pengoi*, a pelagic predator thought to be one of the major threats to biodiversity of inland, brackish and marine environments (Ojaveer and Lumberg, 1995; Maclsaac, 1999; Luque et al., 2014; Einberg et al., 2020). Our result implies that *C. pengoi* has a large native niche that remains to be filled in the invaded range, suggesting that the species may keep spreading in the future. Complementarily, we also review areas where it may be established but has not yet been recorded or is overlooked by mapping where it can potentially invade.

Accordingly, from updated modelling procedures, we used *C. pengoi* as a model to investigate a regional and transoceanic invasion followed by a significant population decrease in native areas. The case presented here is the first assessment into a deep understanding of the invasion success of *C. pengoi* through integrated niche characterisation analysis.

Our niche analyses unveil a niche unfilling during the invasion process of *C. pengoi*, which indicates that there is a broad environmental space only occupied in the native range and available in the introduced range. In the first invasion step, when the species was introduced from Porto-Caspean to the Baltic Sea, niche comparison analyses reveal that *C. pengoi* would have only partially occupied the ancestral niche. In addition, its climatic niche would have expanded following the second axis (Fig. 3B, E). This result is in line with a regional geographic range expansion to Russian waterways (Lazareva, 2019a,b) with the occupancy of novel and previously non-existing native climatic niches or novel occupancy of existing but underestimated native climatic niches.

These geographical expansions across Russian waters may be promoted by ballast water from connected areas in the native range, rising concerns on human-driven alterations favouring the establishment of invasive species. Also, it should be noted that *C. pengoi,* in its native range, seems to be occupying a larger climatic space especially when compared with the non-native area Inv 2 (Fig. 3A, B).

In this second introduction event following transoceanic movement into Great Lakes, the higher niche similarity and overlap between Inv 1 and Inv 2 led us to hypothesise that a propagule reservoir from the Inv 1 range (the Baltic Sea) probably spread into the North American range. This event is also in support of the more intense propagule pressure supposed to occur between these areas considering trade rates. This pattern is also shown by the closer climatic similarities between these invaded ranges (Fig. 4). Nevertheless, it could reveal the effect of mixing the imported pools from both ranges separately, which confers a clear ecological advantage, especially considering adaptive traits in short-life cycle organisms as cladocerans (Gustafsson et al., 2005).

Invasive species are most commonly introduced in low numbers reflecting a small sample of the entire genetic diversity of the native population leading to genetic impoverishment and processes such as Allee effects that can hamper the expansion to other environmentally suitable areas. Dispersal barriers and biotic interactions are other examples of processes that can slow the spread of invaders and result in a niche unfilling during the invasion process (Taylor & Hastings, 2005; Strubbe et al., 2013). This non-equilibrium relation of the invader with the exotic climate (Guisan et al., 2014; Hill et al., 2017) deserves special attention from monitoring programs to control the spread of *C. pengoi* into climatic areas that are occupied in the native range but not yet in non-native areas. Accordingly, the elevated degree of unfilling found in our analysis must predict an also high expansion potential of this species.

However, movement may be limiting this species to stablish in novel climatically susceptible areas. The high prevalence of niche unfilling in freshwater organisms might be due to the inability of these organisms to colonise all suitable habitats (Torres et al., 2018). Moreover, limiting its dispersion is fundamental in the case of *C. pengoi*, as multiple introduction events could rescue its entire genetic pool and create new ones, favouring the complete occupation of realised niche in novel suitable areas. Since cladocerans depend on wind, drift, and other animals for dispersal of their propagules (adult form or resting stages), it is mainly human-assisted dispersal that will promote their spread at a large scale, yet enhanced by their characteristics mentioned above.

Furthermore, the accurate and high performed projections calibrated in the Inv2 (Table 2; Fig. 5C) may suggest that the species could have survived and established following preadapted conditions from the environmental match with both native and Inv1 source ranges. This also falls into the assumptions of the better performance of suitable ares based on native and invasive ranges together (ref). Finally, particular features of the niche of *C. pengoi* could also be suggested: Populations preadapted to the INV2 could access areas not currently suitable for European populations from both native and INV1 if reverse dispersion occurs. In other words, populations from INV2 showed larger appropriate regions of Eurasia and North Africa.

Surpassing these occupancy restritions, some surveillance priority areas can be pointed out aiming more efficient control strategies for *C. pengoi* invasion. Starting from areas close to the source environments in America, we suggest special attention to novel introductions in Florida following Mississippi River flow and in the Bahama Archipelago following ballast water from the continental source. Also, in the plains of Quebec, Canada. On the other hand, in Europe, we suggest higher efforts in the North of Europe (Sweeden, Finland, Denmark, and the UK), also Russian water bodies which have been invaded by zooplankton organisms through global trade (Zhdanova, 2016; Lazareva & Zhdanova, 2018) and are targeted of novel commercial ship routes in the Arctic (ref). Also, the Mediterranean Sea, where *C. pengoi* is currently absent (Zenetos & Galanidi, 2020), especially regarding the fragile and yet not complete known biodiversity of shallow ponds and new species descriptions in the area (e.g., Alonso et al., 2021). Curiously, *C. pengoi* is not present at established invasive populations elsewhere in the world out from the areas investigated in this study. This condition could be due to the extensive control and monitoring activities in the source areas. The colonisation of new environments in the invaded range not occupied in the native range could result from the absence of biotic interactions, such as enemy release or the absence of competition (Catford, Jansson, & Nilsson, 2009). Still, more recently, the invasion success of *C. pengoi* was supported to be more attached to environmental filters than to biotic interactions (Golubkov et al., 2020).

None of other related cladoceran species have successfully invaded more temperate regions north of Baltic and Great Lakes, even though others have been present and widespread for decades (e.g., *Bytothrephes longimanus*). According to Katajisto et al. (2013), the spatial distribution of *C. pengoi* populations in plankton and its egg bank in sediments had higher abundances in the Gulf of Finland than in the Gulf of Bothnia during the period spanning 1997–2008, probably reflecting its invasion history in the Baltic Sea (Krylov et al., 1998; Krylov et al. 1999, Uitto et al. 1999, Antsulevich & Välipakka, 2000). Accordingly, in the Bothnian Bay, it showed to occur irregularly in plankton samples in 2 of the nine sampling years carried by Katajisto et al. (2013). This finding could be due to the lower climatic suitability than what we observed in the Gulf of Finland, considering training data in native and INV1 ranges (Fig. 5A, B). This result raises another exciting hypothesis of whether resitting egg banks may be more associated with less suitable areas as sexual reproduction in cladocerans are adaptive strategies to population maintenance under unfavourable conditions (Panov et al., 2004, Riccardi et al., 2004), including *C. pengoi* in the eastern Gulf of Finland (Krylov & Panov, 1998). Also, from genetic analyses, Cristescu et al. (2001) suggest that *C. pengoi* was further introduced to the Laurentian Great Lakes in North America from the Baltic sea.

However, biotic interaction with another invasive species may ressussit these ideas. Alarming evidence of the absence of native populations of *C. pengoi* and other Cercopagids were reported by studies within the southern portion of the Caspian Sea (native area; Roohi et al., 2008; Bagheri et al., 2014) following the introduction of the invasive gelatinous zooplankter *Mnemopsis leydii*. However, whether the absence of *C. pengoi* and other zooplankton populations can be attributed solely to *M. leidyi* presence or other anthropogenic disturbances (e.g., nutrient enrichment, pollution, and climate change) remains unclear. Nonetheless, *M. leidyi* is a voracious planktivorous species capable of feeding directly on *C. pengoi* and on many organisms that would otherwise play a role as prey for *C. pengoi*. Also, the Aral Sea salinisation following upstream water withdraws in the 1960s (10 to 100 ‰; Micklin, 2007) extirpated *C. pengoi* populations (Rivier 1998, as cited in Panov et al. 2007). A conservation paradox arises from the presence of *C. pengoi* in non-native areas, yet threatened in its native areas, leading non-native areas to play a role as an invasive refugee (Marchetti & Engstrom, 2016). It is important to note that studies in its native area are scarce (especially in the northern and central portions of the Caspian Sea) or restricted to local journals (Roohi et al., 2008). Also, the ability to produce diapause eggs trigged by predation pressure is found in cladocerans (Sopanen, 2008) hatch and re-establish a population in native ranges after *M.*

leidyi eradication. Nonetheless, future studies must assess the current conservation status of *C. pengoi* in its native area, mainly because different selective pressures could improve its invasiveness in suitable non-native areas.

5. CONCLUSION

We found that climatic information on native ranges of *Cercopagis pengoi* was not enough to fully explain/predict its distributional patterns of invasion. The niche overlaps revealed that invaded fundamental niches are subsets of the native but occupancy of climates not found across native ranges increased the potential invasive areas of *C pengoi.* Although geographically restricted in invaded ranges, it is not climatically constrained to localities of its known current distribution, showing more significant portions to be potently occupied if control policies weaken. We suggest the inclusion of information on pre-selective traits (genetic and morphological) from non-native occurrences on invasion risk assessments based on species distribution modelling. In doing so we could elucidate mechanisms of success and failure of invasion processes of *C. pengoi.* The high invasion potential of *C. pengoi*, currently listed as one of the “100 World’s Worst invasive species” due to its impacts on zooplankton and fish larvae through active feeding, highlights the urgency of strategies to anticipate its impact on native aquatic communities and ecosystem services.

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ARTICLE FIVE

Submitted to WATER RESEARCH

Highlights

Globally, 16 holoplanktonic invasive species have cost $5.8 billion since 1970s.

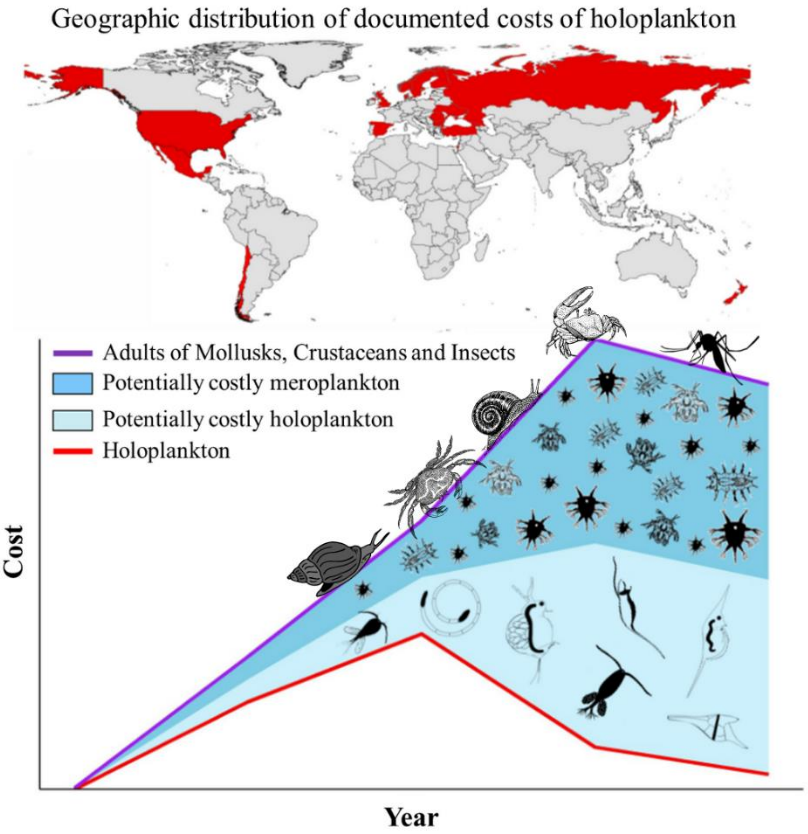
Annual costs peak in 1995 and unrealistically decreased through the 21st century.

Fishery was the most impacted economic sector, $5.5 billion.

Costs estimates grossly overlooked damage done to water quality and quantity.

Impact reporting towards meroplanktonic stages is urgently needed.

Graphical abstract



The global social-economic dimension of biological invasions by plankton: grossly underestimated costs but a rising concern for water quality benefits?

Rafael L. Macêdo, Ana Clara S. Franco, Betina Kozlowsky-Suzuki, Stefano Mammola, Tatenda Dalu, Odete Rocha

Abstract

Planktonic invasive species cause adverse effects on biodiversity and ecosystem services. However, these impacts are often underestimated because of unresolved taxonomic issues and limited biogeographic knowledge. Accordingly, it is pivotal to start a rigorous quantification of direct impacts of planktonic invasive species on global ecological systems and economies. We used the *InvaCost* database, the most up-to-date database of economic cost estimates of biological invasions worldwide, to produce a first critical assessment of the economic dimension of biological invasions caused by planktonic taxa. We found that in 1960–2021, the cumulative global cost of plankton invasions was US$ 5.8 billion for permanent plankton (holoplankton) from what viruses encompassed nearly 93%. Cumulative global costs of invasive meroplanktonic organisms (i.e. those with early planktonic stages) was US$ 98 billion. Apart from viruses, we found more costs related to zooplankton (US$ 297 million) than to the other groups summed, namely myco- (US$ 73 million), phyto- (34 million), and bacterioplankton (US$ 0.7 million). However, costs are likely to be underestimated due to the limited sample of investigated invasive taxa and several knowledge gaps regarding the autoecology and invasion dynamics of most of these planktonic organisms. Strikingly, harmful and potentially toxic cyanobacteria and dinoflagellates are completely absent from the database. Furthermore, we observed a decrease in costs over time, which is probably an artifact as a sharp rise of novel planktonic alien species has gained international attention only in the last two decades. Also, assessments of the impacts of larval planktonic stages of littoral and benthic invertebrates that exert ecological pressures at several compartments of the aquatic ecosystems are not only lacking but largely neglected. Considering the challenges and perspectives of increasing impacts by plankton invasions with global climate change, the assessment of the ecological and economic impacts of invasive species should be of high priority.

Keywords: Alien plankton; ecosystem services; *InvaCost*; monetary loss; non-native; pelagic invaders

Introduction

Plankton has a pivotal ecological role in both marine and inland waters where they dictate biogeochemical cycles and mediate energy flow (Kerfoot et al., 1988; Anderson et al., 2018; Armengol et al., 2019; Naselli-Flores and Padisák, 2022). It has been also efficiently used in monitoring programs tracking changes in their abundance and biomass as they indicate environmental changes through bottom-up or top-down regulation (Suttle, 2007; Jeppesen et al., 2011; Špoljar et al., 2018; Feitosa et al., 2019). In addition to the strong and complex trophic links that characterize planktonic relationships, it's high diversity of taxa, living forms and stages (e.g., the interplays between holo- vs meroplankton in the vertical transport of nutrients), more recently, the non-native planktonic species emerged as a challenge for the complete understanding of ecosystem functioning and the context-dependency of their impacts (Havens and Karl, 2002; Stecker et al., 2011; Jokela et al., 2017).

Invasion scientists, managers, and stakeholders have reported high and rising impacts of invasive species on ecosystems and economies worldwide (Bellard et al., 2016; Diagne et al., 2020a; Cuthbert et al., 2021). In the context of the Anthropocene, invasive planktonic species are continuously proliferating as result of the global transport of goods and people, electronic commerce (e.g., Casas-Monroy et al., 2015; Ricciardi and MacIsaac, 2022), accelerated over the course of the COVID-19 pandemic, and owing to anthropogenic environmental changes (Bellard et al., 2016; Seebens et al., 2021; Macêdo et al., 2021). Likely, the abundant early planktonic stages (meroplankton, i.e. organisms with a non-planktonic adult life stage) of aquatic invaders drifting with the currents show high propagule pressure colonizing new environments (e.g., Czerniawski and Krepski, 2021) and are the most frequent life forms in ballast water discharges. However, there has been an appeal to expand our understanding of the impacts of biological invasions at different biological organization levels (Crystal-Ornelas and Lockwood, 2020), and through an interdisciplinary context (Ricciardi et al., 2020, Diagne et al., 2020b).

Water quality is affected by both the diversity and abundance of invasive species, therefore management actions taken to monitor and control these "neobiota" are very important. For example, phytoplanktonic invaders cause widespread impacts on biodiversity and human health through phycotoxin release, water quality deterioration, massive fish kills through oxygen depletion and histological damage, and bottom-up disruptions of trophic relationships (Amorim and Mouna, 2020; Pacheco et al., 2021; González-Madina et al., 2021). Zooplankton invaders can act as vectors transmitting novel pathogens, such as the fungi-like fish parasite and viral hemorrhagic septicemia dispersed by *Moina macrocopa*, or the planktonic copepod *Mesocyclops ogunnus* which hosts and disperse the nematode *Dracunculus medinensis,* a crippling parasite affecting people in rural, deprived and isolated communities depending mainly on open surface water sources such as ponds for drinking water (Bimi, 2001; Vanjare et al., 2010; Ito and Olesen, 2017). To date, invasive plankton impact evaluations are scarce or are biased towards few taxa that caused impacts in developed counties (Luque et al., 2014; Dexter and Bollens, 2019) or toward laboratory experiments with limiting extrapolation power (e.g., Oliveira et al., 2019) but see Dexter and Bollens (2019). Moreover, impacts of planktonic invaders can be caused by indirect changes in habitat conditions e.g. turbidity (Walsh et al., 2016) or impacts from sudden population outbreaks posing risks for water resources (e.g., Spear et al., 2021; Corrêa et al., 2022), yet lacking a clear definition of which response variables to measure, thresholds, and different temporal and spatial scales, is still debatable, as for other invasive species (Jeschke et al., 2014).

In an economically connected world, advancing our knowledge of monetary costs of aquatic invasion impacts, fosters the need of a comprehensive assessment of their description and quantifications for efficient and sustainable management invasive taxa and invaded habitats. With aquatic ecosystems more vulnerable to anthropogenic impacts and consequently more prone to invasions during the 21st century, costs of plankton invasions may be disproportionately low due to a mismatch between high number of non-native species and impact quantification assessment (Crystal-Ornelas and Lockwood, 2020; Cuthbert et al., 2021; 2022). Also, studies of economic aspects showed overlooked values even for the most investigated taxonomic groups e.g., invasive fish and macroinvertebrates (Pimentel et al., 2005; Cuthbert et al., 2021; Haubrock et al., 2022a,b; Kouba et al., 2022). This lack of knowledge is a major concern when it comes to the pelagic habitats, considering planktonic organisms, which have many features that remain primarily neglected worldwide e.g., abundance, diversity and distribution.

At present, we assume that knowledge gaps on the economic costs of plankton invasions may be a result of the considerable underestimation of their destructive potential, especially if we consider indirect effects and assessment limitations. Here, to understand the current economic dimension of this problem, we evaluated the global costs of alien invasive planktonic taxa using the *InvaCost* database (Diagne et al., 2020c). We used a subset of this database focusing on aquatic environments where the costs were estimated and where the invasive species lives, independently of where the cost occurred, to address the following questions: 1) What are the documented economic costs of planktonic species invasion globally? 2) How does these costs change over time and how are they distributed among main economic activities? 3) What are the costliest invasive species among them all? This framework also aims to discuss the complex causal interactions between different compartments of aquatic ecosystems in the context of biological invasions aiming to shed light on possible institutional and scientific solutions for costly negative effects (Perrings et al., 2002; Ricciardi et al., 2020).

Materials and methods

Data collection

We compared the economic costs of handling invasive holoplanktonic species and organisms with those of meroplanktonic stages using the *InvaCost* database. The *InvaCost* is a comprehensive compilation and description of economic cost estimates of biological invasions worldwide (Diagne et al. 2020b,c). The database was developed following a systematic and standardized methodology to extract information from scientific articles, grey literature, stakeholders, and expert elicitation. All methods and procedures for data search, retention, extraction, validation, collation, and improvements are available in Diagne et al. (2020a,c).

We used the most up-to-date version of *InvaCost* (version 4.0, doi: 10.6084/m9.figshare.12668570), which contains 13,123 cost entries referring to a unique cost value (both in local currencies and 2017 US$ rates). There is also a set of specific descriptors of the cost's spatial and temporal information, the taxonomy of the invasive species, the cost typology, the impacted sectors, and the document reporting the cost

(Diagne et al. 2020a). We classified all holo- and meroplanktonic organisms, which fell into the following groups: virioplankton (DNA and RNA viruses with few nanometers in diameter), bacterioplankton (Gram-negative bacteria belonging to Aeromonadaceae family), mycoplankton (fungi-like pathogens, especially oomycetes, with microscopic filamentous dimension), phytoplankton (unicellular algae from families Raphidophyceae, Prymnesiaceae and Cymbellaceae with dimension 10–45 μm), zooplankton (Platyhelminthes 0.5–1.0 mm, Branchiopoda: Cladocera and Anostraca with dimensions 10–15mm, Scyphozoa and Ctenophora with dimension 14–18 cm), and meroplankton (which included animals with early stages in the pelagic zone such as Mollusks, Crustaceans, and some Insects. We extracted all economic costs associated with aquatic organisms filtering the information on the descriptive field "environment". We checked the data subset to remove any missing data on the economic costs. Our final databases had 43 entries of planktonic species and 714 entries of meroplankton. Due to the small number of resulting cost information for holoplanktonic species, we also included data classified as having low reliability (*n* = 8; e.g., not fully accessible information) and as potential implementation (*n* = 13; observed or expected through modeling or extrapolations), following Adelino et al. (2021). For meroplanktonic data, we instead retained only the costs classified as "observed" and also those of high reliability (column "method reliability", see Diagne et al. (2020a) for further details). For model analyses, we used the final subset for meroplanktonic organisms (597 entries).

We classified the groups according to the typology of the costs they have promoted, namely: *damage/loss* – for economic losses due to the impact of invaders (e.g., infrastructure alteration, medical care or damage repair); *management* – for economic resources allocated to actions towards avoiding the invasion or dealing with established invaders, (e.g., prevention, control or eradication); *mixed* – when the cost includes both damage and management elements. We also categorized data on which societal or market sectors were impacted by each group, using data from the "impacted sector" descriptive field. *Agriculture* (food and other useful products produced by human activities through using natural and/plant resources from their ecosystems), *authorities/stakeholders* (governmental services and/or official organizations dedicated to management of biological invasions), *environment* (impacts on natural resources and/or ecosystem services), *fishery* (impacts on fisheries and aquaculture), *health* (cost related to the sanitary demands of people), *public and social welfare* (activities or services related to the human well-being at a broader sense such as personal goods or quality of life), and *mixed* (when more than a single sector was involved).

We have included a glossary of terms and definitions to facilitate comprehension of the hypothesized causes for the suggested underestimation of monetary costs by plankton (Table 1). Although a clear understanding of the terminology of invasion biology is essential, this glossary is focused on the further ecological concepts that emerge from each term and not specifically on their uses and misuses in invasion science literature.

Table 1. Glossary defining our usage of invasion biology terms in this article along with their literature sources.

Term	**Definition**	**Source**
Non-native species	Animals, plants, or microorganisms introduced in environments outside of their native range	Lockwood et al. 2007
Invasive Species (IS)	Non-native species with history of impact or high population abundance.	Lockwood et al. 2007
Potentially IS	A non-native species whose populations are established but not yet widely invasive; e.g. silent or sleeper invaders.	Bradley et al. 2018; Spear et al., 2021
Pelagic zone	An ecological compartment of aquatic ecosystems that includes the entire water column in the ocean and inland habitats.	Belgrano et al., 2013
Planktonic species	A diverse group of organisms (animals, algae, bacteria, protozoa, viruses) of different shapes	Belgrano et al., 2013

	and sizes that drift in the pelagic zone of aquatic habitats.	
Holoplankton	Planktonic species that spend their entire life cycle as drifters in the pelagic compartment.	Belgrano et al., 2013
Meroplankton	A wide variety of aquatic organisms drifting in the water column that are not planktonic in their advanced or adult stages, e.g., benthic; temporary plankton.	Belgrano et al., 2013

Data analysis

We performed all analyses in R version 4.1.2 (R Core Team, 2021), using the *InvaCost* R package (Leroy et al. 2020) for analyses and “ggplot2” version 3.3.5 (Wickham 2011) for data visualization. We first compared the economic costs reported for each group (holo- and meroplankton) using the above classification scheme. Then, we examined annual variations in economic costs. Considering that some of the entries in the database described total costs over multiple years, we used the function "expandYearlyCosts" to determine the annual costs. This function divides the total cost by the number of years and converts it to a cost per year, removing entries with an unspecified period in the database.

We first derived the annual trend of costs caused by planktonic invasive species through the function “summarizeCosts”. This function provides a summary of the cumulative costs and the average annual costs of invasive alien species and divides it into regular periods (1970–2020), based on cost estimates as they appeared in the *InvaCost* database. To estimate and predict the trend of the economic costs of invasive planktonic species over time, we fitted models of annual costs using the function "modelCosts" on the $\log_{10}$-transformed cost estimates per year. This function performs different modeling techniques: "ordinary least squares regressions” (linear and quadratic), “robust regressions” (linear and quadratic), “generalized additive models” (GAM), and other analyses not applied to our data—but see Diagne et al. (2020a). We calibrated all models to follow a robust linear regression using cost data as a response variable and time as the predictor. Considering that our subsets for holo- (n = 43) and meroplankton (n = 597) are too small to make reliable predictions, we used the model approach to detect tendencies for each group. In doing so, we could subsidize our discussion based on the effects of insufficient data on the perceived threat posed by a group of species.

Results

The cost of holoplanktonic species was assessed in 17 countries in North America (the United States and Mexico), Central America + Chile, Eastern Europe (Bulgaria, Georgia, Romania, Russia, Turkey, and Ukraine) + Israel, Central Europe (Spain and Scotland), Northern Europe (Denmark, Sweden, Finland, and Norway) and New Zealand. Our sample included three viruses, three fungal-like organisms (Oomycetes), one bacterium, three phytoplankton, and eight zooplankton taxa (Fig. 1). Geographical and taxonomic disparities associated with costs were perceived, for example, a single species caused damages that cost up to US$ 8 million in New Zealand (one entry), while 8 species in Northern Europe cost altogether US$ 149 million (Table 2).

Table 2. Quantitative summary of the cost data and estimates considered in this study for the holoplanktonic (virio-, bacterio-, myco-, phyto-, and zooplankton). Total costs per taxa (between 1960 and 2021) are provided in 2017-equivalent US$ million. A brief description of the effects caused by holoplanktonic invasive species is also provided. Diverse/Unspecified and pooled species were excluded from the individual-specific analysis (see Methods section for further details).

Holoplankton

Family	**Group**	**Taxa**	**Total cost per taxa (US$)**	**N (entries)**	**Impact**
Aeromonadaceae	Bacterioplankton	*Aeromonas salmonicida* (Lehmann and Neumann 1896) Griffin et al. 1953	717,924.52	2	an important pathogen in salmonid aquaculture
Leptolegniaceae	Mycoplankton	*Aphanomyces astaci* Schikora, 1906	73,140,300.95	2	an emerging filamentous oomycete parasite affecting freshwater crayfish
Artemiidae	Zooplankton	*Artemia franciscana* Kellogg, 1906	3,442.33	1	Brine shrimp used extensively in aquaculture, the aquarium trade, affecting food webs and primary production in hypersaline ecosystems
Batrachochytriaceae	Mycoplankton	*Batrachochytrium dendrobatidis* Longcore et al. 1999	10,965.11	4	a zoosporic pathogenic chytrid fungus in amphibians and grows
Cercopagididae	Zooplankton	*Bythotrephes longimanus* Leydig, 1860	6,383,131.87	1	spiny predatory waterflea with direct and indirect cascade effects
Cercopagididae	Zooplankton	*Cercopagis pengoi*	104,101.01	2	fishhook waterflea, cited in the WWIS list significant top-down effects on

		Ostroumov, 1891			zooplankton
Vacuolariaceae	Phytoplankton	*Chattonella* sp. Biecheler, 1936	2,745,894.88	1	marine raphidophytes associated with red tides
Cymbellaceae	Phytoplankton	*Didymosphenia geminata* M.Schmidt, 1899	8,165,085.43	13	diatom that produces nuisance growths in stream habitats
Gyrodactylidae	Zooplankton	*Gyrodactylus salaris* Malmberg, 1957	241,328,572.08	6	ectoparasite of freshwater fish
Parvoviridae	Virioplankton	IHHN DNA virus	1,348,595,782.92	1	a hematopoietic necrosis virus that affects crustaceans
Bolinopsidae	Zooplankton	*Mnemiopsis leidyi* Agassiz, 1860	49,463,799.47	2	ctenophore and major zooplankton predator associated with fishery depletion
Prymnesiaceae	Phytoplankton	*Prymnesium polylepis* Manton and Parke, 1962	27,347,843.19	1	Potentially toxic marine flagellate algae, found to affect the of other algae, zooplankton, fish and benthic invertebrates

Florenciellales	Phytoplankton	*Pseudochattonella verruculosa* Hara and Chihara, 1994	5,042,068.53	1	phytoflagellate associated with significant impact on the fishing industry
Rhizostomatidae	Zooplankton	*Rhopilema nomadica* Galil, Spannier and Ferguson, 1990	59,109.85	1	Scyphomedusa with impacts on tourism, human health and fisheries
Dicistroviridae	Virioplankton	TSV (RNA virus)	2,620,354,258.22	1	a virus disease of penaeid shrimp
Nimaviridae	Virioplankton	WSSV (DNA virus)	1,478,290,764.26	2	a virus that causes mass mortalities in the aquaculture of shrimps

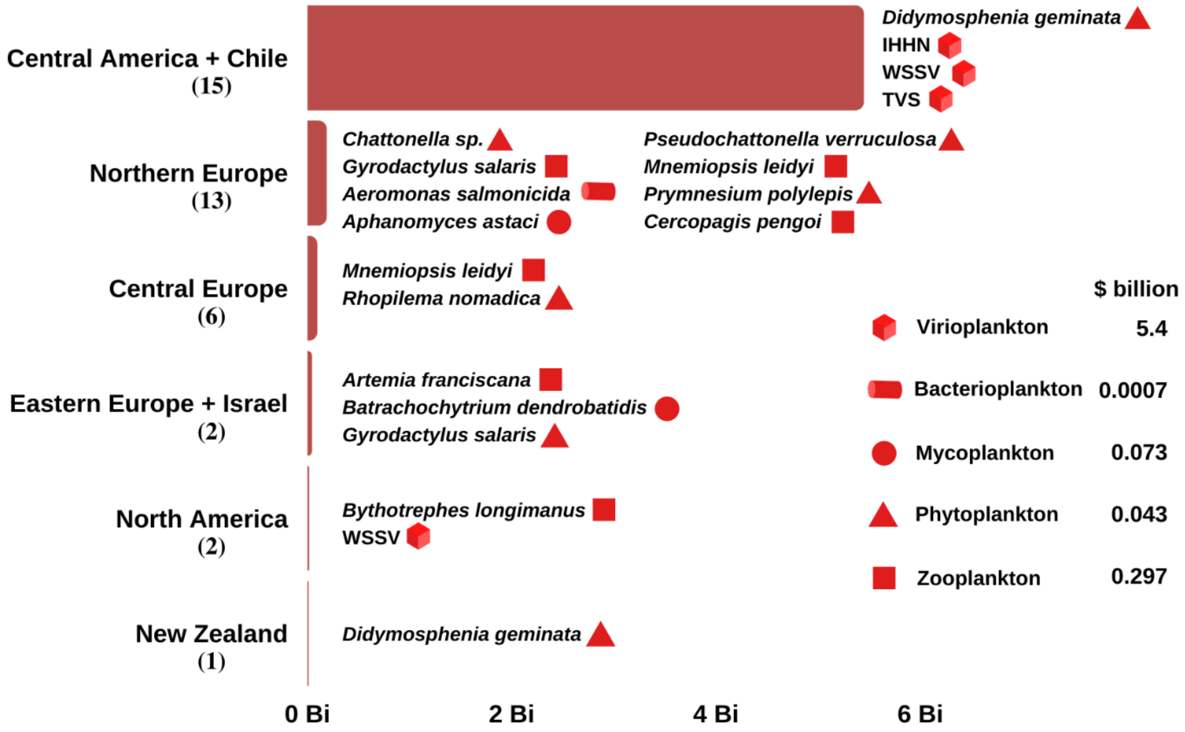


Figure 1. Global distribution of total economic costs (in billions) for aquatic invasive holoplanktonic taxa per geographic region. For details of taxa and their individual costs and impacts see Table 2. The number of studies assessing costs is shown in brackets. Costs attributable to more than one country are summed to the corresponding geographic region.

Holoplanktonic taxa listed in the *InvaCost* database were from 13 systematic orders, excluding viruses (Table 2). Estimated costs and brief descriptive notes of their impacts are provided in Table 2. All reported costs were from non-urban areas, and only one was from a protected island (Canary Islands) attributable to *Artemia franciscana* Kellogg, 1906 (Anostraca: Crustacea). Crustaceans (10 taxa), insects (2 taxa), and molluscans (13 taxa) were found among organisms with meroplanktonic stages. The costliest species from these groups were respectively *Paralithodes camtschaticus* Tilesius 1815, *Lissorhoptrus brevirostris* Suffrian 1871, and *Dreissena polymorpha* Pallas 1771.

Altogether holoplanktonic invasive species were responsible for costs around US$ 5.883 billion. The majority of the reported cost estimates was associated with “damage/loss” (US$ 5.877 billion) rather than “management” costs (US$ 0.005 billion) (Fig. 2). This pattern was consistent across groups, except for bacterioplankton, which had slightly larger costs directed to manage invasions and/or to mitigate their impacts

(54.1 %). Virioplankton was the costliest (US$ 5.4 billion) group and together with mycoplankton (99.9 %) had the largest share in “damage/loss” costs. The estimated global cost of meroplanktonic species reached US$ 98 billion, mainly attributed to "damage/loss" (US$ 82 billion). Most costs associated with Insecta (89.7 %) and Crustacea (81.9 %) were also directed to "damage/loss". In contrast, the costs related to Mollusca were nearly equally attributed to "damage/loss" (55 %) and mixed (41.8 %), with the latter being related to control measures.

The greatest impact of holoplanktonic invasions was on fishery (US$ 5.5 billion), with virioplankton being responsible for the majority of the costs, followed by phytoplanktonic species (Fig. 2). Many impacts were shared among sectors (US$ 317.9 million), but all of them included fishery. Interventions by the public and private sectors (authorities’/stakeholders’ category) were responsible for 54.1% of the costs related to bacterioplankton. Meroplanktonic species had the highest costs attributed to mixed sectors (US$ 74.5 billion), where public and social welfare was present in most of them, due to effects related to the insect group. Mollusks have caused an economic loss of US$ 16.5 billion, mainly spent by authorities and stakeholders (US$ 6.2 billion; 37.9 %) and on public and social welfare (US$ 4.8 billion; 28.9 %). The lowest costs were attributed to crustaceans (US$ 384 million), mostly related to the fishery sector (36.3 %). Health expenditures were exclusively related to the insect group (US$ 6.3 billion) and represented 7.8 % of the total cost caused by this group worldwide (US$ 81 billion). Environmental costs were underrepresented and accounted for less than 1 % as associated with zooplankton, molluscan, and crustacean species.

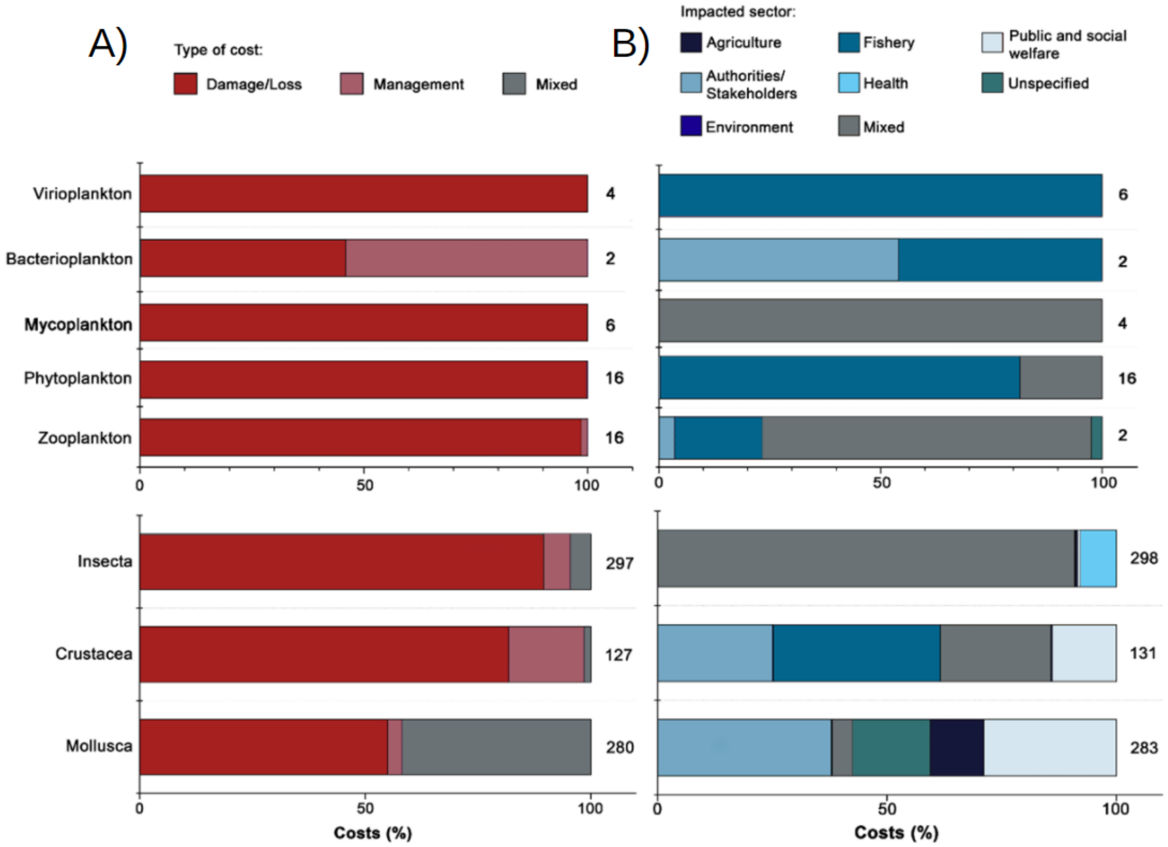


Figure 2. Distribution of observed costs (using the conservative subset) by type of cost **A)** and impacted sector **B)** for each group within holoplankton and late stages of meroplankton. The number of entries of each observed cost are given aside the bars. Brief explanation of the cost type and the impacted sectors are provided in material and methods section, but for details and examples mentioned in *Invacost* see Tables 1 and 2 in Diagne et al. (2020).

The costs of biological invasions of holoplanktonic organisms exponentially increased until the '90s, reaching a peak in 1995 and then steadily decreased towards 2020. During this period, invasions cost on average US$ 142.9 million per year (Figure 3). Costs generated by meroplanktonic invasions have, however, exponentially increased, with a mean annual cost of US$ 2 billion. The 2000–2010 decade was the costliest, reaching US$ 8 billion of annual costs, followed by the 2010–2020 year period where nearly US$ 6.5 billion were spent per year to deal with meroplankton invasions. During the 2010–2019 period costs with invasive meroplanktonic organisms were estimated to be 14 times higher than with holoplanktonic taxa.

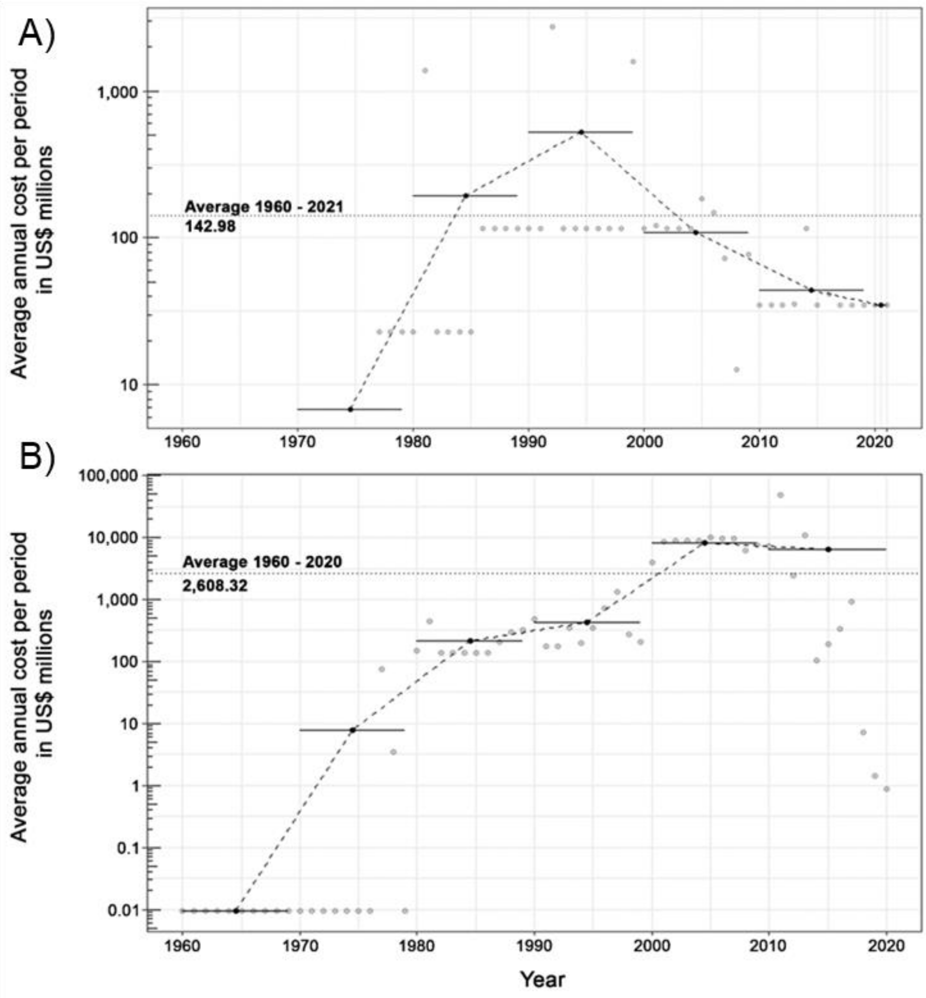


Figure 3. Temporal trends (1960–2020) of mean annual costs (in year 2017 rate equivalents – US$ millions) of A) holoplankton and adults with meroplanktonic stages B). We considered the amounts provided for each decade in the conservative subset (excluding “low reliability” and “potential” from the meroplankton database, see Methods for further details)

Models showed a similar trend for holo- and meroplankton, with a higher explained variance for models with meroplankton data (greater than 70 %; Fig. 4). All modeling techniques confirmed that costs have continuously increased each year since 1970 for meroplanktonic organisms. However, models indicated a quadratic tendency for holoplankton with a decrease in costs from the 2000s forward.

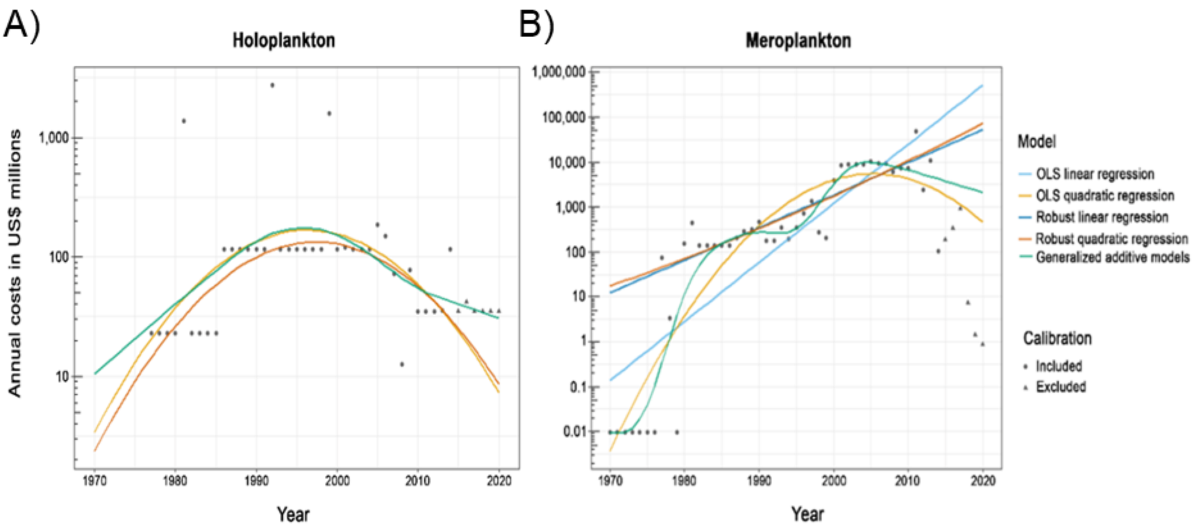


Figure 4. Temporal trends (1970–2020) of costs (in 2017 equivalent rates –US$ millions) using model predictions for A) holoplankton and adults with meroplanktonic stages B). Cost estimates were $\log_{10}$-transformed, and models were calibrated and fitted with at least 75% of cost data completeness from the dataset. OLS: ordinary least-squares.

Discussion

Our global assessment on the economic impacts of plankton invasions identified costs of up to US$ 5 billion (holoplankton), between 1960 and 2021. The current economic costs of holoplankton were compiled solely from 16 invasive species, here split within virio- (3 taxa), bacterio- (1), myco- (2 taxa), phyto- (4 taxa), and zooplankton (6 taxa). Our results indicate much higher and consistent costs towards fishery, caused by microbial pathogens, and “mixed” sectors, where reported cases were not clearly distinguished. These costs are likely expected to be underreported as the aforementioned taxa can substantially impact e.g., the environment sector through disrupting biodiversity — ecosystem functioning relationships (Walsh et al., 2016; Dexter et al., 2020a, Pacheco et al., 2021; González-Madina et al., 2021). Indeed, shifts in water quality and biological diversity may account for higher overall costs as they indirectly effect some overlooked economic sectors (e.g., health, environment and public/social welfare).

Reported costs with holoplankton were driven mainly by damage/loss rather than expenses incurred for management. These results are in line with the overall pattern found for the pool of invasive species in *InvaCost* database, indicating insufficient management and the urgent need to increase spending towards more cost-efficient actions, particularly pre-invasion management (Sarnele et al., 2010; Ewerts et al., 2014; Cuthbert et al., 2022; Zhang et al., 2022).

In the 21st century, the documentation about the presence and expansion of harmful or potentially invasive planktonic species is on a rise (Antunes et al., 2015; Dexter and Bollens, 2019, Dexter et al., 2020b; Macêdo et al., 2020). However, the low number of reported costs with planktonic invasions likely reflects the difficulties in translating their indirect impacts into monetary expenditures, particularly considering the effects of algae blooms that may lead to anoxia, production of toxins or subjective effects such as the aesthetics of waterbodies (e.g. Jochmsen et al., 1998; Naselli-Flores and Padisák, 2022). Also, invasive phytoplankters and their impacts on pelagic biodiversity are sometimes not investigated through the lens of biological invasions (Amorim and Moura, 2020) or not considered as potential threats to valuable aquatic ecosystem services (Naselli-Flores and Padisák, 2022).

On the positive side, anticipating invasions of small aquatic non-native plankton can rely on alternative technologies such as molecular tools e.g. environmental DNA and metagenomics (e.g., de Vargas et al., 2015; Hirai et al., 2017; La Rosa et al., 2020; MacKeigan et al., 2022), that although not yet sufficiently affordable for most developing countries, can be primarily helpful in the detection of cryptic species, immature stages of zooplankton and larvae of benthic taxa (de Vargas et al., 2015; Hirai et al., 2017). In addition, modern tools for analyzing the environmental requirements of planktonic species improve our monitoring protocols and our predictive capacity to deal with invasions of tiny invaders of the diverse pelagic division (e.g., Ricciardi et al., 1995; Jaturapruek et al., 2021; Macêdo et al., 2021; 2022).

Geographical distribution of costs

We detected an unevenly spatial distribution of costs worldwide with a significant discrepancy between developing and developed countries. Disproportionately more data are available in the “Global North” (Bellard and Jeschke, 2015; Bellard et al. 2016, Dexter and Bollens, 2019). Despite these biased geographical cost estimates, plankton costs represent a higher fraction when compared to the total costs for all groups of aquatic and terrestrial alien species of some regional assessments (e.g., Italy; Haubrock et al., 2021a, México; Rico-Sánchez, et al., 2021, and Singapore; Haubrock et al., 2021b).

Investments in management of invasive species, such as those arising from infectious diseases caused by pathogens (mainly viruses and bacteria) were also geographically skewed towards North America, Europe and Oceania (Haubrock et al., 2022c), although Central America and Chile showed the highest reported costs exclusively handling viruses. In Chile and New Zealand, we found enormous costs associated with a single species of a diatom (*Didymosphenia geminata*) while Northern Europe was the only geographical area that had costs with at least one taxon from each of the holoplanktonic groups. The lack of reported costs for Africa and Asia, as well as the few entries from North America and Oceania, are notable. However, several recent studies have shown that biological invasions are a raising problem in Australia (Bradshaw et al., 2021), China and India (Liu et al., 2021) or Southern and Eastern Africa (Diagne et al., 2021b). Costs of planktonic invasive species were also scarce in South America e.g., in Brazil that harbors a significant portion of natural resources with extensive wetlands, groundwater and irrigation systems. Contradictorily, information on the expansion of invasive plankton species in Brazil is rising (Matsumura-Tundisi and Silva, 2002; Anderson et al., 2012; Macêdo et al., 2020; Severiano et a., 2021), but the quantification of their associated impacts were never documented.

Temporal gaps

Historically, monetary costs of plankton introductions started with Platyhelminthes (*Gyrodactylus salaris*) in 1977, while the most recent register was in 2017 for mycoplankton (*Batrachochytrium dendrobatidis*). There were only two bacterioplankton entries in 2006 and 2009, while phyto- and zooplankton costs were observed mainly in the last two decades. Despite the fact that the harmful effects of algal blooms were recognized as already as the 1970s (Maso and Garces, 2006; Zingone and Enevoldsen, 2000) and some reports of impacts by zooplankton were from the early 1980s (Moller, 1984; Shiganova et al., 2001), there is a delay in bringing taxa invasion to the attention of the broad scientific community and managers. This may be in part due to misidentifications (e.g., *Mesocyclops ogunus*, Matsumura-Tundisi and Silva, 2002) or due to delays in labelling as "invasive" species extensively reported in a given area (e.g., the case of *Kellicottia bostoniensis* in Mexico; Nandini et al., 2022).

While cost estimates of holoplankton have been decreasing over time there is an increasing trend with costs with meroplankton and other invasive species included in *Invacost* (Diagne et al., 2020a). Thus we assume that the decrease in global economic costs of planktonic species shown in the model estimates to be an artifact because of lack of data and research effort. Although our estimations are based on the impact of adult stages of meroplanktonic taxa, combining holo- and meroplanktonic populations than holoplankton alone may show a more realistic trend of costs and potential harmful impacts for the pelagic habitats worldwide.

Taxonomic gaps

Monetary costs are available for only 16 holoplanktonic species, stressing our plea on the underestimation of their costs worldwide due to taxonomic issues. For example, Dexter and Bollens (2019) in their review on zooplankton invasions pointed out 139 holoplanktonic IS and approximately half of the surveyed publications concerned solely four species: *Bythotrephes longimanus* (Leydig, 1860), *Mnemioposis leidyi*, *Cercopagis pengoi*, (Ostroumov, 1891), and *Daphnia lumholtzi* (absent in the Invacost database). In addition, only 4.3% of the 139 studies informed on their economic impacts. Also, multiple zooplankton species have shown much higher non-native distributions than previously reported e.g., *Pseudodiaptomus forbesi*, *Oithona davisae*, *Bosmina coregon* (Dexter et al., 2020b). Similarly, much greater distribution extent has been updated for phytoplankton invasive species (e.g., the potentially toxic *Raphidiopsis raciborskii* Padisák et al., 2016 and the large-sized dinoflagellate *Ceratium furcoides* Pacheco et al., 2021; Severiano et al., 2021).

Phytoplankton was poorly represented in the *InvaCost* database with only four taxa listed (see Table 1). However, the European Alien Species Database alone lists 51 phytoplankton species as alien to European coastal waters: 22 dinoflagellates, 20 diatoms, seven raphidophytes, one prymnesiophyte, and one phaeophyte. These numbers indicate the gap between the information available on costs estimates and the number of harmful species already established in aquatic ecosystems around the world. According to Wolf and Klaiber (2017), most of the state and local governments of the United States considered harmful algal blooms to be “somewhat serious” or “very serious” issues. Economic losses related to eutrophication and cyanobacterial blooms have been addressed in several cases (e.g. Dodds et al., 2009; Wolf and Klaiber, 2017; Wurtsbaugh et al., 2019), though in many largely unmeasured or not properly quantified (Carmichael and Boyer, 2016). However, costs of invasive cyanobacteria are lacking in the *InvaCost* database. The potential negative impacts, and underlying neglected costs, of invasive cyanobacteria might be overwhelming and include changes in the abiotic environment and biogeochemical cycles, shifts in microbial communities, not to mention the effect of single or multiple toxins on biodiversity by acute and sub-lethal effects on consumers and potential competitors (Sukenik et al., 2012; Sukenik et al., 2015). Additionally, the co-occurrence of multiple invasive species (Kokocinski and Soininen 2019) and harmful impacts in freshwaters of remote oceanic islands (Costa et al., 2021) set the alert for even overwhelming effects of invasive cyanobacteria.

The parasitic copepod *Lernaea cyprinacea*, which infests commercially important fishes, (Soares et al., 2018), and the dinoflagellate *Ceratium furcoides*, whose frequent blooming negatively affect economically important fish (Pacheco et al., 2021) are also missing from *InvaCost*. Despite their broad tolerance, highly invasive species such as *Cercopagis pengoi*, *Bythotrephes longimanus*, *Artemia franciscana*, *Mysis relicta*, *Rhopilema nomadica* and *Mnemiopsis leidyi* are still largely neglected regarding costs across a global assessment (Diagne et al., 2020a; Haubrock et al., 2021; Zenni et al., 2021). *Artemia franciscana* is capable of spreading cysts of protozoan parasites (e.g., *Giardia*) that infect a wide range of vertebrates including humans (Mendez-Hermida et al., 2006). As the most common live food used for fish and invertebrate production for human consumption, it can further act as a disease vector rising economic and public health concerns. *Cercopagis pengoi* was responsible for US$ 5 million of economic costs related to impacts on fisheries (Pimentel, 2005), however its indirect impacts on environment and ecosystem services are yet not quantified. Meanwhile, another predatory cladoceran, *Bythotrephes longimanus,* whose cascading effect through a lake food web led to losses of US$ 86.5–163 million (Walsh et al., 2016) for restoring water clarity. Water quality is a key ecosystem service commonly affected by eutrophication, albeit commonly associated with phytoplankton blooms and not to the effect of invasive species (e.g., Amorim and Moura, 2020; Naselli-Flores and Padisák, 2022).

We illustrated higher potential impacts (US$ 98 billion) by meroplanktonic organisms (crustaceans, insects, and mollusks) that disperse via planktonic larvae in their early stages. Costs of their larval stages are absent in *InvaCost* database and studies concerning invasions of meroplanktonic organisms are scarce (Bollens et al., 2002), despite the increasing trend of costs with their adult stages in recent decades (Dexter and Bollens, 2019). Free-living life-forms are relevant for our understanding of the trophic relationships in pelagic environments and are most likely to interact with and impact other species e.g., responsible for biomass decline and trophic disruptions (Bowen et al., 2018; Javidpour et al., 2020). Also, early and juvenile stages are more readily dispersed propagules (Flannery et al., 2016; Javidpour et al., 2020), easily transported by several pathways (e.g., as epifauna, within body cavities, via water currents, or ballast water discharges) (Viard et al., 2006). Furthermore, climate change is expected to influence the geographic range, abundance, ontogeny and ultimately the intensity of meroplanktonic invasions by influencing the success of early stages (Walther et al., 2009; Ernandes-Silva et al., 2016; Denley and Metaxas, 2017; Beaury et al., 2020). Therefore, here we suggest some emerging holoplanktonic species of concern for future assessment of costs (Fig. 5) and also advocate that meroplanktonic organisms become a target and priority for invasion early warning (Ernandes-Silva et al., 2016), partly contributing to avoid or minimize the massive negative impact of their adult stages on waters quality and economies (mollusks, Haubrock et al., 2022a; insects, Bradshaw et al., 2021; fish, Haubrock et al., 2022b).

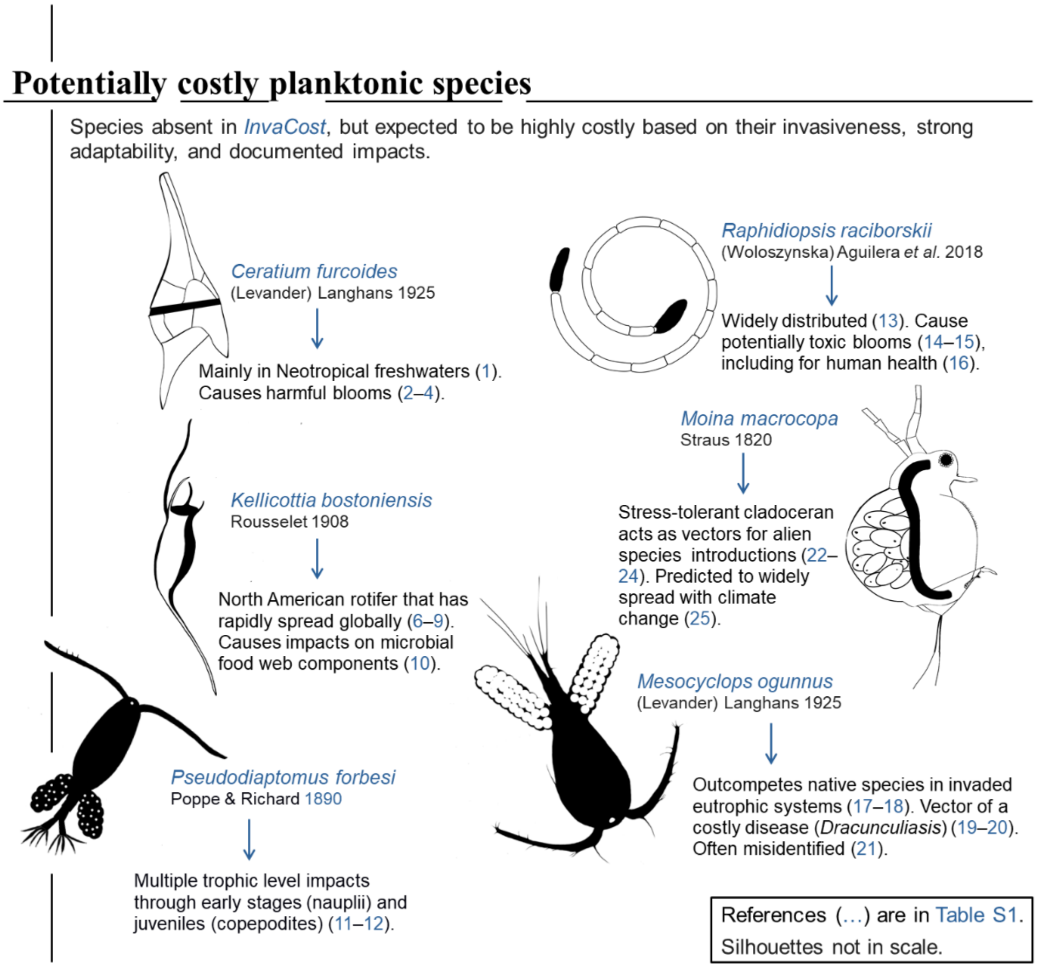


Figure 5. Potentially costly holoplanktonic invaders not recorded in the *InvaCost* database. We short-listed these species considering their potential to exert dual effects: a direct impact on ecosystem services and economies and an indirect impact through biodiversity loss, which in turn can generate monetary costs to restore ecosystem services.

Conclusions

Our study highlights an uneven distribution of data in reporting costs of holoplanktonic invasions, mainly due to the low number of investigated species (taxonomic gap). While it is difficult to predict and reliably interpret costs of aquatic invaders, a continuous and rising introduction of several groups of planktonic taxa is expected and possibly enhanced by synergistic effects of other environmental human-driven alterations.

As cost types were generally higher for damage/loss than for control or management, we advocate for higher efforts in early detection to avoid or minimize the spread and establishment of invasive populations. By doing so, we could substantially reduce the costs of plankton invasive species in the future, an issue that reaches beyond a shift in trophic alterations and goes on to affect water quality worldwide.

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7. FINAL CONSIDERATIONS

Plankton drives productivity and life under water regarding numerous vital ecosystem services. However, our knowledge on planktonic organisms is limited, to the point that most species are still supposed to be distributed across large areas of the planet, and a higher number of species than expected from the available resources can coexist. For these reasons, planktonic organisms have not received much attention in the context of biological invasions, although their ubiquity and short life spans make them promising model organisms for research on this topic.

Despite some alien planktonic species are increasingly recognized as harmful by international efforts such as IUCN's 100 of the World's Worst Invasive Alien Species list, they are currently underrepresented both taxonomically and geographically, as are their impacts. Consequently, even impactful plankton invasions often remain silent for a long time, making it difficult and costly to take effective management actions. Small planktonic organisms are generally overlooked or are solely recognized as threats during bloom episodes, e.g. red tides, or seen as consequences of eutrophication, nor invasion.

Social-economic costs of invasive plankton also seem to be more- timely reported by local environmental authorities than by scientists, whereas a fraction of these data are yet not made publicly accessible. Early detection and approaches that unveils risky and environmental suitable areas for invasion have been efficient in minimizing impacts.

In this sense, our models have revealed a pool of useful statistical approaches and making learning methods applicable to planktonic taxa and to investigate how rapidly invasive species may shift its climatic ranges in space and time and to what extent they are expanding their fundamental niche. Although most predictive studies, including ours, consider often environmental variables, additional factors such as reduced biological pressure, habitat type, and natural and anthropogenic disturbances should be added since they might affect species invasiveness in novel non-native areas. In this sense, we would likely suggest i) to build SDMs that incorporate quantitative information on cells density or biovolume, ii) to investigate whether the species realized niche is conserved over space (iii) Whether extinction in plankton can be caused by alien planktonic taxa or can native plankton taxa be extirpated or extinct as consequence of biological invasions? (iv) What is the role of genetic composition and bottle necks following plankton invasion mechanisms of plankters? (v) Is plankton abundance a useful metric to classify plankton impact? and the most important (vi) How can we define impact categories of harmful planktonic invasive species?

This more in-depth knowledge would be helpful to define surveillance areas and mitigate the potential impacts in areas where the invasion could potentially be reported. Also, to prevent the uneven distribution of data in reporting costs of planktonic invasions, mainly due to the low number of investigated species (taxonomic gap) and area under sampling. By doing so, we could substantially reduce the costs of plankton invasive species in the future, an issue that reaches beyond a shift in trophic alterations and goes on to affect water quality worldwide.