Contents lists available at ScienceDirect

Ecological Indicators

Original Articles

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

Rafael Lacerda Macêdo [a,b,*], Ana Clara Sampaio Franco [c,d], Philip Russo [e], Tim Collart [f], Stefano Mammola [g,h], Erik Jeppesen [i,j,k,l], Christina Wyss Castelo Branco [a,c], Luciano Neves dos Santos [c,d], Odete Rocha [b]

[a] Neotropical Limnology Group (NEL), Federal University of Rio de Janeiro State, Av. Pasteur, 458, 22290-240 Rio de Janeiro, RJ, Brazil
[b] Graduate Program in Ecology and Natural Resources, and Department of Ecology and Evolutionary Biology, Federal University of São Carlos - UFSCar, São Carlos, Brazil
[c] Programa de Pós-graduação em Biodiversidade Neotropical, Universidade Federal do Estado do Rio de Janeiro (UNIRIO), Av. Pasteur, 458 - R314A, 22290-240 Rio de Janeiro, RJ, Brazil
[d] Laboratório de Ictiologia Teórica e Aplicada, Universidade Federal do Estado do Rio de Janeiro (UNIRIO), Av. Pasteur, 458 - R314A, 22290-240 Rio de Janeiro, RJ, Brazil
[e] Departamento de Zoologia, Universidade Federal de Minas Gerais (UFMG), Av. Antônio Carlos, 662, 31270-901 - Pampulha, Belo Horizonte, MG, Brazil
[f] Ghent University, Department of Geology, Campus Sterre, building S8, Krijgslaan 281, 9000 Gent, Belgium
[g] Water Research Institute, National Research Council of Italy (CNR), Verbania Pallanza, Italy
[h] Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland
[i] Department of Bioscience and WATEC, Aarhus University, DK-8600 Silkeborg, Denmark
[j] Sino-Danish Centre for Education and Research (SDC), 100049 Beijing, China
[k] Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem Research and Implementation, Middle East Technical University, 06800 Ankara, Turkey
[l] Institute of Marine Sciences, Middle East Technical University, 33731 Edemli-Mersin, Turkey

ARTICLE INFO

ABSTRACT

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.

1. 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-Hernández et al., 2021).Fig. 1.

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 non-native 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; Macèdo 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
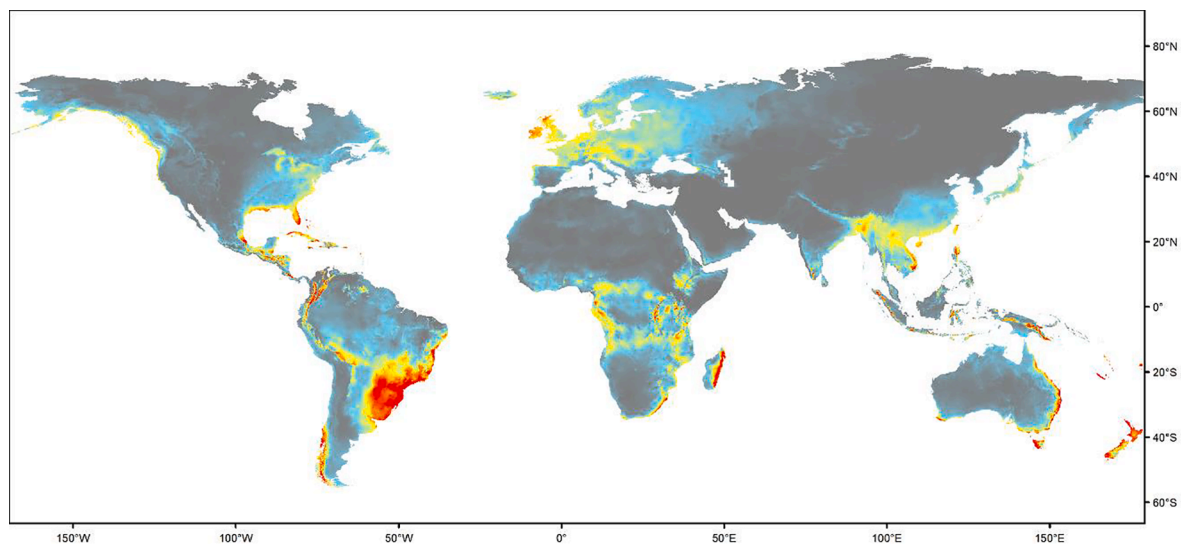

Fig. 1. Consensus map showing the most climate susceptible areas to invasion of *Ceratium furcoies* in the future. The estimated climate suitability of *C. furcoides* was based on the average of all the predicted future scenarios of climate change and includes both the native and invaded range of the species.

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 (Jiménez-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., 2021). 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.

2. Methods

2.1. 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.

2.2. 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 (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, GFDL-ESM4, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0), namely multi-model future climate projections based on alternative scenarios of future CO_2 and aerosol emission rates (https://www.worldclim.org/data/cmip6/cmip6climate.html). Nine bioclimatic future models were generated for SSP126 and SSP370 scenarios of CO_2 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*.

2.3. 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* (Macèdo 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 Macèdo 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).

2.4. 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; Macèdo 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).

3. Results

3.1. 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 (Figure S1; Table S2). 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; Figure S1). 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.

3.2. 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 Macèdo 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).

3.3. 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 (Figures S2 and S3). Temperature seasonality (bio4) was the most important variable for explaining the suitability of an area for *C. furcoides* occurrence in all four models (Figure S3). 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.

3.4. 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.
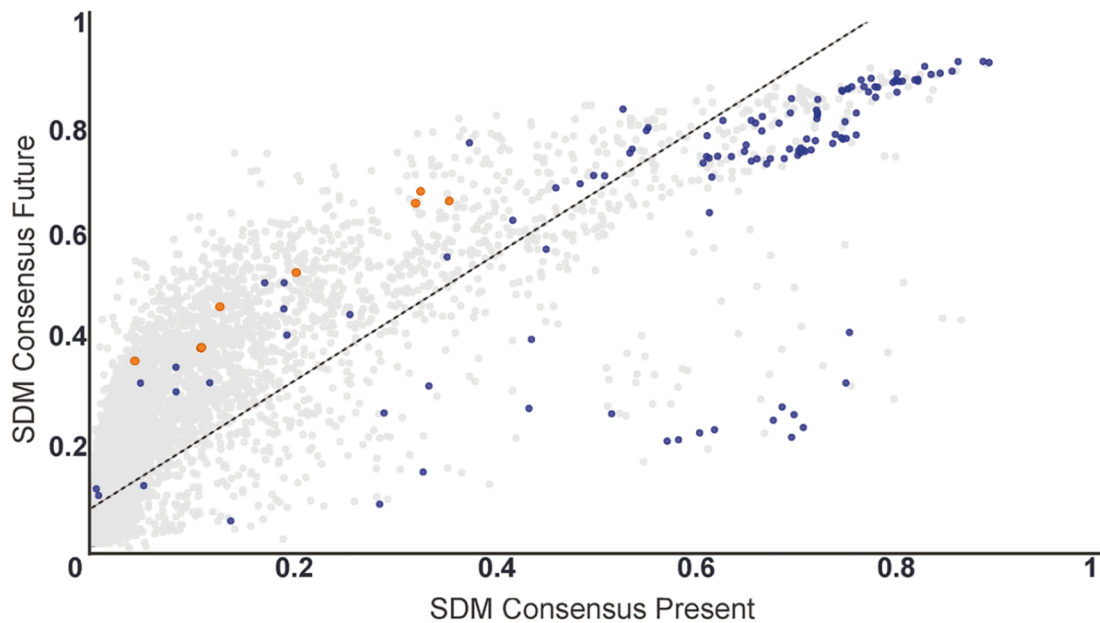
Fig. 2. Probability values of presence of *Ceratium furcoides* at both present and future scenarios. Background data (or pseudo-absence) are represented by gray circles, native records are in orange and non-native records in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
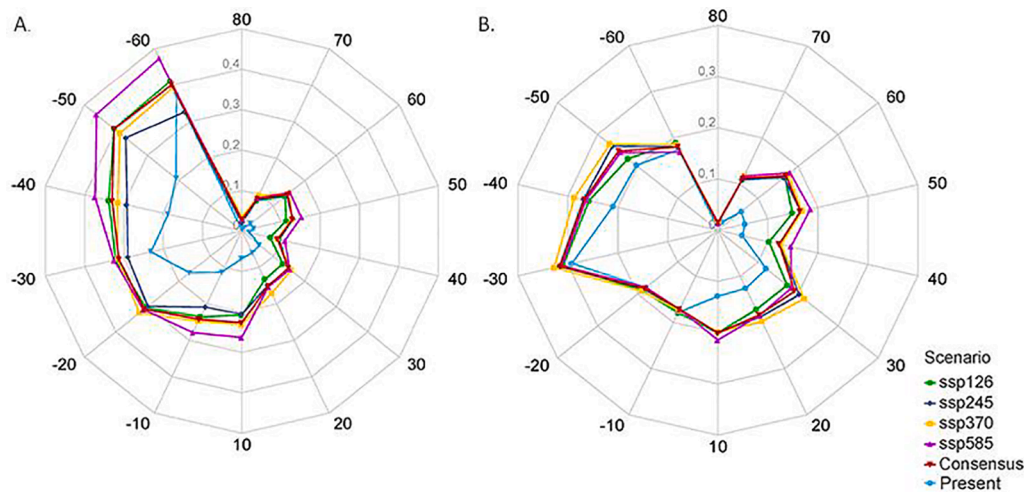

Fig. 3. Radar graphs showing the expansion of *Ceratium furcoides*' range across the geographical space (sorted by latitudinal bands). Average A), and standard deviation B) of suitability values are shown. Colors represent the different projected scenarios: the four future scenarios of climate change, the consensus of these four scenarios and the present model.

4. 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 mixo-trophy), 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-
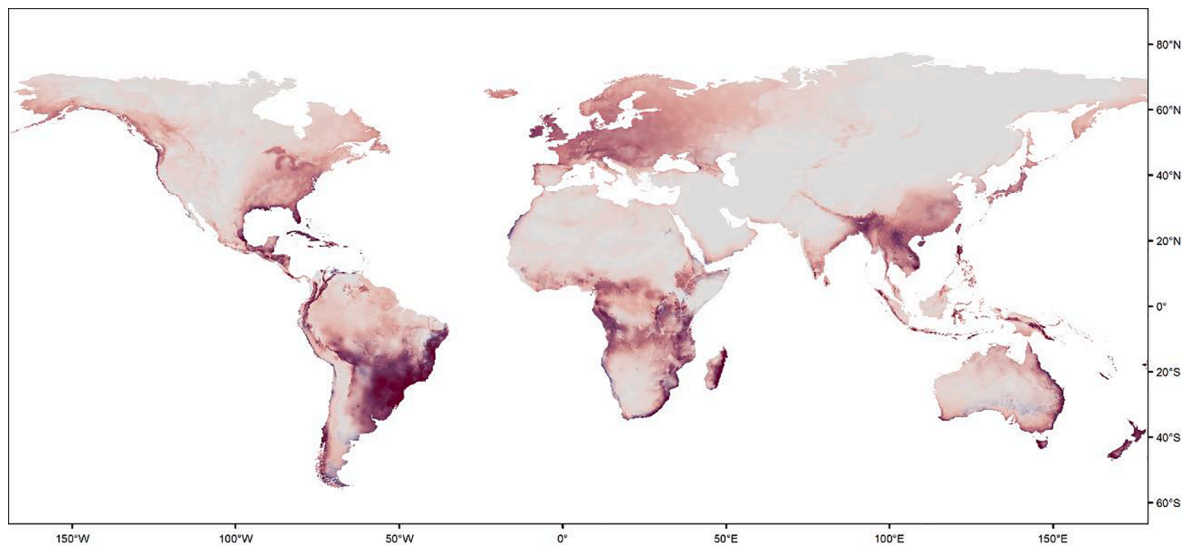
Fig. 4. Map comparing the future global range expansion of *Ceratium furcoides* with the present suitability model. The purple shades indicate an overlap between the present (blue) and the future (red) projections. Darker tons represent higher overlap between present and future projections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
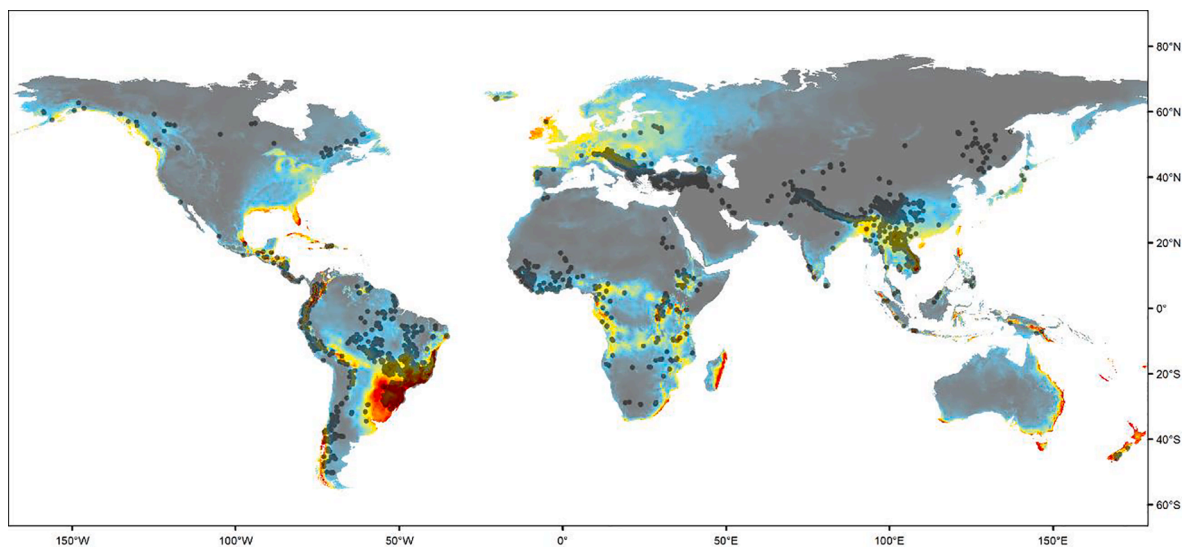

Fig. 5. Consensus map of fundamental niche in future scenarios (2041–2060) overlapping the dam construction projection predicted until 2030.

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 (Macèdo 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 (Sánchez-Fernández 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; Macêdo 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 (Macêdo 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 Paraná 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). In 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 & Padisák, 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; Macêdo 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.

5. Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

CRediT authorship contribution statement

Rafael Lacerda Macêdo: Conceptualization, Data curation, Writing – original draft, Methodology. **Ana Clara Sampaio Franco:** Writing – original draft. **Philip Russo:** Software, Visualization. **Tim Collart:** Writing – review & editing. **Stefano Mammola:** Writing – review & editing. **Erik Jeppesen:** Writing – review & editing, Validation. **Christina Wyss Castelo Branco:** Writing – review & editing. **Luciano Neves dos Santos:** Conceptualization, Writing – review & editing. **Odete Rocha:** Conceptualization, Supervision.

Declaration of Competing Interest

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

Acknowledgment

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108408.

References

R. Abell M.L. Thieme C. Revenga M. Bryer M. Kottelat N. Bogutskaya B. Coad N. Mandrak S.C. Balderas W. Bussing M.L.J. Stiassny P. Skelton G.R. Allen P. Unmack A. Naseka R. Ng N. Sindorf J. Robertson E. Armijo J.V. Higgins T.J. Heibel E. Wikramanayake D. Olson H.L. López R.E. Reis J.G. Lundberg M.H. Sabaj Pérez P. Petry Freshwater Ecoregions of the World: A New Map of Biogeographic Units for Freshwater Biodiversity Conservation 58 5 2008 2008 403 414 10.1641/B580507.

Accattatis, V., Piccini, C., Huber, P., Metz, S., Rueda, E., Devercelli, M., 2020. Identifying invaders: the case of *Ceratium furcoides* (Gonyaulacales, Dinophyceae) in South America. J. Phycol. https://doi.org/10.1111/jpy.13015.

Almeida, C.R., Spiandorello, F.B., Giroldo, D., Yunes, J.S., 2016. The effectiveness of conventional water treatment in removing *Ceratium furcoides* (Levander) Langhans, *Microcystis sp.* and microcystins. Water S.A. 42 (4), 606–611. https://doi.org/10.4314/wsa.v42i4.11.

Amorim, C.A., Moura, A., do N., 2020. Ecological impacts of freshwater algal blooms on water quality, plankton biodiversity, structure, and ecosystem functioning. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2020.143605.

Anderson, R.P., Lew, D., Peterson, A.T., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol. Model. 162, 211–232.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377.

Birk, S., Chapman, D., Carvalho, L., Spears, B.M., Andersen, H.E., Argillier, C., Auer, S., Baattrup-Pedersen, A., Banin, L., Beklioğlu, M., Bondar-Kunze, E., Borja, A., Branco, P., Bucak, T., Buijse, A.D., Cardoso, A.C., Couture, R.M., Cremona, F., de Zwart, D., Feld, C.K., Ferreira, M.T., Feuchtmayr, H., Gessner, M.O., Gieswein, A., Globevnik, L., Graeber, D., Graf, W., Gutiérrez-Cánovas, C., Hanganu, J., Işkın, U., Järvinen, M., Jeppesen, E., Kotamäki, N., Kuijper, M., Lemm, J.U., Lu, S., Solheim, A.L., Mischke, U., Moe, S.J., Nõges, P., Nõges, T., Ormerod, S.J., Panagopoulos, Y., Phillips, G., Posthuma, L., Pouso, S., Prudhomme, C., Rankinen, K., Rasmussen, J.J., Richardson, J., Sagouis, A., Santos, J.M., Schäfer, R.B., Schinegger, R., Schmutz, S., Schneider, S.C., Schülting, L., Segurado, P., Stefanidis, K., Sures, B., Thackeray, S.J., Turunen, J., Uyarra, M.C., Venohr, M., von der Ohe, P.C., Willby, N., Hering, D., 2020. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. Nat. Ecol. Evol. 4 (8), 1060–1068. https://doi.org/10.1038/s41559-020-1216-4. Epub 2020 Jun 15 PMID: 32541802.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Model. 157 (2-3), 281–300.

Branco, C.W.C., Leal, João.José.F., Huszar, V.Lúcia.de.M., Farias, D.da.S., Saint'Pierre, T.D., Sousa-Filho, I.F., de Palermo, E.F.de.A., Guarino, A.W.S., Gomes, A.R., Kozlowsky-Suzuki, B., 2019. New lake in a changing world: the construction and filling of a small hydropower reservoir in the tropics (Rio de Janeiro, Brazil). Environ. Sci. Pollut. Res. 26 (35), 36007–36022. https://doi.org/10.1007/s11356-019-06665-y.

Breslin, P. B., Wojciechowski, M. F., Albuquerque, F. (2020). Projected climate change threatens significant range contraction of *Cochemiea halei* (Cactaceae), an island endemic, serpentine-adapted plant species at risk of extinction. *Ecology and Evolution,* 29;10(23):13211-13224. doi: 10.1002/ece3.6914.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T., Guisan, A., 2007. Evidence of climatic niche shift during biological invasion. Ecol. Lett. 10 (8), 701–709. https://doi.org/10.1111/ele.2007.10.issue-810.1111/j.1461-0248.2007.01060.x.

Browne, L., Markesteijn, L., Engelbrecht, B.M.J., Jones, F.A., Lewis, O.T., Manzané-Pinzón, E., Wright, S.J., Comita, L.S., 2021. Increased mortality of tropical tree seedlings during the extreme 2015–16 El Niño. Glob. Change Biol. 27 (20), 5043–5053. https://doi.org/10.1111/gcb.v27.2010.1111/gcb.15809.

Bustamante-Gil, C., Ramírez-Restrepo, J.J., Boltovskoy, A., Vallejo, A., 2012. Spatial and temporal change characterization of *Ceratium furcoides* (Dinophyta) in the equatorial reservoir Riogrande II, Colombia. Acta Limnol. Bras. 24, 207–219.

Cao, Q., Yu, D., Georgescu, M., Wu, J., 2018. Substantial impacts of landscape changes on summer climate with major regional differences: the case of China. Sci. Total Environ. 625, 416–427.

Casco, María.A., Labollita, Héctor.A., Cano, María.G., 2014. Phytoplankton of the reservoirs of Central and North Patagonia. – Adv. Limnol. 65, 293–307. https://doi.org/10.1127/1612-166X/2014/0065-0047.

Casco, María.A., Mac Donagh, María.E., 2014. Reservoirs of the Peri-Pampean region. 65, 215–231. https://doi.org/10.1127/1612-166X/2014/0065-0043.

Cassol, APV., Pereira Filho, W., Oliveira, MA., Domingues, AL., Correa, FS., Buriol, GA., 2014. First record of a bloom of the invasive species *Ceratium furcoides* (Levander) Langhans 1925 in Rio Grande do Sul state. Brazil. *Brazilian Journal of Biology* 74 (2), 515–517.

Cavalcante, K.P., Zanotelli, J.C., Müller, C.C., Scherer, K.D., Frizzo, J.K., Ludwig, T.A.V., Cardoso, L.S., 2013. First record of expansive *Ceratium* Schrank, 1793 species (Dinophyceae) in Southern Brazil, with notes on their dispersive patterns in Brazilian environments. Check List 9, 862–866.

Çelekli, A., Lekesiz, Ömer, 2021. Limno-ecological assessment of lentic ecosystems in the western Mediterranean basin (Turkey) using phytoplankton indices. Environ. Sci. Pollut. Res. 28 (3), 3719–3736. https://doi.org/10.1007/s11356-020-10697-0.

Chapman, D.S., Makra, László, Albertini, R., Bonini, M., Páldy, A., Rodinkova, V., Šikoparija, B., Weryszko-Chmielewska, E., Bullock, J.M., 2016. Modelling the introduction and spread of non-native species: international trade and climate change drive ragweed invasion. Glob. Change Biol. 22 (9), 3067–3079. https://doi.org/10.1111/gcb.2016.22.issue-910.1111/gcb.13220.

Corrêa, R.F., Macêdo, R.L., Fonseca, K.N., Ribeiro, M.G., Miranda, V.B.S., Orsi, M.L., Portugal, S.G.M., Branco, C.W.C., 2021. Detection paradigms for impact evaluation of *Ceratium furcoides*: concerns for the world's largest water treatment plant for domestic supply. Submitted in *Lakes & Reservoirs: Science, Policy and Management for Sustainable Use*.

Costa, M.R.A., Attayde, J.L., Becker, V., 2016. Effects of water level reduction on the dynamics of phytoplankton functional groups in tropical semi-arid shallow lakes. Hydrobiologia 778, 75–89.

Costa, M.R.A., Menezes, R.F., Sarmento, H., Attayde, José.L., Sternberg, L.da.S.L., Becker, V., 2019. Extreme drought favors potential mixotrophic organisms in tropical semi-arid reservoirs. Hydrobiologia 831 (1), 43–54. https://doi.org/10.1007/s10750-018-3583-2.

Crossetti, L.O., Bicudo, D.de.C., Bini, L.M., Dala-Corte, R.B., Ferragut, C., de Mattos Bicudo, C.E., 2019. Phytoplankton species interactions and invasion by *Ceratium furcoides* are influenced by extreme drought and water-hyacinth removal in a shallow tropical reservoir. Hydrobiologia 831 (1), 71–85. https://doi.org/10.1007/s10750-018-3607-y.

Vanessa S. Daga Valter M. Azevedo-Santos Fernando M. Pelicice Philip M. Fearnside Gilmar Perbiche-Neves Lucas R. P. Paschoal Daniel C. Cavallari José Erickson Ana M. C. Ruocco Igor Oliveira André A. Padial Jean R. S. Vitule 49 1 2020 165 172.

Darwall, W., Smith, K., Allen, D., Seddon, M., Mc Gregor Reid, G., Clausnitzer, V., Kalkman, V. (2009). Freshwater biodiversity—A hidden resource under threat. In The 2008 Review of the IUCN Red List of Threatened Species; Vié, J.C., Hilton-Taylor, C., Stuart, S.N., Eds.; IUCN: Gland, Switzerland; pp. 43–53.

Darki, B.Z., Krakhmalnyi, A.F., 2019. Biotic and Abiotic Factors Affecting the Population Dynamics of *Ceratium hirundinella*, *Peridinium cinctum*, and *Peridiniopsis elpatiewskyi*. Diversity 11 (8), 137. https://doi.org/10.3390/d11080137.

Deng, J., Paerl, H.W., Qin, B., Zhang, Y., Zhu, G., Jeppesen, E., Cai, Y., Xu, H., 2018. Climatically-modulated decline in wind speed may strongly affect eutrophication in shallow lakes. Sci. Total Environ. 645, 1361–1370.

Dinis, M., Vicente, J., César de Sá, N., López-Núñez, F.A., Marchante, E., Marchante, H., 2020. Can Niche Dynamics and Distribution Modelling Predict the Success of Invasive Species Management Using Biocontrol? Insights From *Acacia longifolia* in Portugal. Frontiers in Ecology and Evolution 8. https://doi.org/10.3389/fevo.2020.576667.

Dodds, W.K., Bouska, W.W., Eitzmann, J.L., Pilger, T.J., Pitts, K.L., Riley, A.J., Schloesser, J.T., Thornbrugh, D.J., 2009. Eutrophication of U.S. Freshwaters: Analysis of Potential Economic Damages. Environ. Sci. Technol. 43 (1), 12–19. https://doi.org/10.1021/es801217q.

Emerson, S., Bollens, S., Counihan, T., 2015. Seasonal dynamics of zooplankton in Columbia-Snake River reservoirs, with special emphasis on the invasive copepod *Pseudodiaptomus forbesi*. Aquat. Invasions 10 (1), 25–40. https://doi.org/10.3391/ai10.3391/ai.2015.10.110.3391/ai.2015.10.1.03.

Essl, F., Lenzner, B., Bacher, S., Bailey, S., Capinha, C., Daehler, C., Dullinger, S., Genovesi, P., Hui, C., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., Kühn, I., Leung, B., Liebhold, A., Liu, C., MacIsaac, H.J., Meyerson, L.A., Nuñez, M.A., Pauchard, A., Pyšek, P., Rabitsch, W., Richardson, D.M., Roy, H.E., Ruiz, G.M., Russell, J.C., Sanders, N.J., Sax, D.F., Scalera, R., Seebens, H., Springborn, M., Turbelin, A., Kleunen, M., Holle, B., Winter, M., Zenni, R.D., Mattsson, B.J., Roura-Pascual, N., 2020. Drivers of future alien species impacts: An expert-based assessment. Glob. Change Biol. 26 (9), 4880–4893. https://doi.org/10.1111/gcb.v26.910.1111/gcb.15199.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.2017.37.issue-1210.1002/joc.5086.

Finni, T., Kononen, K., Olsonen, R., Wallström, K., 2001. The History of Cyanobacterial Blooms in the Baltic Sea. *Ambio: A Journal of the Human.* Environment 30 (4), 172–178.

Franco, A.C.S., García-Berthou, E., Santos, L.N.dos., 2021. Ecological impacts of an invasive top predator fish across South America. Sci. Total Environ. 761, 143296. https://doi.org/10.1016/j.scitotenv.2020.143296.

Frankham, R., 2005. Resolving the genetic paradox in invasive species. Heredity (Edinb). 94 (4), 385. https://doi.org/10.1038/sj.hdy.6800634. PMID: 15602569.

Gallien, L., Mazel, F., Lavergne, S., Renaud, J., Douzet, R., Thuiller, W., 2015. Contrasting the effects of environment, dispersal and biotic interactions to explain the distribution of invasive plants in alpine communities. Biol. Invasions 17 (5), 1407–1423. https://doi.org/10.1007/s10530-014-0803-1.

Gobler, C.J., 2020. Climate Change and Harmful Algal Blooms: Insights and perspective. Harmful Algae. 91, 101731. https://doi.org/10.1016/j.hal.2019.101731.

Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C., Kuefer, C., 2014. Unifying niche shif studies: insights from biological invasions. Trends Ecol. Evol. 29, 260–269.

Hamilton, W.D., Lenton, T.M., 1998. Spora and Gaia: How microbes fly with their clouds. Ethology Ecology & Evolution 10 (1), 1–16.

Hansen, G., Cramer, W., 2015. Global distribution of observed climate change impacts. Nat. Clim. Change 5 (3), 182–185. https://doi.org/10.1038/nclimate2529.

Hart, R., Wragg, P., 2009. Recent blooms of the dinoflagellate *Ceratium* in Albert Falls Dam (KZN): History, causes, spatial features and impacts on a reservoir ecosystem and its zooplankton. Water SA 35 (4). https://doi.org/10.4314/wsa.v35i4.76807.

Hassan, B., Qadri, H., Ali, M.N., Khan, N.A., Yatoo, A.M., 2020. In: Fresh Water Pollution Dynamics and Remediation. Springer Singapore, Singapore, pp. 105–121. https://doi.org/10.1007/978-981-13-8277-2_7.

HAVEL, JOHN.E., LEE, CAROL.EUNMI., VANDER ZANDEN, M.JAKE., 2005. Do reservoirs facilitate invasions into landscapes? Bioscience 55 (6), 518. https://doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2.0.CO;2.

Havel, J.E., Medley, K.A., 2006. Biological invasions across spatial scales: intercontinental, regional and local dispersal of cladoceran zooplankton. Biol. Invasions 8 (3), 459–473.

Heino, J., Culp, J.M., Erkinaro, J., Goedkoop, W., Lento, J., Rühland, K.M., Smol, J.P., 2020. Abruptly and irreversibly changing Arctic freshwaters urgently require standardized monitoring. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13645, 57, 7, (1192-1198).

Hellmann, J.J., Byers, J.E., Bierwagner, B.G., Dukes, J.S., 2008. Five Potential Consequences of Climate Change for Invasive Species. Conserv. Biol. 22 (3), 534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x.

Hirabayashi, Y., Tanoue, M., Sasaki, O., Zhou, X., Yamazaki, D., 2021. Global exposure to flooding from the new CMIP6 climate model projections. Sci. Rep. 11 (1), 3740. https://doi.org/10.1038/s41598-021-83279-w.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199 (2), 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.0.

Honti, M., Gao, C., Istvánovics, V., Clement, A., 2020. Lessons Learnt from the Long-Term Management of a Large (Re)constructed Wetland, the Kis-Balaton Protection System (Hungary). Water. 12 (3), 659. https://doi.org/10.3390/w12030659.

Howeth, J.G., Weis, J.J., Brodersen, J., Hatton, E.C., Post, D.M., 2013. Intraspecific phenotypic variation in a fish predator affects multitrophic lake metacommunity structure. Ecol. Evol. 3 (15), 5031–5044. https://doi.org/10.1002/ece3.2013.3.issue-1510.1002/ece3.878.

Martiny, J.B., Bohannan, B.J., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Ovreås, L., Reysenbach, A.L., Smith, V.H., Staley, J.T., 2006. Microbial biogeography: putting microorganisms on the map. Nature Review Microbiology. 4 (2), 102–112. https://doi.org/10.1038/nrmicro1341.

IMA, 2015. Parecer Técnico DILAB 003/2015.

IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.

Iwamura, T., Guzman-Holst, A., Murray, K.A., 2020. Accelerating invasion potential of disease vector *Aedes aegypti* under climate change. Nat. Commun. 11, 2130. https://doi.org/10.1038/s41467-020-16010-4.

Jasechko, S., Perrone, D., 2021. Global groundwater wells at risk of running dry. Science 372 (6540), 418–421.

Jeppesen, E., Brucet, S., Naselli-Flores, L., Papastergiadou, E., Stefanidis, K., Nõges, T., Nõges, P., Attayde, José.L., Zohary, T., Coppens, J., Bucak, T., Menezes, R.F., Freitas, F.R.S., Kernan, M., Søndergaard, M., Beklioğlu, M., 2015. Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. Hydrobiologia 750 (1), 201–227. https://doi.org/10.1007/s10750-014-2169-x.

Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecologica 31 (3), 361–369. https://doi.org/10.1016/j.actao.2007.02.001.

Johnson, P.T.J., Olden, J.D., Vander Zanden, M.J., 2008. Dam invaders: Impoundments facilitate biological invasions into freshwaters. Front. Ecol. Environ. 6 (7), 357–363. https://doi.org/10.1890/070156.

Kling, M.M., Ackerly, D.D., 2020. Global wind patterns and the vulnerability of wind-dispersed species to climate change. Nat. Clim. Change 10 (9), 868–875. https://doi.org/10.1038/s41558-020-0848-3.

Knouft, J.H., Ficklin, D.L., 2017. The Potential Impacts of Climate Change on Biodiversity in Flowing Freshwater Systems. Annual Review of Ecology, *Evolution,*

and Systematics 48 (1), 111–133. https://doi.org/10.1146/ecolsys.2017.48.issue-110.1146/annurev-ecolsys-110316-022803.

Kristiansen, J., 1996. Dispersal of freshwater algae — a review. Hydrobiologia 336, 151–157. https://doi.org/10.1007/BF00010829.

Kruk, C., Piccini, C., Devercelli, M., Nogueira, L., Accattatis, V., Sampognaro, Lía, Segura, A.M., 2021. A trait-based approach predicting community assembly and dominance of microbial invasive species. Oikos 130 (4), 571–586. https://doi.org/10.1111/oik.2021.v130.i410.1111/oik.07694.

Lennon, J.T., Smith, V.H., Williams, K., 2001. Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success. J. Plankton Res. 23 (4), 425–433.

Liu, X., Blackburn, T.M., Song, T., Wang, X., Huang, C., Li, Y., 2020. Animal invaders threaten protected areas worldwide. Nat. Commun. 11 (1), 1–9.

Loo, S.E., MacNally, R., Lake, P.S., 2007. Forecasting New Zealand mudsnail invasion range: model comparison using native and invaded ranges. Ecol. Appl. 17, 181–189.

Macêdo, R. L., A. C. S. Franco, R. F. Corrêa, K. do N. Costa, L. G. Pereira, F. D. M. de Oliveira, G. Klippel, B. D. Cordeiro, M. G. R. Thiago, M. I. A. Rocha, V. L. M. Huszar, L. N dos Santos & C. W. C. Branco, (2021a). Spreading of the invasive dinoflagellate *Ceratium furcoides* (Levander) Langhans across Paraiba do Sul ecoregion, South America, Brazil. *Limnetica.* https://doi.org/10.23818/limn.40.16.

Macêdo, R.L., Russo, P., Corrêa, R.F., Rocha, O., dos Santos Neves, L., Branco, C.W.C., 2021b. The drifting dinoflagellate *Ceratium furcoides* (Levander) Langhans 1925: fundamental niche shift during global invasion. Hydrobiologia 848, 2105–2117. https://doi.org/10.1007/s10750-020-04495-5.

Manjarrés-Hernández, A., Guisande, Cástor, García-Roselló, E., Heine, J., Pelayo-Villamil, P., Pérez-Costas, E., González-Vilas, L., González-Dacosta, J., R. Duque, S., Granado-Lorencio, C., Lobo, J.M., 2021. Predicting the effects of climate change on future freshwater fish diversity at global scale. Nature Conservation 43, 1–24. https://doi.org/10.3897/natureconservation.43.5899710.3897/natureconservation.43.58997.suppl110.3897/natureconservation.43.58997.suppl210.3897/natureconservation.43.58997.suppl310.3897/natureconservation.43.58997.suppl4.

Mammola, S., Milano, F., Vignal, M., Andrieu, J., Isaia, M., Fleishman, E., 2019. Associations between habitat quality, body size and reproductive fitness in the alpine endemic spider Vesubia jugorum. Glob. Ecol. Biogeogr. 28 (9), 1325–1335.

Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38, 921–931.

Marengo, J.A., Alves, L.M., 2005. Tendências hidrológicas da bacia do rio Paraíba do Sul. Revista Brasileira de Meteorologia 20, 215–226.

Mathieu Marmion Miia Parviainen Miska Luoto Risto K. Heikkinen Wilfried Thuiller 15 1 2009 59 69.

Maureaud, A., Andersen, K.H., Zhang, L., Lindegren, M., Thébault, E., 2020. Trait-based food web model reveals the underlying mechanisms of biodiversity-ecosystem functioning relationships. J. Anim. Ecol. 89 (6), 1497–1510. https://doi.org/10.1111/jane.v89.610.1111/1365-2656.13207.

Narkis S. Morales Ignacio C. Fernández Victoria Baca-González MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? 5 2017 e3093 10.7717/peerj.3093 10.7717/peerj.3093/fig-1 10.7717/peerj.3093/fig-2 10.7717/peerj.3093/fig-3 10.7717/peerj.3093/fig-4 10.7717/peerj.3093/table-1 10.7717/peerj.3093/table-2 10.7717/peerj.3093/supp-1 10.7717/peerj.3093/supp-2 10.7717/peerj.3093/supp-3 10.7717/peerj.3093/supp-4 10.7717/peerj.3093/supp-5.

Moon, S., Ha, K.-J., 2020. Future changes in monsoon duration and precipitation using CMIP6. Npj *Climate and Atmospheric.* Science 3 (1). https://doi.org/10.1038/s41612-020-00151-w.

Luigi Naselli-Flores Judit Padisák 764 1 2016 303 313.

Pacheco, J.P., Iglesias Frizzera, C., Goyenola, G., Teixeira de-Mello, F., Fosalba, C., Baattrup-Pedersen, A., Meerhoff, M., Jeppesen, E., 2021. Invasion of *Ceratium furcoides* in subtropical lakes in Uruguay: Environmental drivers and fish kill record during its bloom. Biol. Invasions 23 (11), 3597–3612. https://doi.org/10.1007/s10530-021-02600-w.

Paerl, H.W., Huisman, J., 2008. CLIMATE: Blooms Like It Hot. Science 320 (5872), 57–58. https://doi.org/10.1126/science.1155398.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T. D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J. M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science (New York, N.Y.) 355 (6332). https://doi.org/10.1126/science:aai9214.

Peterson, A.T., Vieglais, D.A., 2001. Predicting Species Invasions Using Ecological Niche Modeling: New Approaches from Bioinformatics Attack a Pressing Problem. Bioscience 51 (5), 363. https://doi.org/10.1641/0006-3568(2001)051[0363:psiuen]2.0.co.

Piano, E., Doretto, A., Mammola, S., Falasco, E., Fenoglio, S., Bona, F., 2020. Taxonomic and functional homogenisation of macroinvertebrate communities in recently intermittent Alpine watercourses. Freshw. Biol. 65 (12), 2096–2107.

Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. PNAS 104 (14), 5732–5737. https://doi.org/10.1073/pnas.0609812104.

N.N. Rabalais R.E. Turner R.J. Diaz D, Justic. Global change and eutrophication of coastal waters ICES Journal of Marine of Science 66 2008 000 000.

Radinger, J., García-Berthou, E., 2020. The role of connectivity in the interplay between climate change and the spread of alien fish in a large Mediterranean river. Glob.

Change Biol. 26 (11), 6383–6398. https://doi.org/10.1111/gcb.v26.1110.1111/gcb.15320.

Rahel, F.J., Olden, J.D., 2008. Assessing the Effects of Climate Change on Aquatic Invasive Species. Conserv. Biol. 22 (3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x.

Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biol. Rev. 94 (3), 849–873. https://doi.org/10.1111/brv.2019.94.issue-310.1111/brv.12480.

Ricciardi, A., Iacarella, J.C., Aldridge, D.C., Blackburn, T.M., Carlton, J.T., Catford, J.A., Dick, J.T.A., Hulme, P.E., Jeschke, J.M., Liebhold, A.M., Lockwood, J.L., MacIsaac, H.J., Meyerson, L.A., Pyšek, P., Richardson, D.M., Ruiz, G.M., Simberloff, D., Vilà, M., Wardle, D.A., 2021. Four priority areas to advance invasion science in the face of rapid environmental change. Environmental Reviews. 29 (2), 119–141. https://doi.org/10.1139/er-2020-0088.

Robinson, T.B., Martin, N., Loureiro, T.G., Matikinca, P., Robertson, M.P. (2020). Double trouble: the implications of climate change for biological invasions. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM. *NeoBiota* 62: 463-487. https://doi.org/10.3897/neobiota.62.55729.

Rogers, J.B., Stein, E.D., Beck, M.W., Ambrose, R.F., Jones, J.A., 2020. The impact of climate change induced alterations of streamflow and stream temperature on the distribution of riparian species. PLoS ONE 15 (11), e0242682. https://doi.org/10.1371/journal.pone.024268210.1371/journal.pone.0242682.g00110.1371/journal.pone.0242682.g00210.1371/journal.pone.0242682.g00310.1371/journal.pone.0242682.g00410.1371/journal.pone.0242682.g00510.1371/journal.pone.0242682.g00610.1371/journal.pone.0242682.t00110.1371/journal.pone.0242682.t00210.1371/journal.pone.0242682.t00310.1371/journal.pone.0242682.t00410.1371/journal.pone.0242682.t00510.1371/journal.pone.0242682.s00110.1371/journal.pone.0242682.s00210.1371/journal.pone.0242682.s00310.1371/journal.pone.0242682.r00110.1371/journal.pone.0242682.r00210.1371/journal.pone.0242682.r00310.1371/journal.pone.0242682.r004.

Sánchez-Fernández, D., Galassi, D.M.P., Wynne, J.J., Cardoso, P., Mammola, S., 2021. Don't forget subterranean ecosystems in climate change agendas. Nat. Clim. Change 11 (6), 458–459.

Sax, D.F., Early, R., Bellemare, J., 2013. Niche syndromes, species extinction risks, and management under climate change. Trends Ecol. Evol. 28 (9), 517–523. https://doi.org/10.1016/j.tree.2013.05.010.

Juliana dos Santos Severiano Emmanuelly da Silva Oliveira Daniely de Lucena-Silva Gustavo Correia de Moura Elizabeth Amorim da Silva José Etham de Lucena Barbosa Invasion of the dinoflagellate Ceratium furcoides (Levander) Langhans 1925 in South America: record of the pattern of expansion and persistence in tropical reservoirs in Northeastern Brazil 10.1007/s10530-021-02641-1.

Sexton, J.P., Montiel, J., Shay, J.E., Stephens, M.R., Slatyer, R.A., 2017. Evolution of Ecological Niche Breadth. Annu. Rev. Ecol. Evol. Syst. 48 (1), 183–206. https://doi.org/10.1146/ecolsys.2017.48.issue-110.1146/annurev-ecolsys-110316-023003.

Sharma, N.K., Rai, A.K., Singh, S., Brown, R.M., 2007. Airborne algae: their present status and relevance. J. Phycol. 43 (4), 615–627. https://doi.org/10.1111/j.1529-8817.2007.00373.x.

Silva, W.José.da., Nogueira, I.de.S., Melo-Magalhães, E.M.de., Benício, S.H.M., Pessoa, S. Magalhães., Menezes, M., 2018. Expansion of invasive Ceratium furcoides (Dinophyta) toward north-central brazil: New records in tropical environments. Acta Limnol. Bras. 30 (0) https://doi.org/10.1590/s2179-975x5917.

Sobek-Swant, S., Kluza, D.A., Cuddington, K., Lyons, D.B., 2012. Potential distribution of emerald ash borer: What can we learn from ecological niche models using Maxent and GARP? For. Ecol. Manage. 281, 23–31. https://doi.org/10.1016/j.foreco.2012.06.017.

Spear, M.J., Walsh, J.R., Ricciardi, A., Vander Zanden, J.M., 2021. The Invasion Ecology of Sleeper Populations: Prevalence. Persistence, and Abrupt Shifts, *BioScience* 71 (4), 357–369. https://doi.org/10.1093/biosci/biaa168.

Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Linking climate change and biological invasions: oceanwarming facilitates non-indigenous species invasions. PNAS 99, 15497–15500.

V. Srivastava 14 020 2019 10.1079/PAVSNNR201914020.

Matsumura-Tundisi, T., Tundisi, J., Luzia, A., Degani, R., 2010. Occurrence of *Ceratium furcoides* (Levander) Langhans 1925 bloom at the Billings Reservoir, São Paulo State. Brazil. *Brazilian Journal of Biology* 70 (3 suppl), 825–829. https://doi.org/10.1590/s1519-69842010000400013.

Tundisi, J.G., Matsumura Tundisi, T., Ciminelli, V.S., Barbosa, F.A., 2015. Water availability, water quality, water governance: the future ahead. Proc. Int. Assoc. Hydrol. Sci. 366, 75–79. https://doi.org/10.5194/piahs-366-75-2015.

F. van der Plas Biodiversity and ecosystem functioning in naturally assembled communities Biological Reviews brv.12499 2019 doi.org/10.1111/brv.12499 https://.

Vanderploeg, H.A., Liebig, J.R., Carmichael, W.W., Agy, M.A., Johengen, T.H., Fahnenstiel, G.L., Nalepa, T.F., 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic Microcystis blooms In Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. 58 (6), 1208–1221. https://doi.org/10.1139/f01-066.

Varol, M., 2016. External morphological variations and temporal distribution of the dinoflagellate *Ceratium hirundinella* in two dam reservoirs in the Tigris River basin (Turkey). Turk. J. Bot. 40, 112–119. https://doi.org/10.3906/bot-1412-8.

Xie, P., Iwakuma, T., Fujii, K., 1998. Changes in the structure of a zooplankton community during a *Ceratium* (dinoflagellate) bloom in a eutrophic fishless pond. J. Plankton Res. 20 (9), 1663–1678. https://doi.org/10.1093/plankt/20.9.1663.

Xiong, W., Wang, H., Wang, Q., Tang, J., Bowler, P., Xie, D., Pan, L., Wang, Z., 2018. Non-native species in the Three Gorges Dam Reservoir: status and risks. BioInvasions Records. 7 (2), 153–158.

Walsh, J.R., Lathrop, R.C., Vander Zanden, M.J., 2016. Invasive invertebrate predator, Bythotrephes longimanus, reverses trophic cascade in a north-temperate lake. Limnol. Oceanogr. 62, 2498–2509.

Weiskopf, S.R., Rubenstein, M.A., Crozier, L.G., Gaichas, S., Griffis, R., Halofsky, J.E., Hyde, K.J.W., Morelli, T.L., Morisette, J.T., Muñoz, R.C., Pershing, A.J., Peterson, D. L., Poudel, R., Staudinger, M.D., Sutton-Grier, A.E., Thompson, L., Vose, J., Weltzin, J.F., Whyte, K.P., 2020. Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. Sci. Total Environ. 733, 137782. https://doi.org/10.1016/j.scitotenv.2020.137782.

Wilken, S., Huisman, J., Naus-Wiezer, S., Van Donk, E., Fussmann, G., 2013. Mixotrophic organisms become more heterotrophic with rising temperature. Ecol. Lett. 16 (2), 225–233.

Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philosophical transactions of the Royal Society of London.* Series B 365, 2093–2106.

H. Zanowski A. Jahn M.M. Holland Arctic Ocean Freshwater in CMIP6 Ensembles: Declining Sea Ice, Increasing Ocean Storage, and Export Journal of Geophysical Research: Oceans 126, Issue 4 2021 article id e16930 10.1029/2020JC016930.

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2015. A global boom in hydropower dam construction. Aquat. Sci. 77 (1), 161–170.

Zhai, J., Mondal, S.K., Fischer, T., Wang, Y., Su, B., Huang, J., Tao, H., Wang, G., Ullah, W., Uddin, M.J., 2020. Future drought characteristics through a multi-model ensemble from CMIP6 over South Asia. Atmos. Res. 246, 105111. https://doi.org/10.1016/j.atmosres.2020.105111.

Zhang, Z., Mammola, S., McLay, C.L., Capinha, César, Yokota, M., 2020. To invade or not to invade? Exploring the niche-based processes underlying the failure of a biological invasion using the invasive Chinese mitten crab. Sci. Total Environ. 728, 138815. https://doi.org/10.1016/j.scitotenv.2020.138815.