

Direct and indirect effects of climate change on distribution and community composition of macrophytes in lentic systems

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ABSTRACT

Macrophytes are an important part of freshwater ecosystems and they have direct and indirect roles in keeping the water clear and providing structure and habitats for other aquatic organisms. Currently, climate change is posing a major threat to macrophyte communities by altering the many drivers that determine macrophyte abundance and composition. We synthesise current literature to examine the direct effects of climate change (i.e. changes in CO₂, temperature, and precipitation patterns) on aquatic macrophytes in lakes as well as indirect effects *via* invasive species and nutrient dynamics. The combined effects of climate change are likely to lead to an increased abundance and distribution of emergent and floating species, and a decreased abundance and distribution of submerged macrophytes. In small shallow lakes, these processes are likely to be faster than in deep temperate lakes; with lower light levels, water level fluctuations and increases in temperature, the systems will become dominated by algae. In general, specialized macrophyte species in high-latitude and high-altitude areas will decrease in number while more competitive invasive species are likely to outcompete native species. Given that the majority of endemic species reside in tropical lakes, climate change, together with other anthropogenic pressures, might cause the extinction of a large number of endemic species. Lakes at higher altitudes in tropical areas could therefore potentially be a hotspot for future conservation efforts for protecting endemic macrophyte species. In response to a combination of climate-change induced threats, the macrophyte community might collapse, which will change the status of lakes and may initiate a negative feedback loop that will affect entire lake ecosystems.

Key words: aquatic plants, climate change, CO₂, invasive species, lakes, macrophytes

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I. INTRODUCTION

Aquatic macrophytes are an important component of many freshwater ecosystems, providing many essential nutritional, structural and biological resources (Chambers *et al.*, 2008). As primary producers, macrophytes are an important part of the food web and play a key role in keeping lake waters clear. They increase denitrification and prevent phytoplankton growth by decreasing the availability of nitrogenous compounds, and not only have a direct role in biochemical cycles, but also serve an indirect role by providing a large surface area for periphyton (van Donk & van de Bund, 2002; Bornette & Puijalon, 2011). Macrophytes can be classified into a number of broad functional groups or morphotypes (e.g. Sculthorpe, 1967) with different growth, architecture, and ecology: (i) submerged with floating leaves; (ii) rooted-submerged, (iii) free-floating; (iv) emergent; and (v) free-floating-submerged (Fig. 1). Variation within groups can be large. For example, rooted-submerged macrophytes include both the slow-growing isoëtids (i.e. small plants with relatively thick and stiff leaves in a basal rosette and a large proportion of below-ground biomass; Smolders, Lucassen & Roelofs, 2002), as well as the fast-growing elodeids (*Elodea* spp.) that have scattered leaves along tall upright stems and can fill entire water bodies.

Many organisms depend on macrophytes for structure and shelter, including zooplankton, plant-associated invertebrates, and vertebrates [e.g. frogs and fish (Lubbers, Boynton & Kemp, 1990; Paterson, 1993; Schriver *et al.*, 1995; van Donk & van de Bund, 2002; Martín, Luque-Larena & López, 2005)]. In shallow eutrophic lakes, the presence of macrophytes is one of the most important factors structuring fish communities. Different fish species have a range of preferences regarding the use of

macrophytes for egg deposition and as food sources (van Donk & van de Bund, 2002). Sediment dynamics and hydrology in lakes are influenced by the presence of macrophytes since they can lower the current velocity, cause particle trapping, and inhibit resuspension of sediments and erosion (Madsen *et al.*, 2001). Furthermore, macrophytes may influence sinking losses (i.e. the sinking velocity of algae divided by the thickness of the epilimnion), light conditions for phytoplankton and produce allelopathic substances (Gao *et al.*, 2017).

While biodiversity is declining across the world, this decline is much greater in fresh waters than in the most affected terrestrial ecosystems (Dudgeon *et al.*, 2006). The loss of aquatic vegetation is accelerating, especially for submerged vegetation in lakes larger than 50 km² (Zhang *et al.*, 2017). Aquatic macrophytes are vulnerable to anthropogenic stressors such as habitat loss, pollution, eutrophication and climate change (Kundzewicz *et al.*, 2008; Smith *et al.*, 2014). Climate change is a major stressor with severe implications for freshwater ecosystems (Sala *et al.*, 2000). The concentration of atmospheric greenhouse gases is currently at the highest levels for at least 800,000 years, and 1983–2012 was likely the warmest 30-year period in the Northern Hemisphere over the last 800 years (IPCC, 2014). Further changes in global climate are projected to have significant effects on the interactions between, and distributions of, aquatic species (Carpenter *et al.*, 1992; Sala *et al.*, 2000; Heino, Virkkala & Toivonen, 2009).

Previous reviews of the effects of climate change on lentic systems have focused on freshwater biota and ecosystems (Carpenter *et al.*, 1992; Wrona *et al.*, 2006; Jeppesen *et al.*, 2015), the consequences of algal blooms (Elliott, 2012; El-Shehawey *et al.*, 2012; O’Neil *et al.*, 2012), or on specific regions including North America (Schindler, 1997), The Netherlands (Mooij *et al.*, 2005), Finland (Heino *et al.*, 2009),

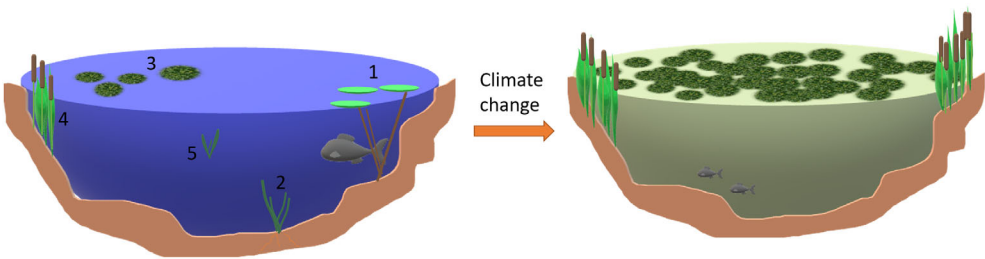


Fig. 1. Deep water lakes at high altitude or latitude are subject to the direct effects of climate change *via* direct increases in temperature, precipitation, and CO₂ levels, and to indirect effects involving nutrient and humic run-off, and invasives. Together, these will result in a decrease in native populations of submerged species and an increase in emergent and floating invasive macrophytes as well as increased phytoplankton abundance and decreased light levels. The end result will be similar in shallow lakes in dry areas, but the pathways and rates of change will differ. Classification of macrophytes: (1) submerged with floating leaves; (2) rooted-submerged; (3) free-floating; (4) emergent; (5) free-floating-submerged.

and boreal regions (Alahuhta, Heino & Luoto, 2011). Other reviews have documented macrophyte distributions, but without considering the impacts of climate change (Chambers *et al.*, 2008; Murphy *et al.*, 2019). There is currently no global review of the direct and indirect effects of climate change on macrophytes, despite the fact that these effects are likely to impact lake ecosystems around the globe (Adrian *et al.*, 2009). Considering the significant role macrophytes play in freshwater ecosystems, it is important to understand what determines their current and future distribution patterns and to identify knowledge gaps. Our objective herein is to synthesise the macrophyte literature and examine the direct effects of changes in CO₂, temperature and precipitation patterns, as well as indirect effects of invasive species and nutrient dynamics. Given the large number of lakes in the northern hemisphere, there is a bias in the literature towards northern regions. Thus, our current knowledge does not reflect the anticipated severity of climate change effects on macrophytes in the southern hemisphere. This review provides insight into the current global status of aquatic macrophytes and facilitates an understanding of the future challenges that face this important group of plants.

II. BACKGROUND

(1) The global distribution of macrophytes

There are an estimated 3,457 species of aquatic macrophytes in the world, with the richest global hotspot for alpha diversity located in Brazil (Murphy *et al.*, 2019) (Fig. 2). In general, macrophyte species richness decreases with increasing latitude and altitude, while lake surface area, shoreline length, littoral zone areas and river channel width show a positive relationship with species richness (Alahuhta *et al.*, 2021). The generally accepted hypothesis was that freshwater aquatic plants have large distribution ranges that tend to be restricted by geographical barriers and are aligned broadly with climatic regions (Cook, 1985; Santamaría, 2002; Les *et al.*, 2003). Similarities among regions have been explained by: (i) aquatic habitats being quite uniform over different geographical areas; (ii) widespread clonality; and (iii) high phenotypic plasticity (Santamaría, 2002). Macrophytes are also a relatively young group and their distribution has been linked to dispersal by birds rather than reflecting their geological history (Cook, 1985; Les *et al.*, 2003). However, these assumptions are based on studies considering only a small proportion of the total number of identified species (Cook, 1985; Santamaría, 2002). By contrast, Murphy *et al.* (2019) found in a worldwide study that most macrophyte species have a narrow global distribution; only 42 species had a broad range (>50% of total grid cell area for the six ecozones considered; Table 1), while species with restricted ranges represent the greatest proportion of macrophyte diversity. According to the IUCN (2020) *Red List*, there is a high endemism in Sub-Saharan Africa, with the largest number of endangered species found in this region (Fig. 2). Endemism among macrophytes seems to be correlated with warmer

conditions, with most endemic species found in tropical and subtropical areas (Murphy *et al.*, 2019). There is also evidence that macrophyte species from higher latitudes have larger geographical ranges than species closer to the equator (the Rapoport effect) (Murphy *et al.*, 2020). However, Sand-Jensen *et al.* (2000) showed that the freshwater flora in northwest Europe includes a large number of rare species. For a comprehensive overview of macrophyte diversity in different regions, see Chambers *et al.* (2008) and Murphy *et al.* (2019).

(2) Current and future climate change

Global climate change is driven by the release of greenhouse gases, mainly carbon dioxide (CO₂), methane (CH₄), nitrous oxide (N₂O) and fluorinated gases (Hartmann *et al.*, 2013). In 2017, human-induced climate warming reached ~1 °C above pre-industrial levels, and is likely to reach 1.5 °C between 2030 and 2052 if it continues to increase at current rates. In northern latitudes, however, some areas have experienced 2–3 times higher rates of warming than the global average (IPCC, 2018). With further climate change, all regions are projected to experience increases in air temperatures, and heavy precipitation with associated floods is likely to intensify and become more frequent in most regions in Africa and Asia (IPCC, 2019). Global average annual precipitation is predicted to increase, but there will be substantial differences among regions, with decreased rainfall in dry, mid-latitudes and dry tropical areas (Kundzewicz *et al.*, 2008), and more precipitation falling as rain instead of snow in high-latitude and high-altitude areas. Heavy rainfall will also cause considerable seasonal shifts in streamflow and changes in run-off patterns in northern areas, which may result in flooding and lower water levels in lakes during the summer (Kundzewicz *et al.*, 2008; Heino *et al.*, 2009). Increased precipitation will result in increased transport of humic substances from terrestrial to aquatic systems, thereby increasing the brownification of freshwater systems (Weyhenmeyer *et al.*, 2016).

Lakes are likely sensitive to changes in climate, although the individual responses of lake chemistry and thermal structure will be lake specific, overall trends may be identified for similar types of lakes. For example, the amount of heat that a lake can absorb or release depends on its depth, implying that shallower lakes (such as many small Mediterranean lakes) will be more severely affected by warming (Poff, 2002; Lacoul & Freedman, 2006a). Lakes are also important emitters of CO₂, CH₄, and N₂O to the atmosphere, which will increase if productivity increases (DelSontro, Beaulieu & Downing, 2018). As they warm, cold-water lakes will emit more CO₂, potentially changing from sink to source status (Kosten *et al.*, 2010; Weyhenmeyer *et al.*, 2015). Even though lakes typically emit CO₂, they can also store carbon in their sediments and climate change will influence both of these processes (Kosten *et al.*, 2010; Short *et al.*, 2016).

A number of studies exemplify the trend for warming lakes (Rosenzweig *et al.*, 2007; O'Reilly *et al.*, 2015; Hintz *et al.*, 2020). In a global study, O'Reilly *et al.* (2015) found an increase in lake surface water temperature of 0.34 °C

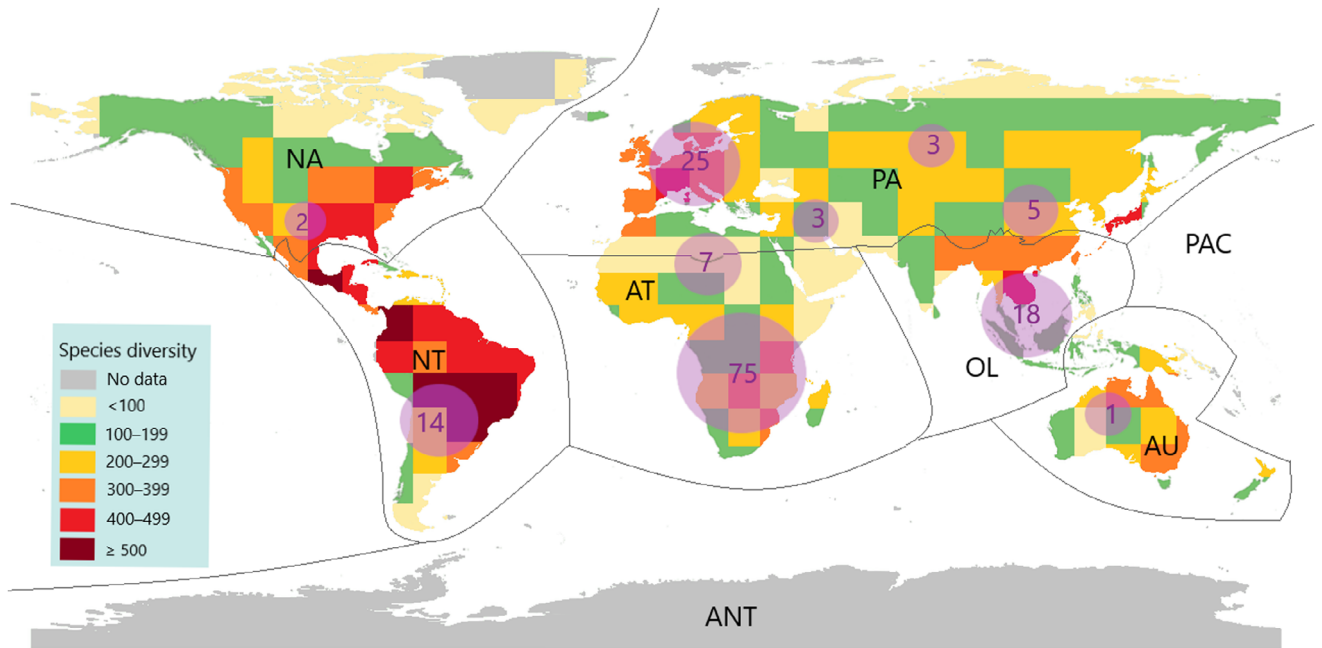


Fig. 2. Macrophyte α -diversity, modified from Murphy *et al.* (2019), combined with the total number of macrophytes (hydrophytes within freshwater systems) that have been assessed as threatened (i.e. categories Critically Endangered, Endangered and Vulnerable) for different regions according to the IUCN (2020) *Red List* (indicated by shaded circles of different sizes). The number of macrophyte species per biogeographic region modified from Chambers *et al.* (2008) is also indicated. Biogeographic regions: ANT, Antarctic (12); AT, Afrotropical (614); AU, Australasian (439); NA, Nearctic (644); NT, Neotropical (984); OL, Oriental (664); PA, Palearctic (497); PAC, Pacific Oceanic Islands (108).

Table 1. Extent of occurrence of the ten most common broad-ranging macrophyte species (expressed as percentage occurrence in 248 10 × 10 degree latitude × longitude grid units in six major land biogeographical regions). Data sourced from supplementary information in Murphy *et al.* (2019)

Family	Species	Species world range (% of grid cells)
Cyperaceae	<i>Cyperus rotundus</i>	77.0
Polygonaceae	<i>Persicaria lapathifolia</i>	76.7
Ceratophyllaceae	<i>Ceratophyllum demersum</i>	76.6
Poaceae	<i>Echinochloa crus-galli</i>	75.8
Poaceae	<i>Phragmites australis</i>	73.9
Juncaceae	<i>Juncus bufonius</i>	68.8
Typhaceae	<i>Typha domingensis</i>	68.3
Poaceae	<i>Echinochloa colona</i>	68.2
Potamogetonaceae	<i>Stuckenia pectinata</i>	67.5
Cyperaceae	<i>Fimbristylis dichotoma</i>	66.6

decade⁻¹ (95% CI 0.16–0.52 °C decade⁻¹). Such temperature increases could have a variety of effects on lakes (Figs. 1 and 3). During a warm year, water temperatures increase, water loss increases, the thermocline becomes shallower, and summer stratification occurs earlier. Warming of northern lakes leads to a longer ice-free season, resulting in altered thermal structure and lake chemistry (Hondzo & Stefan, 1991). In some lakes in Europe and North America,

summer stratification has advanced by up to 20 days, and lengthened by 2–3 weeks since the 1960s (Rosenzweig *et al.*, 2007). This could potentially have major effects: ~78% of all lakes over 10 ha are located in the northern frigid and northern cool areas, and 99.8% have a seasonal ice cover (Maberly *et al.*, 2020).

Increased thermal stability reduces mixing depth and water movement across the thermocline, thereby diminishing essential deep-water nutrient inputs to surface waters. Many lakes are predicted to experience a reduction in mixing frequency or even to become permanently stratified (Woolway & Merchant, 2019). For example, in small tropical lakes there has been an expansion of anoxic waters due to an increase in thermal stability (Saulnier-Talbot *et al.*, 2014). In a study of 393 temperate lakes, Jane *et al.* (2021) found a widespread decline in dissolved oxygen levels from 1941 to 2017, in some cases due to stronger thermal stratification.

Changes in climate will affect lake water quantity and quality, either directly by observed and projected rising CO₂ concentrations and associated changes in temperature, or indirectly through regional and global changes in precipitation regimes, sea-level variability, and melting glaciers and ice cover (Lemke *et al.*, 2007; Meehl *et al.*, 2007; Kundzewicz *et al.*, 2008). Below we focus on the effects of increasing temperature, increasing CO₂ concentration, and changes in precipitation and subsequent run-off on aquatic macrophytes (Fig. 3).

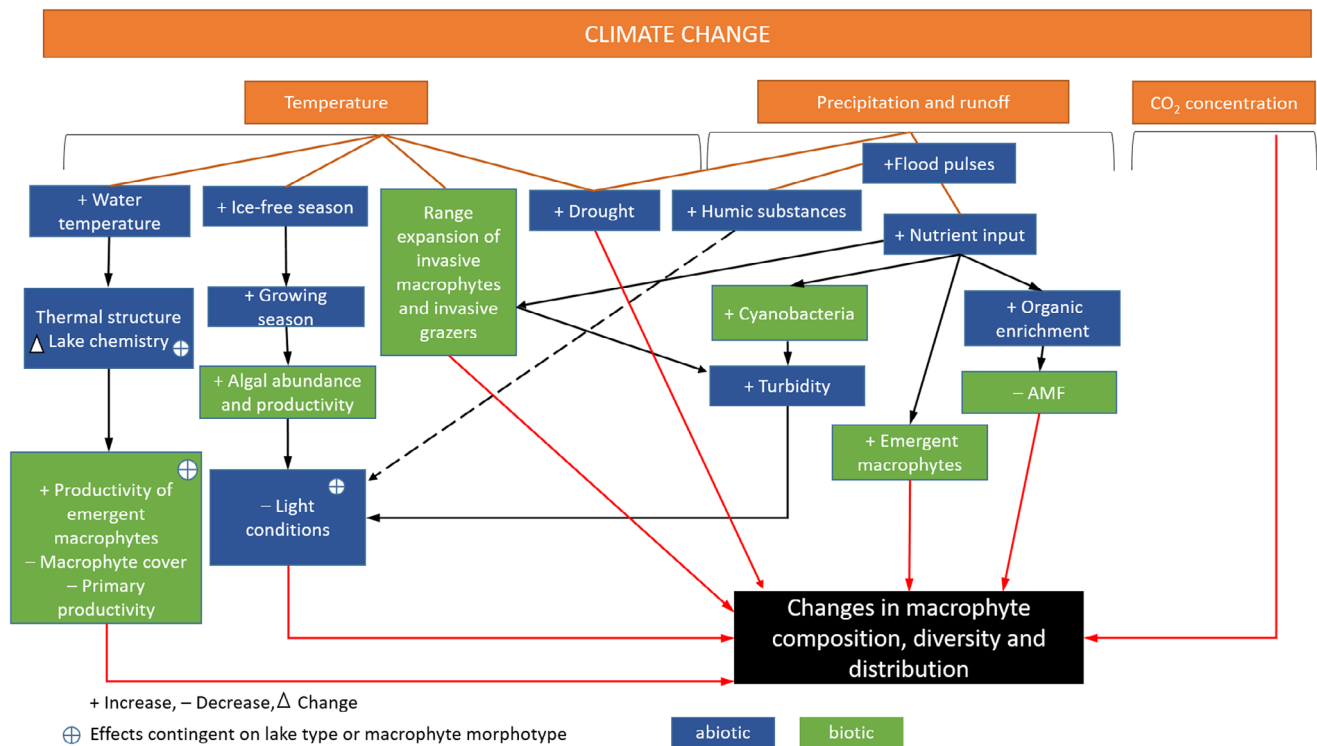


Fig. 3. Flow chart illustrating different biotic and abiotic effects resulting from climate change (as temperature, precipitation and runoff and CO₂ concentration) on macrophyte composition and diversity. AMF, arbuscular mycorrhizal fungi.

III. IMPACTS OF ELEVATED TEMPERATURES ON MACROPHYTES

(1) Effects on macrophytes from changes in lake temperature

As temperature rises, it will affect the community composition, phenology, abundance, productivity, distribution and migration of aquatic plants (Battarbee *et al.*, 2002; Karst-Riddoch, Pisaric & Smol, 2005) (Table 2). However, such effects are expected to be species specific, with a rise in temperature stimulating the growth of some species to a greater extent. For example, *Lagarosiphon major* and *Elodea canadensis* exposed in a growing chamber to different temperature treatments that mimicked different seasons (+3 °C above ambient temperature) showed different growth responses (Silveira & Thiébaud, 2017).

Macrophytes also show variation in responses to elevated temperatures depending on their growth form and location (Fig. 3); floating macrophytes and those that inhabit shallow areas are exposed more to elevated temperatures than are deep-water plants (McKee *et al.*, 2002; Santamaría, 2002). For example, in an outdoor mesocosm experiment in Sweden, charophytes thrived in shallow lakes following a slight increase in temperature, but as light levels decreased through brownification, the charophytes subsequently declined (Fig. 3) (Choudhury *et al.*, 2019).

By using species distribution models (SDMs) with future climate scenarios for Switzerland, Joye & Rey-Boissezon (2015)

predicted a decrease in the occurrence of charophytes in the littoral zone of large deep lakes because of the low number of localities with climatically suitable habitats, while those in small waterbodies increase as they are not deprived of potential favourable ecosystems due to warming. In a warming experiment in Finland that examined littoral habitats using artificial ponds, earlier emergence and higher productivity were observed in four macrophyte species when the temperature was increased by placing a greenhouse over the pond (Kankaala *et al.*, 2000; Table 2). A two-year-long microcosm experiment that mimicked conditions in north temperate ponds and shallow lakes, and used both summer-only warming and continuous warming (+3 °C above ambient temperature), found no significant effects on total abundance of three macrophyte species (*Elodea nuttallii*, *Lagarosiphon major*, and *Potamogeton natans*; McKee *et al.*, 2002; Table 2). However, the community composition changed: the relative proportion of *L. major* increased and this species showed increased growth rate under continuous warming, while *P. natans* showed an increased floating leaf surface area under both warming treatments. In another microcosm-warming experiment conducted in the UK with both summer-only warming and continuous warming (+3 °C above ambient temperature), there was no effect on total macrophyte biomass (McKee *et al.*, 2003), but the experiment did not include any effects of turbidity. On the contrary, a large-scale analysis of 782 lakes identified overall reduced macrophyte cover in response to a warmer climate (Kosten *et al.*, 2009; Table 2).

Table 2. Predicted and observed effects of climate change on macrophytes in lentic systems. AMF, arbuscular mycorrhizal fungi

Effects	Method and location	Reference
Expansion northwards of emergent macrophytes and competitive exclusion of sensitive macrophytes.	Bioclimatic envelope model, Finland	Alahuhta <i>et al.</i> (2011)
No effects on macrophyte biomass but decrease in pH and oxygen saturation with increased frequency of severe deoxygenation.	Microcosm summer warming experiment, UK	McKee <i>et al.</i> (2003)
Growth of <i>Myriophyllum spicatum</i> had a broad thermal tolerance and growth of <i>Egeria densa</i> declined in temperatures >28 °C while growth of <i>Hydrilla verticillata</i> was limited by lower temperatures and increased with increasing temperatures.	Greenhouse experiment, USA	Barko & Smart (1981)
Growth of <i>Vallisneria natans</i> was negatively affected by harmful algal blooms.	Laboratory experiment, China	Jiang <i>et al.</i> (2019)
Biomass and distribution of macrophytes increased with higher temperature and longer growing season.	Lake studies, Canada	Rooney & Kalff (2000)
Increased macrophyte biomass due to warming.	Numerical modelling	Asaeda <i>et al.</i> (2001)
Increased productivity and earlier emergence due to warming.	Warming experiments in artificial ponds, with and without greenhouse cover, Finland	Kankaala <i>et al.</i> (2000)
No abundance effects due to warming, but earlier flowering and increased leaf area. Warming-induced increased proportion of invasive species. One of three species grew better with increased nutrient supply.	Microcosm summer warming experiment, UK	McKee <i>et al.</i> (2002)
Decreased macrophyte cover due to fewer frost days.	782 lakes in Europe, South America and North America	Kosten <i>et al.</i> (2009)
Increased biomass of an invasive free-floating macrophyte, and decreased biomass of a submerged native macrophyte in response to warming.	Mesocosm experiment, The Netherlands	Netten <i>et al.</i> (2010)
Increased of occurrence of free-floating macrophyte (<i>Azolla filiculoides</i>) due to elevated CO ₂ levels.	Greenhouse experiment, The Netherlands	Speelman <i>et al.</i> (2009)
Initial increase in growth of <i>Chara vulgaris</i> due to warming and brownification, followed by a decline in growth with continued increase in temperature and brownification.	Outdoor mesocosm experiment with heaters, Sweden	Choudhury <i>et al.</i> (2019)
Increase of elodeid species and reduction of isoëtids species due to increased CO ₂ levels.	Laboratory experiment in glass containers. Using natural sediments collected in The Netherlands	Spierenburg <i>et al.</i> (2009)
Photosynthesis and nutrient content of an isoëtids decreased in response to organic enrichment of sediments.	Laboratory experiment on sediment turfs from a shallow lake in Sweden, Denmark	Møller & Sand-Jensen (2011)
Decrease in charophytes living in the littoral zone of large deep lakes and an increase of those living in small waterbodies due to increased temperature and decreased precipitation (2 °C increase in mean temperature in July and 15% reduction in precipitation)	Species distribution model (SDM), Switzerland	Joye & Rey-Boissezon (2015)
Colonization of roots of isoëtids with arbuscular mycorrhizal fungi decreased in response to organic enrichment of sediments.	Laboratory aquarium experiment with lake water and sediments from a Swedish lake with <i>Littorella uniflora</i> with and without AMF colonisation	Møller <i>et al.</i> (2013)
Changes in macrophyte community from <i>Chara</i> spp. to vascular plants following a one-year dominance of <i>Chara</i> spp. after a severe drought	Lake study, Lake Okeechobee, Florida, USA	Havens <i>et al.</i> (2004)
Severe drought disturbance caused a decrease in the number of patches colonized by <i>Egeria densa</i> and <i>E. najas</i>	Lake study, Itaipu, Paraguay/Brazil border	Gubiani <i>et al.</i> (2017)
	Lake study, Natural reserve Otamendi, Argentina	O'Farrell <i>et al.</i> (2011)

(Continues)

Table 2. (Cont.)

Effects	Method and location	Reference
Field data showing a shift from free-floating plant dominance to phytoplankton-dominated state during extreme low water levels		
Greater impact on plant growth of climate warming in spring than in summer and late winter on three invasive macrophytes	Containers with macrophytes were added to growth chambers with different temperature treatments. Macrophytes collected in France.	Silveira & Thiébaud (2017)
Comparison of three invasive species subjected to light and temperature treatments showed that <i>Egeria densa</i> is most competitive in warm water and <i>Lagarosiphon major</i> in cold waters, while <i>Elodea canadensis</i> showed the most competitive establishment in all treatments	Outdoor experiment in six tanks with plants from lakes and streams in New Zealand	Riis <i>et al.</i> (2012)
Expansion of suitable habitats for invasive species in Europe and North America while decreasing their native range in South America	SDM	Gillard <i>et al.</i> (2017)

In general, freshwater habitats are buffered against extreme fluctuations in temperature (Santamaría, 2002). However, O'Reilly *et al.* (2003) found a 20% reduction in phytoplankton productivity in Lake Tanganyika since 1800. This fall in productivity was caused by decreased deep-water nutrient upwelling due to increased thermal stability of the water column in combination with reduced mixing (O'Reilly *et al.*, 2003). In many high-latitude and high-altitude lakes reduced ice cover has allowed a longer growing season, resulting in increased algal abundance and productivity (Battarbee *et al.*, 2002; Karst-Riddoch *et al.*, 2005). Increased algal abundance due to fewer frost days leads to lower light availability and, as a consequence, decreased macrophyte cover (Kosten *et al.*, 2009). These changes in temperature and ice cover have caused the phytoplankton spring peak to occur about 4 weeks earlier than 45 years ago (Weyhenmeyer, Blenckner & Pettersson, 1999), decreasing light availability for macrophytes. Photosynthesis rates increase with temperature up to a certain point, beyond which they start to decrease. Hence, when temperatures become very high, there will be a negative impact on net primary production (Tait & Schiel, 2013). Since this response will depend to some extent on the species and growth conditions (Kirschbaum, 2004), increased water temperature is likely to cause major changes in macrophyte community composition and distribution, although the precise responses will be species and region specific. Hence, the effects of climate warming can range from individual responses to the loss of entire macrophyte communities.

(2) Shifts in geographic range

Many taxa are showing range expansions to higher latitudes and altitudes (Parmesan & Yohe, 2003; Hickling *et al.*, 2006), and warming temperatures are also likely to affect the distribution of macrophytes (Hondzo & Stefan, 1991). The response of macrophytes to climate change will depend on their ecophysiology and dispersal ability (Lacoul & Freedman, 2006a; Santamaría, 2002). Bird-mediated dispersal, at least over short distances, facilitates connectivity and gene flow in macrophytes (Coughlan *et al.*, 2017), which might be a key factor in

range shifts and for maintaining genetic diversity in a changing climate. Submerged macrophytes mainly disperse vegetatively and their establishment success therefore depends on the regeneration of plant fragments and whether they can successfully anchor (Heidbüchel & Hussner, 2019).

Longer growing seasons may open up new areas towards higher latitudes for macrophytes potentially to colonize. However, only a few native macrophytes appear to show this pattern to date (Heino *et al.*, 2009). For example, in Finland, *Phragmites australis* and *Typha latifolia* are increasing in extent, pushing their ranges northwards (Alahuhta *et al.*, 2011). With a warmer climate, emergent macrophytes (rooted species with a large proportion of biomass above the water surface) are predicted to spread northwards and cause overgrowth of sensitive submerged or floating macrophytes (Alahuhta *et al.*, 2011). This trend has been documented in Europe and may continue as the climate changes (Partanena & Luoto, 2006). Climate warming could also imply a loss of habitat for macrophytes in dry, mid-latitudes and dry tropical areas where lakes could suffer from dewatering due to increased drought and changes in thermal regime (Poff, 2002; Kundzewicz *et al.*, 2008). For example, in a study of three freshwater macrophytes native to South America (*Egeria densa*, *Myriophyllum aquaticum* and *Ludwigia* spp.), the surface area of suitable habitats in their native ranges is predicted to decrease with climate change (Gillard *et al.*, 2017).

IV. IMPACTS OF ALTERED PRECIPITATION AND NUTRIENT RUN-OFF

Climate change is likely to cause increased variability in the weather, with more droughts and more intense periods of precipitation (Seneviratne *et al.*, 2012). Changes in water levels due to drought will particularly impact aquatic plants that depend on specific hydrological conditions. For example, following a natural drought in a large subtropical lake in Florida, *Chara* spp. rapidly expanded and dominated

near-shore habitats for a year, thereafter, vascular taxa (*Hydrilla verticillata* and *Potamogeton illinoensis*) became dominant (Havens *et al.*, 2004). A severe drought in a floodplain lake in Argentina caused a decrease in dominance of free-floating macrophytes (O'Farrell *et al.*, 2011). Water level increases in shallow Turkish lakes also had a strong negative impact on the occurrence of submerged macrophytes (Tan & Beklioglu, 2005). Hence, studies show that both droughts and heavy rainfall can lead to increases or decreases in macrophyte cover, but generally cause some change to the macrophyte community (O'Farrell *et al.*, 2011; Gubiani *et al.*, 2017).

Increased rainfall and subsequent run-off will transport nutrients from land to water, thereby stimulating emergent macrophytes and potentially leading to overgrowth of freshwater ecosystems (Alahuhta *et al.*, 2011; Egertson, Kopaska & Downing, 2004). Heavy rainfall washes more nutrients (e.g. phosphorus and nitrogen), pathogens, and toxins into water bodies, which can lead to shifts in species composition (Vaithianathan & Richardson, 1999; Confalonieri *et al.*, 2007; Sand-Jensen *et al.*, 2018). Such patterns were described in a study from the Everglades, where species composition changed with P-enrichment (Vaithianathan & Richardson, 1999).

Submerged plants are generally predicted to dominate in a clear-water state, while phytoplankton would dominate in a turbid state. To avoid a turbid state, there is a lower threshold of nutrient levels for maintaining submerged macrophytes in shallow Mediterranean lakes than in temperate shallow lakes, and conservation of macrophytes has become important in these systems (Romo *et al.*, 2004). Again, responses among species can vary, with higher nutrient levels causing a decrease in species richness (Egertson *et al.*, 2004), a reduction in total plant volume, or a reduction in diversity (Barker *et al.*, 2008). In oligotrophic lakes, slight eutrophication can increase diversity (Heino & Toivonen, 2008). However, sensitive slow-growing species, such as isoëtids and stoneworts will disappear early after eutrophication, while fast-growing, nutrient-demanding species can survive (Sand-Jensen *et al.*, 2000). Continued nutrient input will cause hypereutrophic conditions and a decline in macrophyte diversity (Arts, 2002; Heino & Toivonen, 2008). One consequence of eutrophication is organic enrichment of lake sediments and sedimentation of organic matter (Smolders *et al.*, 2002), which can impact isoëtids in oligotrophic, soft-water lakes (Møller & Sand-Jensen, 2011). These species rely on a diverse array of arbuscular mycorrhizal fungi (AMF) (Nielsen *et al.*, 2004; Baar *et al.*, 2011) for uptake of phosphorous. Organic enrichment of sediments reduces AMF colonization (Fig. 3) (Møller, Kjeller & Sand-Jensen, 2013) of *Lobelia dortmanna* due to sediment O₂ depletion, which may explain the high sensitivity of isoëtids to eutrophication.

Nutrient addition resulting from increases in winter precipitation and extreme rainfall events can act as a major trigger for cyanobacteria development (Mooij *et al.*, 2005). Cyanobacterial harmful algal blooms (CyanoHABs) cause increased turbidity and hence restrict light penetration (Paerl & Huisman 2009) (Fig. 3), which suppresses the establishment and growth of aquatic macrophytes (Scheffer

et al., 1993). Macrophytes have an important role in keeping the water clear and thereby create conditions suitable for their own growth since many macrophytes are light limited. In shallow Mediterranean lakes, the year-round persistence of macrophytes increases their competitiveness for light and nutrients (Beklioglu *et al.*, 2007). A decrease in macrophyte abundance could therefore lead to a reduction in water clarity which will feed forward to further losses of macrophytes (Scheffer *et al.*, 1993).

V. IMPACTS OF ALTERED CO₂ CONCENTRATION

A large proportion of atmospheric CO₂ is absorbed by the oceans and other water bodies (Watson *et al.*, 2020). CO₂ enters the pool of dissolved inorganic carbon (DIC, i.e. CO₂, bicarbonate, and carbonate) and reacts with water molecules, producing carbonic acid, which dissolves into a proton (H⁺) and bicarbonate (HCO₃⁻) (Pedersen, Colmer & Sand-Jensen, 2013). The DIC equilibrium depends on pH, but also on temperature, ionic strength and buffering. Thus, the effects of an increase in atmospheric CO₂ concentration will depend strongly on the type of water (Kosten *et al.*, 2009; Bloom *et al.*, 2012; Hussner *et al.*, 2019). Given that the availability of HCO₃⁻ is higher than that of CO₂ in many fresh waters, HCO₃⁻ is the preferred form of inorganic carbon used in the photosynthesis of freshwater charophytes and many macrophytes (Pedersen *et al.*, 2013).

Hence, rising CO₂ concentrations in the atmosphere may increase DIC levels (in the form of CO₂ or HCO₃⁻) and stimulate the photosynthetic rates and productivity of macrophytes (Mormul, Thomaz & Jeppesen, 2020). Waters with massive growth of macrophytes or algae are commonly characterized by a high pH and CO₂ depletion (Sand-Jensen, 1989). In small eutrophic waterbodies, increased atmospheric CO₂ concentration may lead to increased growth of free-floating macrophytes (Speelman *et al.*, 2009). Free-floating macrophytes are superior competitors for light, while submerged plants are stronger competitors for nutrients (Netten *et al.*, 2010). However, free-floating macrophytes profit more from increased CO₂ availability (Speelman *et al.*, 2009), and their resulting increased growth could allow free-floating plants to outcompete submerged plants (Netten *et al.*, 2010).

Softwater lakes, which often occur in boreal and temperate regions and at higher elevations, are bicarbonate-limited systems with low acidity-neutralization capacity (Arts, 2002). The growth of submerged macrophytes in these lakes is therefore often assumed to be carbon limited, and the native isoëtid species are well adapted to these low-carbon conditions (Smolders *et al.*, 2002). Acidification and an increase in CO₂ concentration in softwater lakes can therefore result in large-scale invasions of fast-growing rooted-submerged macrophytes (specifically elodeids), replacing slow-growing rooted-submerged species (i.e. isoëtids) (Arts, 2002). Experiments have linked such changes in species composition to

elevated CO₂ levels (Spierenburg *et al.*, 2009), and Olesen & Madsen (2000) found a positive relative growth rate (RGR; rate of growth per unit time) in *Callitriche cophocarpa* in response to high CO₂ levels and increased temperatures. Rising aquatic CO₂ concentrations in softwater lakes could therefore change these habitats, making them more suitable for elodeid species (Arts, 2002; Smolders *et al.*, 2002). In monocultures or when grown individually, many invasive plants respond positively to elevated CO₂ concentrations (Dukes & Mooney, 1999; Ziska, 2003). Hence, increasing CO₂ emissions will benefit fast-growing species and free-floating macrophytes that outcompete submerged and slow-growing plants (Figs. 1 and 3).

VI. IMPACTS OF INVASIVE SPECIES

It is generally thought that climate change will enhance the invasiveness of exotic species, and simultaneously decrease ecosystem resistance to invasion (McKee *et al.*, 2002; Lacoul & Freedman, 2006b; Thuiller, Richardson & Midgley, 2007). A number of factors contribute to the success of invasive alien macrophytes compared to native plants, including the absence of natural enemies or competitors, and simultaneous increases in disturbances such as eutrophication and altered hydrology (Coetzee & Hill, 2012). Although fresh water only covers less than 1% of the Earth's surface, 15 aquatic taxa, including one macrophyte species (water hyacinth, *Pontederia crassipes*), are listed among the 100 worst invasive plants and animals by the IUCN (Lowe *et al.*, 2004). Many of the species listed under the U.S. Endangered Species Act are considered threatened or at risk primarily due to the presence of invasive species (Pimentel, Zuniga & Morrison, 2005).

In Europe, 33% of all invasive alien plants (36 species) of concern are aquatic (European Commission, 2020). However, to date, 96 invasive aquatic plants are reported for Europe (not all are listed as 'of concern') (Hussner, 2012), 90 in North America (Center of Invasive Species and Ecosystem Health, 2018) and 152 in China (Wang *et al.*, 2016). In Southeast Asia, 30 invasive aquatic plants have been reported (Peh, 2010), while there are apparently many fewer reported in Africa (Darwall *et al.*, 2011). This may be due to lower awareness concerning invasive aquatic plants in developing countries, leading to lower reporting levels, to a greater availability of suitable niches in colder areas as the climate changes, or to a larger number of lakes in the northern hemisphere.

Climate change is predicted to increase the number of invasive alien species in India, eastern China, northwestern USA and northwestern Europe, while a decrease is predicted for Central and South America, Indonesian and the Pacific Islands region, southwestern Europe, central Africa, and eastern Australia (Bellard *et al.*, 2013). This global pattern thus predicts a higher number of invasive species in the northern hemisphere compared to the southern hemisphere, with decreases at lower altitudes in tropical regions. Tropical regions are expected to shift into future extreme climatic

zones and are therefore predicted to be less susceptible to invasion, however, biomes such as temperate forests at higher latitudes will have a less extreme climate and are therefore predicted to experience gains of invasive species (Bellard *et al.*, 2013).

In South Africa, the water hyacinth is currently the most problematic invasive species: it creates dense mats that reduce access to light for submerged plants. New threats are also emerging, such as hydrilla (*Hydrilla verticillata*), which is climatically predicted to thrive in most parts of the country, particularly in eutrophic systems (Coetzee, Hill & Schlange, 2009). *H. verticillata* can grow in complete darkness (Haug, Harris & Richardson, 2019), a trait that increases its competitiveness.

Several studies have reported a geographic range shift of invasive species, for example the invasion of *Ranunculus trichophyllus* into previously non-vegetated, high-elevation Himalayan lakes (Lacoul & Freedman, 2006b), and the northward spread in Europe of the invasive *Elodea canadensis* (Tattersdill, 2017; Heikkinen *et al.*, 2009). Increased temperatures were shown experimentally to favour the spread of *E. canadensis* (Silveira & Thiébaud, 2017), and Netten *et al.* (2010) found that the invasive free-floating *Salvinia natans* benefited from an increased temperature whereas *Elodea nuttallii* decreased in biomass (Table 2). Gilard *et al.* (2017) showed that the invasive ranges of *Egeria densa*, *Myriophyllum aquaticum* and *Ludwigia* spp. may increase up to twofold by 2070, predicting that the climate of Iceland will become suitable for *Egeria densa* and *Myriophyllum aquaticum* under projected future climate conditions (Table 2).

Macrophytes are an important food source for many organisms, and changes in species composition of invasive grazing herbivores such as fish, waterfowl and snails can therefore influence macrophyte communities (Lauridsen, Jeppesen & Østergaard Andersen, 1993; van der Wal *et al.*, 2013; Lei, Chen & Li, 2017). For example, several species of aquatic snail are invasive, including the golden apple snail (*Pomacea canaliculata*) which feeds on aquatic macrophytes (Estebenet & Martin, 2002). This species is among the world's 100 most notorious invasive species (Lowe *et al.*, 2004) and climate change is predicted to facilitate its range expansion (Lei *et al.*, 2017). Herbivorous snails have a strong negative top-down effect on macrophytes, which is amplified by nutrient enrichment (Liu *et al.*, 2020).

Invasive crayfish (Zhang *et al.*, 2020) affect macrophytes by increasing water turbidity, direct consumption and shredding (Lodge & Lorman, 1987; Rodríguez-Villafañe, Becares & Fernández-Aláez, 2003). Crayfish influence macrophyte communities by removing species from the community sequentially, from the most to the least preferred (Carreira, Dias & Rebelo, 2014). Suitable habitat for *Procambarus leniusculus* is predicted to shift poleward and thereby allow its range to increase in North America and Europe, while decreasing in Asia. The suitable climate for *Procambarus clarkii* is predicted to contract in North America and Asia but widen in Europe (Zhang *et al.*, 2020).

VII. FUTURE DIRECTIONS

(1) Distribution, dispersal and threats

Macrophytes play a significant role in freshwater ecosystems and understanding and quantifying the environmental factors that control their distribution is important for implementing management practices. There is a need to establish an overview of potential future threats towards already threatened and endemic species in different regions, and to establish if these species are already present in protected areas, or if further actions are needed. It is important to understand how native and endemic species are dispersed and if their dispersal corridors could benefit the spread of invasive species (Rahel & Olden, 2008). Given the narrow global distribution patterns for the majority of aquatic macrophytes (Murphy *et al.*, 2019), there is a great need for targeted actions to ensure suitable habitat quality for numerous regionally endemic species. To understand how the geographical distribution of aquatic macrophytes has been shaped by evolutionary history, we also need accurate information concerning the phylogenetic relationships among species (Alahuhta *et al.*, 2021).

(2) Limiting the success of invasive species

Once invasive species become established, it can be very difficult and expensive to eradicate them. Humans are often the most important dispersal vector and education of anglers, boaters, people with garden ponds and aquariums, and the general public may be the best way to prevent the future spread of invasive macrophytes in a changing climate (Gillard *et al.*, 2017; Gallardo & Aldridge, 2013). Preventive measures include limiting the trade of invasive and potentially invasive species. SDMs could help us to understand which types of macrophytes need to be specifically targeted (Gillard *et al.*, 2017). Identifying traits in common among highly invasive macrophytes could also help us to predict future invasiveness. The effects of acidification and how invasibility is likely to change in the tropics in response to climate change remain poorly understood and further investigations are needed.

(3) Identifying tipping points

Macrophytes act as bioindicators of environmental change and are therefore sentinels of the current status of freshwater ecosystems (Lacoul & Freedman, 2006a). Macrophytes have a positive feedback on lake ecosystems but we require further studies to establish the tipping points when lake status will change in relation to the projected changes in macrophyte cover and climate change. As lakes cross certain thresholds in warming, light levels and oxygen, rapid changes will likely take place in their macrophyte communities, and we need to understand how simultaneous stressors combine to cause threshold effects.

(4) Ecosystem services

Macrophytes have many direct and indirect effects on lentic ecosystems (van Donk & van de Bund, 2002; Bornette & Puijalon, 2011), but it is still unclear which species are providing the most ecosystem services. Different species can be similar in their functionality and it is important to understand whether richness or functionality represents the most important factor for lake ecosystem status and function. We need to identify key species and species traits in order to make accurate decisions and conduct appropriate management actions.

VIII. CONCLUSIONS

(1) Macrophyte communities are vulnerable to climate change, with the available evidence indicating that many macrophyte species have already exhibited range shifts in response to climate change. Observations from small-scale experiments and inter-annual fluctuations can be difficult to extrapolate to predict long-term changes to macrophyte communities, but we here present an overview based on the data currently available (Fig. 3).

(2) Climate change will have major implications for all freshwater communities. It is predicted that there will be an increase in potential habitats for invasive macrophytes in the northern hemisphere. Native macrophyte communities in northern areas may be threatened by increases in algae cover, but native species richness in these areas is generally low. There are fewer lakes in the southern hemisphere, which is reflected in the number of studies available. However, the majority of endemic species are found in the tropics, and predicted future extreme climates might result in habitat loss in these regions for both native and invasive species. Many specialized endemic species in the southern hemisphere, specifically in shallow lakes, are at risk as climate change is likely to shift the abiotic conditions and thereby habitat suitability for different species. This will result in increased abundance of more opportunistic and generalist species, with changes in climate will favouring productive, disturbance-adapted species with high dispersal ability. Specialized, less disturbance-adapted species are likely to undergo range contractions in response to new biotic and abiotic conditions. For example, macrophyte species in deep, cold-water lakes have a relatively low chance of successful dispersal to another deep cold-water lake. We predict that most macrophyte communities will experience a shift in species composition and abundance as a consequence of climate change.

(3) Geographical shifts in invasive grazers will cause additional pressure on native species, and with increased precipitation and nutrient run-off the effects of herbivorous snails are likely to be amplified.

(4) An increase in invasive species is predicted at high latitudes but not at high altitudes, therefore, lakes at higher altitudes in tropical areas could potentially be a hotspot for future conservation efforts for protecting endemic macrophyte species.

(5) Climate change is likely to challenge the definition of invasive species (Hellmann *et al.*, 2008): some previously non-invasive species might become invasive, while some invasive species may become less so. Native and non-native species will undergo shifts in their geographic distribution and the definition of their natural ranges might have to change. Changes in climate will promote the invasion of exotic species and the current handling of aquatic plants will facilitate this invasion. It is a major challenge to prevent the loss of biodiversity and preventive measures such as education and limiting trade are needed to reduce the impact of invasive species. Climate change is part of that challenge; if species cannot adapt or move to more favourable climates, they will become extinct.

(6) The combination of increase in temperature, CO₂ and nutrient run-off will likely benefit emergent and floating species and negatively affect submerged macrophytes. As climate changes accelerate, algae will dominate lake systems. The speed of these processes will depend on lake depth, size, location, and other anthropogenic pressures. Changes to the macrophyte community might initiate a negative feedback loop that will affect entire lake ecosystems.

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