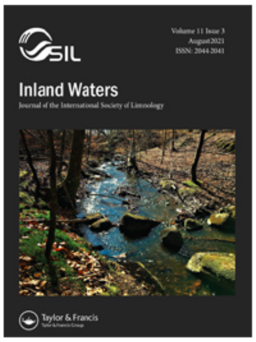

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Feedback between climate change and eutrophication: revisiting the allied attack concept and how to strike back

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ABSTRACT

Despite its well-established negative impacts on society and biodiversity, eutrophication continues to be one of the most pervasive anthropogenic influences along the freshwater to marine continuum. The interaction between eutrophication and climate change, particularly climate warming, was explicitly focused upon a decade ago by Brian Moss and others in "Allied attack: climate change and eutrophication," which called for an integrated response to both problems, given their apparent synergy. In this review, we summarise advances in the theoretical framework and empirical research on this issue and analyse the current understanding of the major drivers and mechanisms by which climate change can enhance eutrophication, and vice versa, with a particular focus on shallow lakes. Climate change can affect nutrient loading through changes at the catchment and landscape levels by affecting hydrological patterns and fire frequency and through temperature effects on nutrient cycling. Biotic communities and their interactions can also be directly and indirectly affected by climate change, leading to an overall weakening of resilience to eutrophication impacts. Increasing empirical evidence now indicates several mechanisms by which eutrophying aquatic systems can increasingly act as important sources of greenhouse gases to the atmosphere, particularly methane. We also highlight potential feedback among eutrophication, cyanobacterial blooms, and climate change. Facing both challenges simultaneously is more pressing than ever. Meaningful and strong measures at the landscape and waterbody levels are therefore required if we are to ensure ecosystem resilience and safe water supply, conserve biodiversity, and decrease the carbon footprint of freshwaters.

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Introduction

The Anthropocene, planetary boundaries, and catastrophic shifts, among other concepts, are increasingly prominent and debated in the scientific literature. These concepts, including the connection between ecosystem and human health, are also becoming relatively frequent in the speeches of managers, policy makers, and politicians, yet most long-standing environmental problems remain largely unresolved.

Several large and often nutrient-poor lakes in temperate and cold regions are showing temporal declines in phosphorus (P) concentration and/or phytoplankton biomass (e.g., Kraemer et al. 2017, Huser et al. 2018). Different restoration efforts at the waterbody or watershed levels are delivering positive results in Europe and Asia (e.g., Jeppesen et al. 2012, Liu et al. 2018). Despite these positive trends, eutrophication continues to be one of the most pervasive anthropogenic impacts

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along the freshwater to marine continuum (Wurtsbaugh et al. 2019). Water quality has deteriorated, and blooms of toxic cyanobacteria, hypoxia, and finfish and shellfish kills are becoming more frequent in many regions of the world. As a result, the contributions of lakes and rivers to human wellbeing are dwindling across the globe regardless of the country's economic status and degree of development.

Climate change, a highly asymmetric but planetary phenomenon, already impacts many ecosystems and human livelihoods around the world (IPCC 2021). In addition to the most commonly described effects of changes in temperature and precipitation patterns, the anticipated change in frequency and intensity of extreme events (heatwaves, storms, extreme rains, and droughts) may also affect ecosystem stability (García-Palacios et al. 2018) and resilience (Pimm et al. 2019) in yet unpredicted ways. The natural self-repairing capacity of ecosystems (or resilience; sensu Folke 2016) may thus weaken, with consequent increases in ecosystem sensitivity to other external stressors, such as elevated nutrient loading from increasing anthropogenic land use (e.g., Paerl et al. 2019).

The interaction between eutrophication and its symptoms with climate change, particularly climate warming, was the focus of the paper by Moss et al. (2011), "Allied attack: climate change and eutrophication," which called for an integrated response to both problems, given their synergy.

Here we review the status and advances on this topic given the different avenues of research in the first decade since the publication of Moss et al. (2011). Although the processes described can apply to any freshwater system, most of the examples refer to shallow lakes. Theoretical and empirical studies have consolidated previously described patterns, confirmed some expectations, and shed light on the complexity of several processes involved in the linkage between eutrophication and climate change. Growing empirical evidence suggests that facing both challenges simultaneously is more pressing than ever but, also, that current measures are not enough.

Theoretical advances potentially relevant for management and policy

The existence of feedback between eutrophication and its symptoms and climate warming has profound implications for the appropriate management of freshwater systems and waterscapes. In addition, the existence and correct identification of dynamic regime shifts around potential tipping points or thresholds is important in management and policy making. Although tipping points have been described for deep lakes in some circumstances (Bruel et al. 2018), thresholds and tipping points have been more intensively studied in shallow lakes.

In shallow lakes, the nutrient thresholds modulating a shift from a clear water to a turbid water state, and for the reverse shift to occur, have been the subject of intensive research and debate, given the diverse effects of climate and other external and internal drivers (e.g., Jeppesen et al. 2007, Scheffer and van Nes 2007). Determining such thresholds for a given region and particular waterbody before the shift has occurred has proved extremely difficult, if not impossible. The challenge increases because not all regime shifts are associated with tipping points (Dakos et al. 2015).

Work focused on early warning signals of regime shifts has flourished in the last decade (Scheffer et al. 2009, Wang et al. 2012, Dakos et al. 2015), as has research aimed at quantifying and measuring ecosystem resilience and stability (Donohue et al. 2016, Pimm et al. 2019). Also in the last decade, the idea of feedback and thresholds for a system to experience a shift or critical transition has upscaled from individual ecosystems (Scheffer et al. 1993, Folke 2016) to the planet itself (Steffen et al. 2018). In particular, the existence of planetary boundaries, and of a safe operating space for humanity and for particular ecosystems, has been the subject of research in the past few years (Rockström et al. 2009, Green et al. 2017). However, these ideas, among other issues, have sparked intense debate and controversy (Montoya et al. 2018, Hillebrand et al. 2020) because of difficulties in identifying those boundaries and translating them into concrete management recommendations.

Empirical advances: climate change enhances eutrophication and its symptoms

In the last decade, mounting empirical evidence has documented temporal changes in phytoplankton biomass (using chlorophyll *a* as proxy), largely using remote sensing techniques, particularly applied to large lakes. Opposite trends have also been documented (Kraemer et al. 2017, Ho et al. 2019), sparking debate on the reliability of different methodologies (e.g., Feng et al. 2021). Some temporal trends do not relate consistently with trends in temperature, precipitation, or fertilizer use (Ho et al. 2019), whereas a combination of positive and negative trends for individual lakes stresses the heterogeneity of lake responses to global change.

Many empirical studies based on either in situ measurements or paleolimnogical approaches have supported the idea that climate change is promoting both eutrophication and many of its symptoms (e.g., Beaulieu et al. 2013, Taranu et al. 2015). Such enhancement is the result of a variety of processes occurring at different spatial and temporal scales (Fig. 1) and biological levels of organization, from the catchment to the waterbody and from ecosystem-scale biogeochemical cycles to food webs, and life history traits of particular species or genotypes. This review describes some of the main expectations from a large to small spatial and ecological scales (Fig. 1).

The watershed level

Human-induced external nutrient loading of surface waters is the key driver of eutrophication. Even under constant anthropogenic practices such as land use, several components of climate change tend to increase eutrophication through direct and indirect mechanisms that have become clearer in the last decade.

Climate change involves changes in precipitation patterns, temperature, wind speed, both in magnitude (means and extreme values) and in the frequency and duration of extreme events. The external nutrient loading entering inland and coastal systems will depend on changes in the regional and local climate as well as future changes in land use governed by future climate, population, and policies.

Major changes in precipitation patterns and amounts are expected worldwide (IPCC 2021). Net precipitation is expected to increase in vast regions of the world but to decrease over parts of the subtropics, limited areas of the tropics, and the Mediterranean (IPCC 2021). With decreased precipitation, despite the resulting reduction in runoff and potentially lower net loads of nutrients, water nutrient concentrations may remain high because a more prolonged residence time can enhance sediment–water column exchange and internal nutrient cycling (Özen et al. 2010). In arid and semiarid climates, climate warming also enhances drought through higher evaporation and evapotranspiration rates (Trenberth et al. 2014, IPCC 2021), with strong implications for water level and salinity in lakes (Beklioğlu et al. 2011, Yılmaz et al. 2021). If prolonged or extreme, drought can transform permanent lakes and ponds into more transient systems (Beklioğlu et al. 2007) or they may disappear altogether. Even if the waterbodies remain permanent, they may become saline to different degrees, with negative effects on aquatic diversity (Brucet et al. 2012) and trophic web structure and functioning (Vidal et al. 2021, Yılmaz et al. 2021). This process may be accelerated when water extraction is increased by enhanced bank filtration for drinking water production and irrigation (Gillefalk et al. 2019, Yılmaz et al. 2021).

By contrast, higher net precipitation is expected in large areas in the north temperate zone, particularly during winter and in several locations of the Southern Hemisphere subtropical zones, while in many places storms are also expected to intensify in frequency and magnitude (IPCC 2021). In such cases, higher net precipitation and more intense precipitation events enhance runoff of sediments, dissolved organic carbon, nutrients, and other substances from the catchments to the waterbodies, particularly in catchments with intense land uses (Paerl et al. 2020). Such increases in external loading may or may not rapidly translate into higher nutrient concentrations in the lakes, depending on their size, flushing rates, water level fluctuations, and sediment characteristics, among others.

Climate change effects act on top of impacts from agricultural land use, often in additive and/or synergistic ways. Through various research approaches, we can now predict that a significant enhancement in diffuse nutrient loadings of P (Jeppesen et al. 2009, Goyenola et al. 2015, Ockenden et al. 2017), nitrogen (N; Jeppesen et al. 2011, Goyenola et al. 2020), and organic matter (Graeber et al. 2015) can be expected from agricultural catchments in areas with increasing precipitation driven by climate change. Obviously, the nutrient legacy in the soils, resulting from historical land use, is a key factor determining the levels of nutrients reaching surface waters (Goyenola et al. 2020). An increase up to 30% of average winter P loads at present-day land use is predicted to occur in temperate rain-fed watersheds by 2050 because of future changes in precipitation (Ockenden et al. 2017).

However, and although this topic needs further investigation, it is unlikely that land use will remain unchanged. Water-demanding, fast-growing crops are expected to increase in locations where precipitation is already increasing or expected to increase in coming years (Olesen et al. 2007). In places where access to water will be limited or more variable in time and space, the selection of drought-resistant crops or crop variants, as well as agricultural practices, is expected, although the reverse pattern (i.e., more water demanding crops fed by irrigation) has unfortunately also been seen in recent decades (Yılmaz et al. 2021). By contrast, climate change mitigation policies, such as land use changes toward reforestation or even afforestation, may eventually lead to improved water quality (Daneshmand et al. 2020), depending on local conditions.

One concern that has emerged in recent years is that the combined effect of changes in precipitation patterns, particularly increased droughts, and climate warming coupled to land use changes have led to an increase in the number and intensity of fires in many places around

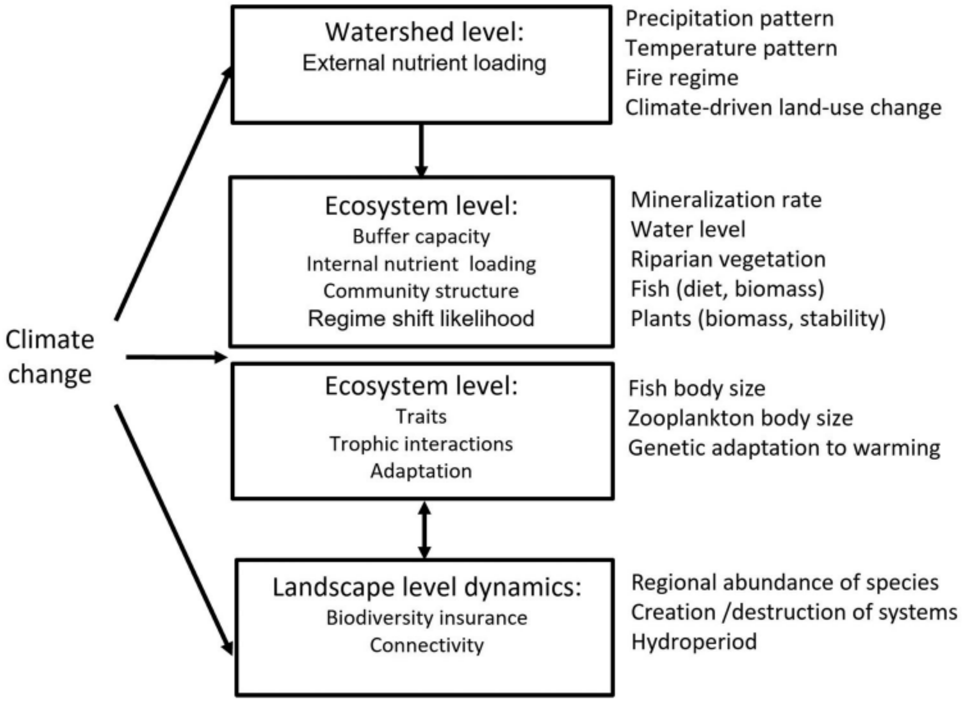

Figure 1. Summary of some of the main climate change-related drivers acting at different spatial and ecological levels that can directly or indirectly promote eutrophication and its symptoms. For each level, direct and indirect changes promoted by climate change are shown inside panels, while some of main system responses enhancing eutrophication and/or its symptoms are shown on the right side.

the world (Stevens-Rumann et al. 2018), impacting fresh waters. One of the multiple effects of fires is the high ash load (Earl and Blinn 2003), which can increase water pH, turbidity, total organic carbon (TOC), and nutrient concentrations as well as reduce dissolved oxygen concentrations (Earl and Blinn 2003, Cerrato et al. 2016). The overall effects differ regionally. The ash and post-fire erosion-related increase in nutrient loading leads to increased primary production (Planas et al. 2000), thus contributing to eutrophication (Fig. 1). Increased fires are assumed to contribute to the increasing occurrence of filamentous algae blooms in the littoral of lakes, even in remote areas (Vadeboncoeur et al. 2021).

The ecosystem level

A decade ago, it was generally accepted that warming may increase in-lake nutrient concentrations through enhanced microbially mediated internal cycling, thereby directly promoting eutrophication (Jeppesen et al. 2009). Warming-induced anoxia events following higher organic matter decomposition and stronger stratification of the water column will also boost sediment release of stored P and N (Søndergaard et al. 2003, 2013).

Now also becoming clear is that the natural shield of lakes and their tributaries, represented by riparian zones (Naiman and Decamps 1997, Vidon et al. 2010), can also be affected by climate change. Owing to their topographic position in the landscape, riparian zones are generally highly exposed to extreme climatic events, such as floods and droughts, which are expected to increase in frequency and intensity in many regions because of climate change (Capon et al. 2013, Paerl et al. 2019). These changes may pose a risk of a decreased buffering capacity to retain, transform, or decrease nutrients before they reach the water (Capon et al. 2013, Pinay et al. 2018).

Both fish and macrophyte communities, key players for pond and shallow lake functioning, can be directly and indirectly affected by climate change, in particular by warming, as identified in Moss et al. (2011). Changes in both communities can promote several cascading effects and, if strong enough, promote ecosystem regime shifts with different effects on ecosystem contributions to societies (Hilt et al. 2017, Janssen et al. 2021).

Significant changes in fish communities are expected with climate warming, due to both direct and indirect effects as observed by different approaches, such as heating experiments, long-term monitoring, time series analyses, and space-for-time substitution (summarized in Jeppesen et al. 2014). One issue that emerged more clearly with the research conducted in the last decade is that fish diet often changes with increasing temperature. At the community level, a decrease in carnivory (i.e., with omnivorous and herbivorous species becoming more abundant and even dominant) within fish communities occurs at lower latitudes and in warmer climates (González-Bergonzoni et al. 2012). A change in diet toward more herbivory with increasing water temperature has been observed at individual, population, and community levels (González-Bergonzoni et al. 2016) following intraannual variations. Food webs in tropical and subtropical lakes are thus more truncated than food webs in similar temperate shallow lakes, as found in comparative studies (Iglesias et al. 2017). Different indicators of fish predation suggest a stronger effect of fish on prey communities such as zooplankton under warmer climates (Meerhoff et al. 2012). Stronger fish predation on macroinvertebrates is also expected with warming (Clemente et al. 2019). Via cascading effects, fish may therefore enhance the growth of phytoplankton and of epiphytic periphyton, thus negatively affecting submerged plants. Top-down–mediated elevated phytoplankton biomass in warmer climates has been observed in many empirical studies along latitudinal gradients or cross-comparisons (Gyllström et al. 2005, Meerhoff et al. 2012), patterns further substantiated with comparisons involving a huge number of lakes (Jeppesen et al. 2020). Experimental results suggest that linear top-down effects may be weaker with warming in cases where fish omnivory (understood as feeding on animal and plant items) is important (He et al. 2021). Changes in precipitation patterns, although much less studied than changes in temperature, may also provoke large changes in lake and pond communities and food webs (Ledger et al. 2013, Romero et al. 2020). Variations in the quantity and evenness of rainfall, resulting in localized droughts or flooding, can potentially erode the base of freshwater food webs, with negative implications for the stability of trophic dynamics (Romero et al. 2020).

Climate warming is also expected to affect macrophytes in many direct and indirect ways. Warming may stimulate macrophyte growth in lakes with ambient temperatures currently below the optimum temperatures for macrophytes (Zhang et al. 2019, Lauridsen et al. 2020). This increase in growth can potentially overcompensate warming-enhanced herbivory (Bakker et al. 2016, Calvo et al. 2019). Warming can also lead to a prolonged macrophyte growing season (Netten et al. 2011), advanced phenology, and/or higher abundance (Velthuis et al. 2018) as well as shifts in species composition and flowering (Li et al. 2017), vegetation type (Peeters et al. 2013), and plant stoichiometry (Velthuis et al. 2017). However, some heating experiments have instead shown a higher risk of a shift from submerged plants to dominance by free-floating plants (Netten et al. 2010) or filamentous algae (Trochine et al. 2011). The future role of submerged macrophytes for maintaining clear water conditions (Scheffer et al. 1993) is unclear but will likely diminish in many systems, as stated in Moss et al. (2011). In addition to negative direct effects, loss of submerged macrophytes can result in indirect negative effects of warming on other communities that can suppress their periphyton and phytoplankton competitors, such as grazer macroinvertebrates (Brucet et al. 2012, Clemente et al. 2019) and zooplankton (Meerhoff et al. 2007a, Havens et al. 2009). Warming may also promote phytoplankton and periphyton growth (Mahdy et al. 2015, Kazanjian et al. 2018) and thereby increase the susceptibility of macrophytes to herbivory (Hidding et al. 2016).

Low water levels due to more frequent or intense drought can lead to increased growth of submerged plants (Bakker and Hilt 2016, Ersoy et al. 2020). However, extreme reductions in water level may lead to submerged macrophyte collapse and substitution by other primary producers, such as floating plants (Moi et al. 2021).

Sudden increases in water turbidity can occur because of the more frequent extreme climatic events (Crisci et al. 2017), including storm-driven particulate and dissolved organic matter loss and transport from watersheds to receiving waterbodies (Brothers et al. 2014). As with macrophytes, turbidity pulses might affect trophic interactions, often more than the increases in temperature (Figueiredo et al. 2019). Moreover, the ash of climate change-enhanced fires has been found to negatively impact zooplankton (Harper et al. 2019) and fish (Silva et al. 2020) in addition to exerting toxic effects on some algae and macrophytes (Silva et al. 2015). Thus, the increase in fires may be yet another way that climate change leads to enhanced eutrophication and may potentially induce regime shifts from the clear-water to the turbid or free-floating plant-dominated regimes.

Trait change in response to climate and eutrophication effects

Earlier we focused on changes in ecosystem rates and biomasses linked to climate change and eutrophication. In addition to changes in biomass, however, the trait values of communities in food webs may also substantially change because of climate warming, as evidenced in recent research. This change can be achieved both through changes in species composition and changes in trait values of the different species within a community. The latter intraspecific variation has multiple components: ontogenetic change (linked to changes in age distribution), phenotypic plasticity (direct response of individuals to higher temperatures), and genetic change (i.e., due to evolution; Govaert et al. 2016).

A classic example involves the change in body size of fish communities resulting from increasing water temperature (Daufresne et al. 2009, Teixeira-de Mello et al. 2009, Jeppesen et al. 2010, Brucet et al. 2013). Although not all fish species show a consistent response to climate (Jeppesen et al. 2010), a smaller mean body size of adult fishes in warmer climates has been confirmed in a comprehensive analysis of a large database along climatic gradients (latitudinal, altitudinal, and water depth) in 356 European lakes (Emmrich et al. 2014). The mechanisms behind a reduction in fish body size with warming, whether direct (physiology driven) or indirect (via trophic web interactions) are the subject of debate (Lefevre et al. 2017). In general, low latitude species also grow faster, mature earlier, have shorter life spans, and reproduce more frequently than high altitude species (reviewed in Meerhoff et al. 2012). A reduction in body size in warmer waters has also been observed for zooplankton, both mediated through changes in species composition (Gianuca et al. 2018) as well as through genetic change (Geerts et al. 2015, Brans et al. 2017). Such changes enhance the positive interaction between climate change and eutrophication, given that smaller zooplankton generally are less efficient grazers than larger-bodied zooplankton (Fig. 2).

Genetic adaptation, however, may also contribute to reduced probability of adverse effects of warming. Van Doorslaer et al. (2009), for instance, provided experimental evidence that an evolutionary trait change upon warming can enhance the capacity of local zooplankton populations to reduce invasion success of pre-adapted immigrants from warmer regions.

From ecosystem back to catchments: landscape-level dynamics

Since the early 2000s, and particularly in the last decade, population persistence, community dynamics, biodiversity, and their impacts on ecosystem functioning have been the focus of empirical and theoretical studies, recognizing their links to the position of a given system in the landscape and the potential connectivity with other systems (Loreau et al. 2003, Leibold et al. 2004, Heino et al. 2015, Thompson et al. 2020). Biodiversity is strongly affected by species dispersal and information fluxes, and ecosystem dynamics are largely determined by the flow of matter and substances among systems (Heino et al. 2021). Connectedness in heterogeneous landscapes can increase local biodiversity and resilience through a spatial insurance effect (Loreau et al. 2003). A recent study by Horváth et al. (2019) showed, through a longitudinal study across more than 50 years, that the disappearance of soda pans at the regional level resulted in a concurrent decline in average local diversity in the remaining pans following the gradual disappearance of less common species. Effective connectedness is indeed not only a function of geographic distances among lakes and ponds, but also of the regional abundance of species, as fewer abundant species occupy fewer available patches. Conversely, high connectedness can under some circumstances also be detrimental to diversity (Scheffer et al. 2012) because anthropogenic disturbances (pollution, exotic species, fire, eutrophication) may affect more systems simultaneously when they are better connected.

Connectivity can be affected by climate change in a myriad of ways. Warming and reduced precipitation can result in the disappearance of ponds and shallow lakes in certain areas, or in a modification of hydroperiod leading to a change in lake type (permanent vs. temporary), resulting in a decrease in local and regional diversity (Horváth et al. 2019). Human interventions to mitigate climate change effects may increase drought stress (e.g., irrigation for agriculture), counteract it (e.g., restoration measures), or substantially change the nature of ponds (e.g., by making temporary ponds deeper and more permanent), depending on the situation. An increase in local water storage capacity (by digging ponds and most frequently by impounding and fragmenting low-order streams and wetlands) is a strategy both farmers and policy makers will likely pursue under the predictions of lower or uncertain water availability. Such strategies are already implemented in several areas fearing future water shortages.

Empirical advances: eutrophication and its symptoms enhance climate change

Moss et al. (2011) hypothesized that eutrophication could promote climate change, but the possibility was still largely an open question. In the past decade, much evidence has accumulated indicating that several manifestations of eutrophication enhance climate change (see review in Li et al. 2021), thus supporting the idea of self-reinforcing feedback between both processes (Fig. 3).

Lake greenhouse gas (GHG) emissions are affected by several external drivers, including changes in temperature (Kosten et al. 2010, Aben et al. 2017) and hydrology (Kosten et al. 2018, Keller et al. 2020). Temperature can be a major driver of GHG emissions. In experiments conducted along a latitudinal gradient in Europe, a decline in net ecosystem production was found, from positive in the colder lakes, implying a net capture of

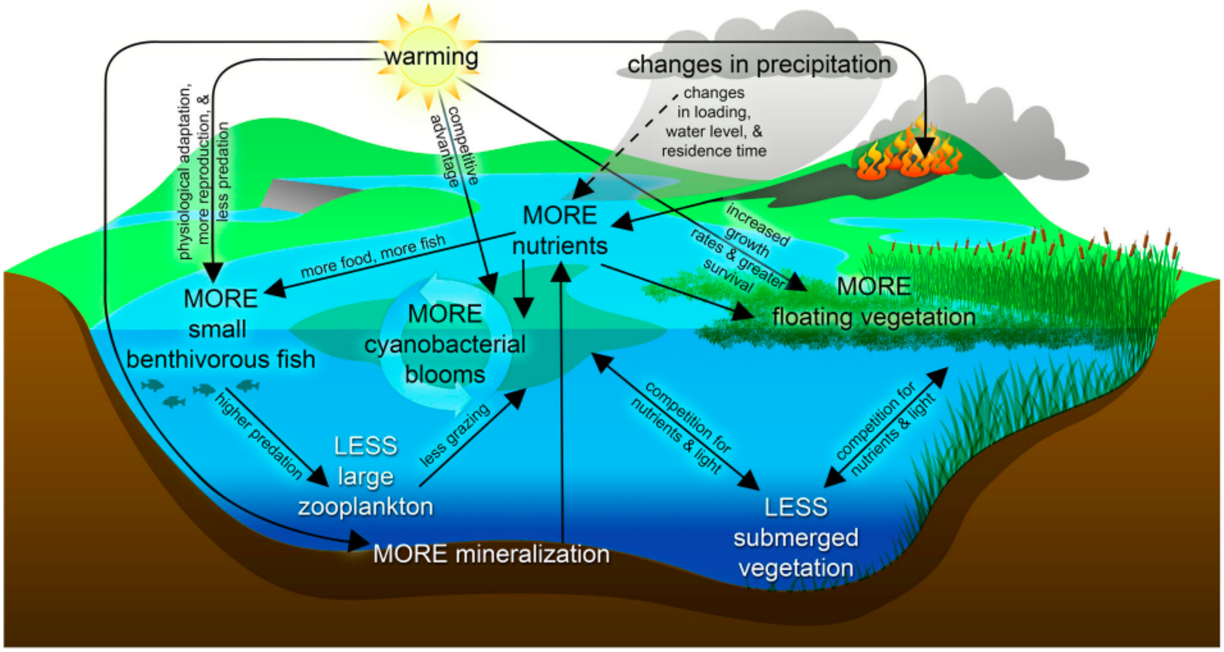

Figure 2. Schematic view of main feedback effects of climate change on eutrophication and its symptoms. Dashed line indicates that changes in precipitation regimes may either lead to higher or lower nutrient and organic carbon loading, depending on local and regional circumstances. Warming intensifies water stratification and nutrient mineralization and directly or indirectly promotes several biological changes, leading to a higher likelihood of free-floating plant and phytoplankton dominance. The resilience against eutrophication is consequently reduced with climate warming, and the likelihood of cyanobacteria blooms, which are self-perpetuating regimes under eutrophic conditions, increases. The resilience of an individual waterbody also depends on landscape processes, including other anthropogenic impacts, such as fragmentation, climate change-promoted fires, and the potential connectivity with other freshwaters. Drawing by Alan R. Joyner, based on Fig. 1 in Moss et al. (2011). Copyright © International Society of Limnology, with permission of Taylor & Francis Ltd.

carbon dioxide (CO_2), to negative, implying a net release of CO_2, in the warmer southern lakes, regardless of nutrient levels (Scharfenberger et al. 2019). The net flux of CO_2 under a eutrophic and warmer scenario seems to depend on regional climate as well as on local abiotic characteristics (Kosten et al. 2010). Changes in hydrology due to changes in precipitation and evaporation patterns may lead to changes in stratification patterns and trophic state and, ultimately, in GHG emissions (Fig. 3). For example, in regions with higher precipitation and consequent higher runoff from catchments to waterbodies, water browning, anoxia, and eutrophication interact, leading to higher CO_2 and methane (CH_4) emissions (Brothers et al. 2014, DelSontro et al. 2018).

Despite the growing evidence of its relevance, eutrophication-induced emissions from natural or artificial lakes and ponds are not included in national GHG inventories or in the Intergovernmental Panel on Climate Change (IPCC) guidelines. This gap is crucial because lakes and ponds are large sources of CH_4 at the global scale. Global estimated emissions from natural lakes and ponds oscillate around 0.012 Pg C yr^{-1} (25–75th percentiles: 0.006–0.015 Pg C yr^{-1}) for only CH_4 diffusive flux (Holgerson and Raymond 2016). Calculated mean annual fluxes for individual artificial ponds vary between 0.1–44.3 g CH_4 m^{-2} yr^{-1} and −36 to 1138 g CO_2 m^{-2} yr^{-1} (Peacock et al. 2021). In addition, a recent synthesis suggests that GHG fluxes vary inversely with lake size, with ∼37% of total lentic CH_4 emissions (diffusive + ebullitive) deriving from systems <0.1 ha (Rosentreter et al. 2021). Growing evidence indicates that CH_4 emissions tend to be increased by eutrophication and climate warming (Davidson et al. 2015, Deemer et al. 2016, Davidson et al. 2018, DelSontro et al. 2018, Sepulveda-Jauregui et al. 2018, Beaulieu et al. 2019). Water chlorophyll *a* or total P concentrations, 2 clear proxies of eutrophication, can often explain CH_4 emissions from lakes and reservoirs (Deemer et al. 2016, DelSontro et al. 2018, Beaulieu et al. 2019). The mechanisms responsible for the increased CH_4 emissions in eutrophic ecosystems are, however, not fully resolved. Under eutrophic conditions, more abundant and more labile organic matter supplies seem to fuel methanogenesis. At the same time, the potential for CH_4 oxidation decreases because

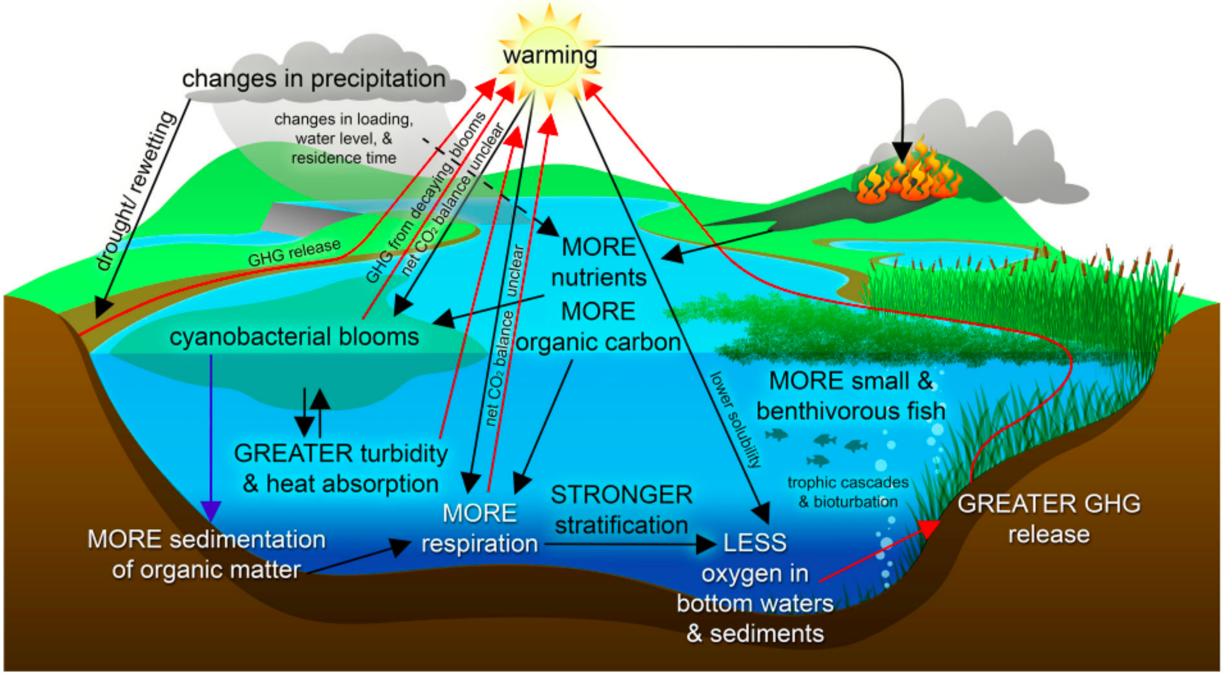

Figure 3. Current understanding of main feedback effects of eutrophication on climate change. The blue arrow indicates carbon sequestration; red arrows indicate carbon emission routes; black arrows indicate other type of effects. The dashed line indicates that changes in precipitation regimes may either lead to higher or lower nutrient and organic carbon loading, depending on local and regional circumstances. Warming and eutrophication intensify water stratification and reduce oxygen concentrations. Direct and indirect changes in biotic interactions under eutrophic conditions promote cyanobacteria dominance, which has its own feedback with climate change. Warming and eutrophication may increase both CO_2 uptake and release, and thus net CO_2 balance is unclear, whereas potential effects on other GHG, particularly CH_4, are evident. Strong fluctuations in water level due to changes in precipitation may lead to cycles of drying–rewetting of sediments, promoting CO_2 release. GHG are produced and released by diffusion across different lake compartments, and CH_4 also by ebullition (bubbles). The role on GHG emissions of key communities, such as macrophytes, fish, and macroinvertebrates, is the subject of intense research. Drawing by Alan R. Joyner, based on Fig. 2 in Moss et al. (2011). Copyright © International Society of Limnology, with permission of Taylor & Francis Ltd.

oxygen is frequently lacking (Zhou et al. 2019). A productive environment, combined with the enhanced metabolic activities caused by higher temperatures (Yvon-Durocher et al. 2010), results in a disproportionate increase in CH_4 emissions (Davidson et al. 2018). Particularly, bubble-mediated emissions increase under eutrophic and warming conditions, transporting CH_4 produced in the sediment directly to the atmosphere with little opportunity for methanotrophic bacteria to transform some of that CH_4 to CO_2 (Fig. 3). Current and expected reduced wind speed in many parts of the world (atmospheric stilling; Mölter et al. 2016) will accelerate lake thermal responses to warming and lengthen stratification (Woolway et al. 2019), further enhancing the risk of having low oxygen concentrations at the sediment surface in shallow lakes (Deng et al. 2018) and thus enhancing the risk of higher CH_4 emissions.

The alternative dominance by phytoplankton, submerged plants, and free-floating vegetation, likely growing under eutrophic conditions, can promote contrasting patterns in CO_2 and other GHG fluxes (Davidson et al. 2015, Almeida et al. 2016, Jeppesen et al. 2016, Audet et al. 2017). While all primary producers take up CO_2 through photosynthesis and release CO_2 through respiration, the effects on CH_4 and N_2O dynamics may differ among phytoplankton and submerged, free-floating, or emergent macrophytes. In the tropics, areas of floodplain lakes dominated by free-floating plants can act as net CO_2 sinks during all seasons because of carbon fixation by plants, whereas open waters generally emit CO_2 following hydrological changes (Peixoto et al. 2016). Macrophytes that root in the sediment may oxygenate the sediment, thereby potentially increasing consumption and decreasing CH_4 production, overall resulting in a decrease in CH_4 emissions (Davidson et al. 2015, 2018). A counteracting effect, however, is that rooted plants with emergent parts (i.e., either emergent macrophytes, or submerged macrophytes with emergent leaves and flowers) may also transport CH_4 from the sediments to the atmosphere, bypassing water column CH_4 oxygenation. In this way, rooted plants may increase CH_4 emissions

(Oliveira Junior et al. 2019). The overall effects of aquatic plants on CH_4 emissions are therefore considerably variable (Kosten et al. 2016, Hilt et al. 2017) and likely depend on species traits and environmental conditions. Overall, however, current evidence suggests that abundant submerged plants may decrease CO_2 efflux (Jeppesen et al. 2016) and tend to decrease CH_4 emissions (Colina et al. 2021b). Plant effects on oxygen conditions in the sediment and in the water column not only affect CH_4 processes, but also the N cycle (Veraart et al. 2011), thereby potentially impacting nitrous oxide (N_2O) emissions. By contrast, phytoplankton blooms have been related to uptake of CO_2 (Jeppesen et al. 2016) but also to high N_2O (Wang et al. 2006) and high GHG emissions in general during the decomposition of decaying blooms of cyanobacteria (Yan et al. 2017).

Different food web configurations, often associated with the alternative regimes in shallow lakes and ponds, may also promote different GHG release patterns. A field of active research currently aims to elucidate the role of trophic interactions, particularly the role of fish trophic and behavioural effects on GHG dynamics (Devlin et al. 2015, Oliveira Junior et al. 2019, Colina et al. 2021a). Under certain conditions, fish predation on zooplankton may indirectly promote CH_4-oxidizing bacteria and thus decrease CH_4 diffusive emissions (Devlin et al. 2015). Benthic fish, whose numbers and biomass typically increase with eutrophication, may promote contrasting processes. Benthivores may either reduce CH_4 emissions because of higher oxygen availability in the sediments through bioturbation (Oliveira Junior et al. 2019) or, by contrast, increase CH_4 production through negative top-down effects on bio-irrigating benthic macroinvertebrates (Colina et al. 2021a).

This review highlights that general patterns are difficult to distill because individual lake emissions are, to a large degree, the result of local morphometric, hydrological, and catchment characteristics, including land uses that affect inputs of dissolved organic matter and suspended sediments, and of dissolved GHGs (Weyhenmeyer et al. 2015). As hotspots for biogeochemical processes, lakes and ponds suffer from the ills of the catchments, both in terms of ecological conditions due to eutrophication but also in terms of potential feedback to climate change.

Eutrophication and climate warming synergy and feedback through cyanobacteria

Despite opposite trends that may be expected in nutrient-poor lakes (e.g., Kraemer et al. 2017), under warmer climate and eutrophic conditions a higher biomass of phytoplankton and dominance by potentially toxic cyanobacteria is expected. This finding is consistent with results emerging from numerous recent studies (Paerl and Huisman 2008, Kosten et al. 2012, Paerl and Paul 2012, Jeppesen et al. 2014, Huisman et al. 2018, Burford et al. 2020) and research approaches such as modelling for individual temperate lakes and basins (Trolle et al. 2011, Kakouei et al. 2021), heating experiments (Hansson et al. 2013; but see Feuchtmayr et al. 2009 and Kratina et al. 2012), and latitudinal gradient and cross-comparative studies (Kosten et al. 2012, Meerhoff et al. 2012). Long-term increases in water temperature have translated to an acceleration in cyanobacterial dominance, as detected in sediment records (Taranu et al. 2015). Cyanobacterial biomass is even increasing in northern nutrient-poor lakes with increases in mean temperature, earlier ice-out, and later ice-on experienced in the last decade (Freeman et al. 2020). Long-term monitoring of phytoplankton composition (along a 25-year period) indicated that climatic changes, including warming and a decrease in long-term wind speed, combined with high N and P loads, were important interactive drivers of changes in phytoplankton community structure and bloom dynamics in eutrophic Lake Taihu in China (Deng et al. 2018, Guo et al. 2019, Paerl et al. 2020). Heat waves also seem to promote cyanobacterial blooms (Jöhnk et al. 2008, Wagner and Adrian 2009, Bartosiewicz et al. 2019).

The interaction of warming and eutrophication may strongly affect other key aspects of blooms. Experiments combining warming with nutrient pulses found higher microcystin concentrations in the combined treatment than under warming alone (Lürling et al. 2018). A strong latitudinal gradient analysis in Europe has shown that direct and indirect effects of temperature are the main drivers of the spatial distribution in the toxins produced by cyanobacteria, both in terms of their diversity and their concentrations (Mantzouki et al. 2018). With climate warming, the direct and indirect effects of increased lake temperatures will likely drive changes in cyanobacterial taxa and their production of cyanobacterial toxins, likely including promoting the selection of a few *Microcystis* species or strains producing highly toxic microcystin-LR (Mantzouki et al. 2018). Despite variations among lakes in a waterscape, a regional increase in microcystin maxima and duration of blooms has also been clearly explained by increasing temperature in central North America (Hayes et al. 2020), with increasing risks to human health.

Growing evidence indicates that cyanobacterial dominance will exert a positive feedback with climate warming (Havens et al. 2016, Paerl et al. 2020). Many cyanobacterial species proliferate on the lake surface, absorbing light, enhancing localized temperature increases, and increasing thermal stratification potential (Kahru et al. 1993). Cyanobacteria promote the release of GHGs, particularly CH_4 (Yan et al. 2017), during the decomposition following the collapse of a bloom. Cyanobacteria also promote remineralization of nutrients during blooms, leading to multiple blooms in a single season. Under eutrophic and warming conditions, cyanobacteria dominance may thus be a self-perpetuating prophecy (Fig. 2 and 3).

Advances in mitigation and adaptation policies

Advances in research and understanding the feedback between eutrophication and climate change, however, have not translated into significant advances in management actions. Despite the current recognition of the integral role lakes and ponds play in GHG emissions (Rosentreter et al. 2021), they are typically not included in national GHG inventories. We call for their inclusion bcause it would contribute to reducing GHG emissions and lead to efforts to promote biodiversity conservation and restoration measures in ponds and lakes. We also call for decision making strategies that build natural resilience, as illustrated for some iconic ecosystems (Scheffer et al. 2015), particularly wetlands (Green et al. 2017).

The best approaches for mitigating the effects of human activity on lake phytoplankton and cyanobacteria depend strongly on lake sensitivity to long-term change and the magnitude of projected climate changes and land use at a given location (Kakouei et al. 2021). Although climate warming may promote eutrophication and its symptoms, eutrophication is still largely human-controlled. The application of appropriate management measures should lead to a reduction in nutrients, despite increasing air temperatures. In the case of lakes and ponds, measures should aim to decrease nutrient exports from the catchments, minimize eutrophication symptoms, and simultaneously protect and/or recover resilient mechanisms at the ecosystem and landscape level, such as the natural hydrological patterns (Fig. 4), buffer zones, and existing landscape connectivity with other waterbodies. Monitoring and restorating lake biodiversity and ecosystem services should also consider that, in addition to individual responses of a given lake or pond, a high degree of dynamism occurs at local, regional, and global spatial scales (Heino et al. 2021). Connected and heterogeneous landscapes allow metacommunity dynamics to build biodiversity resilience against future disturbances driven by climate change, such as fires (Cunillera-Montcusí et al. 2021).

Measures to reduce point sources of nutrients are well known (Moss 1990, Moss et al. 1996, Hamilton et al. 2016), yet in many locations around the globe, sanitation, proper sewage treatment, and disposal of black and grey waters from cities and industries (including confined animal operations) are lacking or largely insufficient. A global decrease in nutrient discharge is only possible when wastewater treatment plants are extended with at least tertiary treatment.

By contrast, measures to reduce diffuse nutrient input are more difficult because they need to be implemented at the catchment level and therefore may require action of many stakeholders (Hamilton et al. 2016). To illustrate the problem, based on a complex combination of models, Ockenden et al. (2017) suggested that the effects of climate change on surface runoff and consequent increase in diffuse P loading to freshwaters might be limited only by large-scale agricultural changes (e.g., 20–80% reduction in current levels of P inputs). Beaulieu et al. (2013) models indicated that under a scenario of atmospheric CO_2 doubling from 1990 levels (resulting in an estimated 3.3 °C increase in surface water), a doubling of cyanobacteria biomass could be expected. Future nutrient loadings should thus be seriously decreased, also considering that a series of reinforcing feedbacks may occur under cyanobacterial dominance, decreasing the nutrient threshold theoretically needed to recover clear water conditions, as also suggested by recent models that incorporate cyanobacteria traits (Chang et al. 2020).

Measures to reduce both N and P loading, particularly in priority catchments (in terms of human uses, such as drinking water sources, or in terms of biodiversity and cultural values), may include (1) promotion of organic or agroecological production of food and feed instead of conventional, chemically based agriculture; (2) formulation and application of fertilisers as determined by crop needs and soil retention capacity as well as weather and climate forecast; (3) improvement of agricultural practices, including minimizing chanelisation to reduce both soil erosion and dissolved nutrient export; (4) recognition of the hydrological cycle of particular lakes and streams, allowing floodplains and wetlands to develop and increase nutrient and organic matter retention; (5) development of climate-smart irrigation systems; and (6) reestablishment of native riparian vegetation along rivers and shores of large lakes. The appropriate management or restoration of ponds within agricultural landscapes can have a secondary positive effect of increasing local and regional biodiversity (Swartz and Miller 2021) and contributing to the potential connectivity among freshwaters.

Measures to reduce loading at the catchment and landscape level are most needed because they deal with

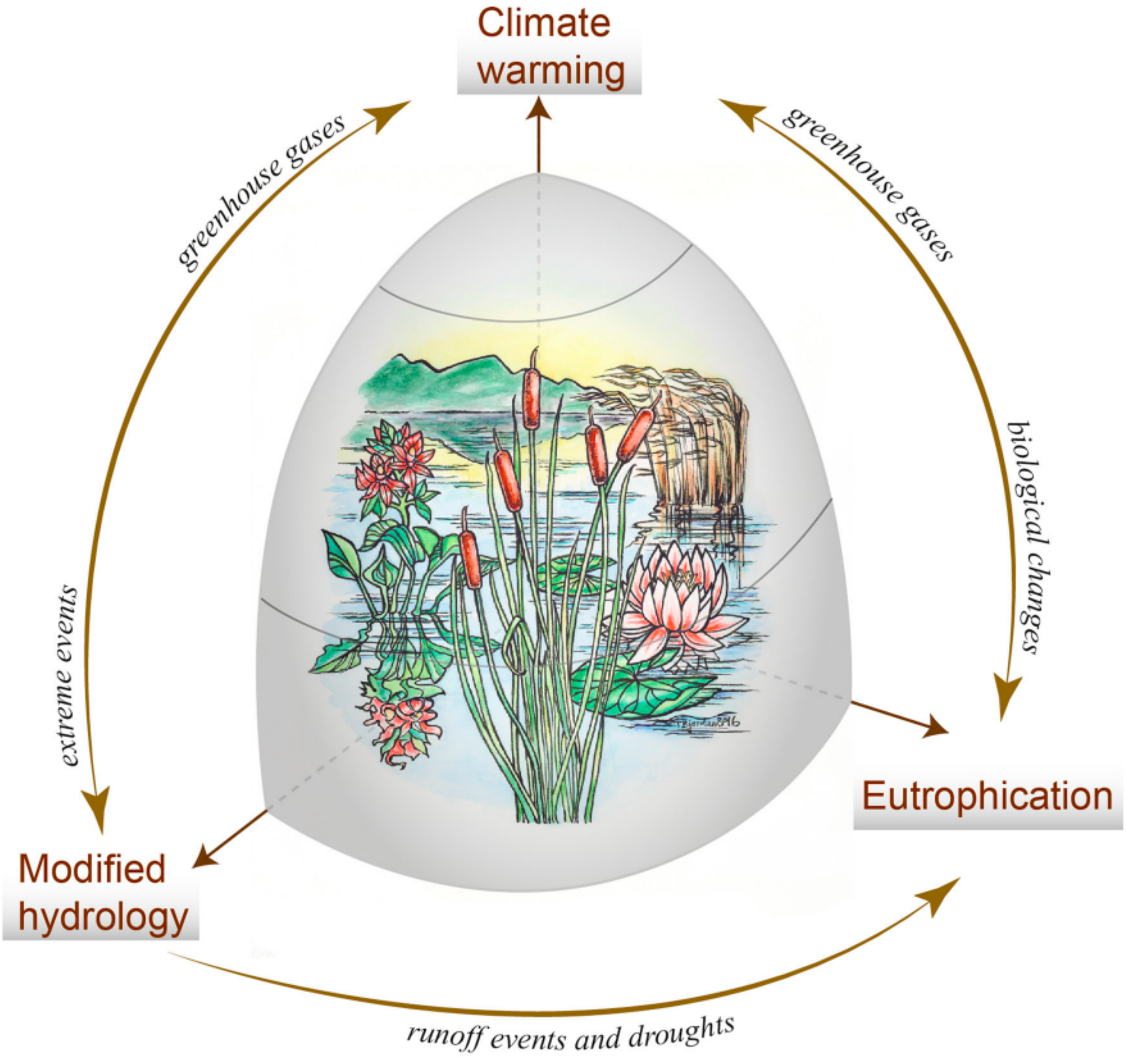

Figure 4. Synergy between climate warming and eutrophication, highlighting some of the feedback, including effects through changes in the hydrological dynamics. Restoring or maintaining lakes and ponds in a state of high biodiversity, clear water, and a low carbon footprint (illustrated as the grey space) as climate change progresses requires a major reduction in nutrient loading and eutrophication symptoms, which often requires measures at landscape and lake levels to maintain, strengthen, or recover resilient mechanisms. See text for the elaboration on drivers and feedback between and within climate warming and eutrophication as well as on other climate change-related effects such as a potential increase in salinization. Based on the safe operating space for wetlands scheme in Green et al. (2017). Copyright by the Ecological Society of America. Painting by Tone Bjordam.

the cause of the problem. However, measures taken at the system level can also enhance its own resilient mechanisms to better cope with climate change effects (e.g., Urrutia-Cordero et al. 2016). Various in-lake measures may also help counteract the synergy between eutrophication and warming. One such method is biomanipulation, including removal of planktivorous and benthivorous fish. In northern temperate lakes in Europe, biomanipulation has had variable long-term effectiveness (Jeppesen et al. 2012), but a shift to clear water and promotion of non-cyanobacterial species, along with submerged plants and higher biodiversity, is frequent (Fox et al. 2020). Biomanipulation in subtropical and tropical lakes is often less successful, mainly because of the trophic web structure (reviewed in Jeppesen et al. 2012), which may indicate that its future success under warmer conditions may be weaker or shorter-lived than needed. Chemical intervention, aimed at precipitating and/or reducing P release from the sediment, has been used to reverse eutrophication (Lürling et al. 2016). A promising alternative for warm and warming, particularly not too shallow, lakes may be to combine fish removal, transplantation of submerged macrophytes, and capping P in the sediment (Liu et al. 2018, Zhang et al. 2021) to potentially lower restoration costs and environmental impacts (via reduced use of chemicals and fewer fish kills). More research is needed on a range of ecosystems and climatic conditions to corroborate these results.

Degraded ecosystems are too often resistant to traditional restoration measures because of constraints on changes in landscape connectivity and organization, loss of native species pools, shifts in guilds dominance, changes in major trophic interactions, invasion by exotic species, and associated changes in biogeochemical processes (Suding et al. 2004). The efforts described would not only help recover good water quality and lead to improved biodiversity, but also decrease the carbon footprints of fresh waters, even turning some waters from net sources to net sinks of GHG, by increasing carbon sequestration while decreasing CH_4 emissions (Taylor et al. 2019), which would also contribute to ecosystem resilience to counter the pressures from climate change. Lake management measures aimed at reducing GHG emissions are starting to be applied, and results need to be monitored (e.g., by water managers in a Dutch waterscape; Motelica-Wagenaar et al. 2020).

Final remarks

The COVID-19 crisis, despite its terrible death toll and health, social, and economic consequences, can be seen as an opportunity to inspire reactions against other global crises, such as the biodiversity and climate crisis. As a global society we have learned that we can respond immediately and dramatically, in ways unthinkable before December 2019. Governments have managed to lock down hundreds of cities, ban international travel, and prevent millions of children from going to school, with huge political, economic, and societal costs. Considering these dramatic changes in our societal habits, how difficult can it be to put a limit to the massive use of agrochemicals, prevent the fragmentation and disappearance of lakes and ponds in connected landscapes, and to promote climate-smart restoration and conservation practices? An integrated response to tackle eutrophication and climate change and their feedback is urgently needed to maintain and recover water quality, protect the remaining biodiversity, and enhance ecosystem resiliency as we jointly engage to mitigate the negative effects of climate change.

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