

Feedbacks 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 influence along the freshwater to marine continuum. The interaction between eutrophication and climate change, particularly climate warming, was explicitly focused upon a decade ago in the paper by Moss et al. (2011), 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 feedbacks between eutrophication, cyanobacterial blooms, and climate change. Facing both challenges at the same time is more pressing than ever. Meaningful and strong measures at the landscape and water body levels are therefore required if we are to ensure ecosystem resilience and safe water supply, conserving biodiversity, and decreasing the carbon footprint of freshwaters.

Key words: nutrients; temperature; feedback; resilience; cyanobacteria; greenhouse gases

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. Still, 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 concentration and/or phytoplankton biomass (e.g., Kraemer et al. 2017; Huser et al. 2018). Different restoration efforts at the water body 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 along the freshwater to marine continuum (Wurtsbaugh et al. 2019). Water quality has deteriorated, and blooms of toxic cyanobacteria, hypoxia, 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 2013). Besides 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, on the one hand, and climate change particularly climate warming, on the other, was the focus of the paper by Moss et al. (2011), which called for an integrated response to both problems, given their synergy.

Here we aim to review the status and advances on this topic given the different avenues of research in the first decade since the publication of the paper by Moss et al. (2011). Even though 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 at the same time is more pressing than ever, but also, that current measures are not enough.

1. Theoretical advances potentially relevant for management and policy

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

In the case of 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 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 water body before the shift has occurred has proven extremely difficult if not impossible. The challenge increases as not all regime shifts are associated with tipping points (Dakos et al. 2015).

The 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 well as 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 feedbacks 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 have sparked intense debate and controversy (Montoya et al. 2018; Hillebrand et al. 2020), among other issues due to difficulties in identifying those boundaries and translating them into concrete management recommendations.

2. Empirical advances: climate change enhances eutrophication and its symptoms

In the last decade, empirical evidence has mounted documenting temporal changes in phytoplankton biomass (using Chlorophyll-a as proxy), largely using remote sensing techniques particularly applied to large lakes. Opposite trends have 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 paleolimnological 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 water body and from ecosystem-scale biogeochemical cycles to food webs and life history traits of particular species or genotypes. The following subsections describe 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, and 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, besides 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). In the latter situation, 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 semi-arid 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 water bodies 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 (Gillefalk et al. 2019; Yılmaz et al. 2021).

In 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, and nutrients and other substances from the catchments to the water bodies, 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 phosphorus (Jeppesen et al. 2009; Goyenola et al. 2015; Ockenden et al. 2017), nitrogen (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 in up to 30% of average winter phosphorus loads at present-day land-use has been predicted to occur in temperate rain-fed watersheds by 2050, due to future changes in precipitation (Ockenden et al. 2017).

However, and although this topic needs to be further investigated, 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, are to be 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). In contrast, climate change-mitigation policies, such as land-use changes towards reforestation or even afforestation may eventually lead to improved water quality (Daneshmand et al. 2020), depending on local conditions.

One of the concerns that has emerged in the last 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 the world (Stevens-Rumann et al. 2018) and that such effect impacts fresh waters. One of the multifold effects of fires is the high load of ashes (Earl and Blinn 2003). High ash loads can increase water pH, turbidity, total organic carbon (TOC) and nutrient concentrations, as well as reduce dissolved O₂ 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 increases in 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 already 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 phosphorus and nitrogen (Søndergaard et al. 2003; Søndergaard et al. 2013).

Now it is also becoming clear 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 due to climate change (Capon et al. 2013; Stocker et al. 2014; 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).

Strong changes in fish communities are expected with climate warming, both due to direct and indirect effects as observed by different approaches, such as heating experiments, long-term monitoring and time series analyses, and space-for-time substitution (summarized in Jeppesen et al. 2014). One of the issues 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 towards more herbivory with increasing water temperature has been observed at individual, population, and community levels (González-Bergonzoni et al. 2016), following intra-annual 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 that are 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 of importance (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 macrophytes' optimum temperatures (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 prolongation of the macrophyte growing season (Netten et al. 2011), advance 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 a 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). Besides from negative direct effects, this can result from 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. 2007b; Havens et al. 2009). Warming may also promote phytoplankton and periphyton growth (Mahdy et al. 2015; Kazanjian et al. 2018) and in this way increase the susceptibility of macrophytes to herbivory (Hidding et al. 2016).

Low water levels due to more frequent or intense drought can lead to an increase in 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 water bodies (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), besides also exerting toxic effects on some algae and macrophytes (Silva et al. 2015). The increase in fires may thus be yet another way in which 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

In the previous section 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 due to climate warming, as has been evidenced in recent research. This 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 large-bodied zooplankton (Fig. 2).

Genetic adaptation, however, may also contribute to reduce the 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

One of the issues that has received a tremendous theoretical and empirical impulse since the early 2000's and particularly in the last decade, is the recognition that population persistence, community dynamics and biodiversity, and their impacts on ecosystem functioning, are deeply affected by 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 will occupy less of the available patches. Conversely, high connectedness can under some circumstances also be

detrimental to diversity (Scheffer et al. 2012), since 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 versus 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., in case of 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 due to fear of future water shortage.

3. Empirical advances: eutrophication and its symptoms enhance climate change

Moss et al. (2011) hypothesized that eutrophication could promote climate change, but that 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 feedbacks between both processes (Fig. 3).

Lake 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 CO₂) to negative (implying a net release of CO₂) in the warmer southern lakes, regardless of nutrient levels (Scharfenberger et al. 2019). The net flux of CO₂ 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 water bodies, water browning, anoxia and eutrophication interact leading to higher CO₂ and CH₄ 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 greenhouse gas inventories or in the IPCC guidelines. This is a crucial gap, as lakes and ponds are large sources of methane 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), only for CH₄ diffusive flux (Holgerson & Raymond, 2016). Calculated mean annual fluxes for individual artificial ponds vary between 0.1 – 44.3 g CH₄ m⁻² yr⁻¹ and -36 – 1138 g CO₂ m⁻² yr⁻¹ (Peacock et al. 2021). A recent synthesis suggests, besides, that GHG fluxes vary inversely with lake size, with ca. 37% of total lentic CH₄ emissions (diffusive + ebullitive) coming from systems <0.1 ha. in size (Rosentreter et al. 2021). Growing evidence indicates that CH₄ 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 Chl-a or TP concentrations, two clear proxies of eutrophication, can often explain CH₄ emissions from lakes

and reservoirs (Deemer et al., 2016; DelSontro et al., 2018; Beaulieu et al., 2019). The mechanisms responsible for the increased CH₄ emissions in eutrophic ecosystems are, however, not fully resolved. Under eutrophic conditions, the more abundant and more labile organic matter supplies seem to fuel methanogenesis. At the same time, the potential for methane oxidation decreases due to a frequent lack of oxygen (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 of CH₄ emissions (Davidson et al. 2018). Particularly, bubble-mediated emissions increase under eutrophic and warming conditions, transporting methane produced in the sediment directly to the atmosphere with little opportunity for methanotrophic bacteria to transform some of that CH₄ to CO₂ (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 CH₄ emissions.

The alternative dominance by phytoplankton, submerged plants, and free-floating vegetation, that are likely under eutrophic conditions, can promote contrasting patterns in CO₂ 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 CO₂ through photosynthesis and release CO₂ through respiration, the effects on CH₄ and N₂O dynamics may differ among phytoplankton, submerged, free-floating, or emergent macrophytes. In the tropics, areas of floodplain lakes dominated by free-floating plants can act as net CO₂ sinks during all seasons due to carbon fixation by plants, whereas open waters generally emit CO₂ following hydrological changes (Peixoto et al. 2016). Macrophytes that root in the sediment may oxygenate the sediment,

thereby potentially increasing consumption and decreasing CH₄ production, overall resulting in a decrease in methane emissions (Davidson et al. 2015; Davidson et al. 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 CH₄ from the sediments to the atmosphere, by-passing water column CH₄ oxygenation. In this way, rooted plants may increase CH₄ emissions (Oliveira Junior et al. 2019). The overall effects of aquatic plants on CH₄ 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 CO₂ efflux (Jeppesen et al. 2016) and tend to decrease CH₄ emissions (Colina et al. 2021b). Plants effects on oxygen conditions in the sediment and in the water column do not only affect CH₄ processes, but also the nitrogen cycle (Veraart et al. 2011), thereby potentially impacting N₂O emissions. In contrast, phytoplankton blooms have been related to uptake of CO₂ (Jeppesen et al. 2016) but to high N₂O emissions (Wang et al. 2006) and to high emissions of GHG 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 very active research currently aims at elucidating the role of trophic interactions and 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 CH₄ oxidizing bacteria and thus decrease CH₄ diffusive emissions (Devlin et al., 2015). Benthic fish, whose numbers and biomass typically increase with eutrophication, may promote contrasting processes. Benthivores may either reduce CH₄

emissions due to higher oxygen availability in the sediments through bioturbation (Oliveira Junior et al. 2019) or, in contrast, lead to an increase in CH₄ production through negative top-down effect on bio-irrigating benthic macroinvertebrates (Colina et al. 2021).

This review highlights that general patterns are still hard to distil, because an individual lake's 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 (DOM) 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 feedbacks to climate change.

4. Eutrophication and climate warming synergy and feedbacks through cyanobacteria

Despite opposite trends 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 a consistent result 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 the dominance by cyanobacteria, as detected in sediment records (Taranu et al. 2015). Cyanobacterial biomass is

even increasing in northern nutrient poor lakes with the 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 nitrogen and phosphorus 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 at 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 and enhancing localized temperature increases and increasing thermal stratification potentials (Kahru et al. 1993). Cyanobacteria promote the release of GHG during the decomposition following the collapse of a bloom, particularly of methane (Yan et al. 2017). 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 (Figs. 2 & 3).

5. Advances in mitigation and adaptation policies

The advances in research and understanding of the feedbacks between eutrophication and climate change, however, have not translated in 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 greenhouse gas inventories. We call for their inclusion, as it would contribute to reduce 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 at decreasing nutrient exports from the catchments and minimizing

eutrophication symptoms and, at the same time, at protecting and/or recovering 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. The monitoring and restoration of lake biodiversity and ecosystem services should also consider that besides the 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). Still, 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.

In contrast, measures to reduce diffuse nutrient input are more difficult, since 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 fresh waters might be limited only by large-scale agricultural changes (e.g., 20-80% reduction in current levels of phosphorus inputs). Beaulieu et al. (2013) models indicated that under a scenario of atmospheric CO₂ 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 chanelization 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) develop 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 & Miller 2021) and contributing to the potential connectivity among freshwaters.

Measures to reduce loading at the catchment and landscape level are the most needed since they deal with 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 due to 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 (Lüring 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 phosphorus in the sediment (Liu et al. 2018; Zhang et al. 2021), with potential lower restoration costs and environmental impacts (via reduced use of chemicals and less fish kills). More research needs to be done on a range of ecosystems and climatic conditions to corroborate these results.

Degraded ecosystems are too often resistant to traditional restoration measures due to 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 above 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 methane emissions (Taylor et al. 2019). This will 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 travels, and prevent millions of children from going to schools, 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 feedbacks 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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References

- Aben RCH, Barros N, van Donk E, Frenken T, Hilt S, Kazanjian G, Lamers LPM, Peeters ETHM, Roelofs JGM, de Senerpont Domis LN et al. 2017. Cross continental increase in methane ebullition under climate change. *Nature Communications*. 8(1):1682.
- Almeida RM, Nóbrega GN, Junger PC, Figueiredo AV, Andrade AS, de Moura CG, Tonetta D, Oliveira Jr ES, Araújo F, Rust F et al. 2016. High primary production contrasts with intense carbon emission in a eutrophic tropical reservoir. *Frontiers in Microbiology*. 7:717.
- Audet J, Neif ÉM, Cao Y, Hoffmann CC, Lauridsen TL, Larsen SE, Søndergaard M, Jeppesen E, Davidson TA. 2017. Heat-wave effects on greenhouse gas emissions from shallow lake mesocosms. *Freshwater Biology*. 62(7):1130-1142.
- Bakker ES, Hilt S. 2016. Impact of water-level fluctuations on cyanobacterial blooms: options for management. *Aquatic Ecology*. 50(3):485-498.
- Bakker ES, Wood KA, Pagès JF, Veen GC, Christianen MJ, Santamaría L, Nolet BA, Hilt S. 2016. Herbivory on freshwater and marine macrophytes: a review and perspective. *Aquatic Botany*. 135:18-36.
- Bartosiewicz M, Przytulska A, Deshpande BN, Antoniadis D, Cortes A, MacIntyre S, Lehmann MF, Laurion I. 2019. Effects of climate change and episodic heat events on cyanobacteria in a eutrophic polymictic lake. *Science of The Total Environment*. 693:133414.
- Beaulieu M, Pick F, Gregory-Eaves I. 2013. Nutrients and water temperature are significant predictors of cyanobacterial biomass in a 1147 lakes data set. *Limnology and Oceanography*. 58(5):1736-46.
- Beaulieu JJ, DelSontro T, Downing JA. 2019. Eutrophication will increase methane emissions from lakes and impoundments during the 21st century. *Nature Communications*. 10(1):1-5.
- Beklioğlu M, Meerhoff M, Søndergaard M, Jeppesen E. 2011. Eutrophication and restoration of shallow lakes from a cold temperate to a warm Mediterranean and a (sub)tropical climate In: Ansari AA, Singh S, Lanza GR et al., editors. *Eutrophication: Causes, Consequences and Control*. Springer; p. 91-108.
- Beklioğlu M, Romo S, Kagalou I, Quintana X, Bécares E. 2007. State of the art in the functioning of shallow Mediterranean lakes: workshop conclusions. *Hydrobiologia*. 584(1):317-326.
- Brans KI, Jansen M, Vanoverbeke J, Tüzün N, Stoks R, De Meester L. 2017. The heat is on: Genetic adaptation to urbanization mediated by thermal tolerance and body size. *Global Change Biology*. 23(12):5218-5227.
- Brothers S, Köhler J, Attermeyer K, Grossart H-P, Mehner T, Meyer N, Scharnweber K, Hilt S. 2014. A feedback loop links brownification and anoxia in a temperate, shallow lake. *Limnology and Oceanography*. 59(4):1388-1398.
- Brucet S, Boix D, Nathansen LW, Quintana XD, Jensen E, Balayla D, Meerhoff M, Jeppesen E. 2012. Effects of temperature, salinity and fish in structuring the macroinvertebrate community in shallow lakes: implications for effects of climate change. *PloS one*. 7(2):e30877.
- Brucet S, Pédrón S, Mehner T, Lauridsen TL, Argillier C, Winfield IJ, Volta P, Emmrich M, Hesthagen T, Holmgren K. 2013. Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures. *Freshwater Biology*. 58(9):1779-1793.

- Bruel R, Marchetto A, Bernard A, Lami A, Sabatier P, Frossard V, Perga ME. 2018. Seeking alternative stable states in a deep lake. *Freshwater Biology*. 63(6):553-68.
- Burford MA, Carey CC, Hamilton DP, Huisman J, Paerl HW, Wood SA, Wulff A. 2020. Perspective: Advancing the research agenda for improving understanding of cyanobacteria in a future of global change. *Harmful Algae*. 91:101601.
- Calvo C, Mormul RP, Figueiredo BR, Cunha ER, Thomaz SM, Meerhoff M. 2019. Herbivory can mitigate, but not counteract, the positive effects of warming on the establishment of the invasive macrophyte *Hydrilla verticillata*. *Biological Invasions*. 21(1):59-66.
- Capon SJ, Chambers LE, Mac Nally R, Naiman RJ, Davies P, Marshall N, Pittock J, Reid M, Capon T, Douglas M. 2013. Riparian ecosystems in the 21st century: hotspots for climate change adaptation? *Ecosystems*. 16(3):359-381.
- Cerrato JM, Blake JM, Hirani C, Clark AL, Ali A-MS, Artyushkova K, Peterson E, Bixby RJ. 2016. Wildfires and water chemistry: effect of metals associated with wood ash. *Environmental Science: Processes and Impacts*. 18(8):1078-1089.
- Chang M, Teurlinx S, Janse JH, Paerl HW, Mooij WM, Janssen AB. 2020. Exploring how cyanobacterial traits affect nutrient loading thresholds in shallow lakes: A modelling approach. *Water*. 12(9):2467.
- Clemente JM, Boll T, Teixeira-de Mello F, Iglesias C, Pedersen AR, Jeppesen E, Meerhoff M. 2019. Role of plant architecture on littoral macroinvertebrates in temperate and subtropical shallow lakes: a comparative manipulative field experiment. *Limnetica*. 38(2):759-772.
- Colina M, Meerhoff M, Pérez G, Veraart AJ, Bodelier P, van der Horst A, Kosten S. 2021.a Trophic and non-trophic effects of fish and macroinvertebrates on carbon emissions. *Freshwater Biology*. 63: 1831.
- Colina M, Kosten S, Silvera N, Clemente JM, Meerhoff M. 2021.b. Carbon fluxes in subtropical shallow lakes with contrasting regimes. *Hydrobiologia* <https://doi.org/10.1007/s10750-021-04752-1>.
- Cunillera-Montcusí D, Borthagaray AI, Boix D, Gascón S, Sala J, Tornero I, Quintana XD, Arim M. 2021. Metacommunity resilience against simulated gradients of wildfire: disturbance intensity and species dispersal ability determine landscape recover capacity. *Ecography*.
- Dakos V, Carpenter SR, van Nes EH, Scheffer M. 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 370(1659):20130263.
- Daneshmand H, Alaghmand S, Camporese M, Talei A, Yeh PJ, Daly E. 2020. Long-term impacts of partial afforestation on water and salt dynamics of an intermittent catchment under climate change. *Water*. 12(4):1067.
- Daufresne M, Lengfellner K, Sommer U. 2009. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*. 106(31):12788-12793.
- Davidson TA, Audet J, Jeppesen E, Landkildehus F, Lauridsen TL, Søndergaard M, Syväranta J. 2018. Synergy between nutrients and warming enhances methane ebullition from experimental lakes. *Nature Climate Change*. 8(2):156-160.
- Davidson TA, Audet J, Svenning JC, Lauridsen TL, Søndergaard M, Landkildehus F, Larsen SE, Jeppesen E. 2015. Eutrophication effects on greenhouse gas fluxes from shallow-lake mesocosms override those of climate warming. *Global Change Biology*. 21(12):4449-4463.
- Deemer BR, Harrison JA, Li S, Beaulieu JJ, DelSontro T, Barros N, Bezerra-Neto JF, Powers SM, Dos Santos MA, Vonk JA. 2016. Greenhouse gas emissions from reservoir water surfaces: a new global synthesis. *BioScience*. 66(11):949-964.

- DelSontro T, Beaulieu JJ, Downing JA. 2018. Greenhouse gas emissions from lakes and impoundments: Upscaling in the face of global change. *Limnology and Oceanography Letters*. 3(3):64-75.
- Deng J, Paerl HW, Qin B, Zhang Y, Zhu G, Jeppesen E, Cai Y, Xu H. 2018. Climatically-modulated decline in wind speed may strongly affect eutrophication in shallow lakes. *Science of The Total Environment*. 645:1361-1370.
- Devlin SP, Saarenheimo J, Syväranta J, Jones RI. 2015. Top consumer abundance influences lake methane efflux. *Nature Communications*. 6(1):1-7.
- Donohue I, Hillebrand H, Montoya JM, Petchey OL, Pimm SL, Fowler MS, Healy K, Jackson AL, Lurgi M, McClean D. 2016. Navigating the complexity of ecological stability. *Ecology Letters*. 19(9):1172-1185.
- Earl SR, Blinn DW. 2003. Effects of wildfire ash on water chemistry and biota in South-Western USA streams. *Freshwater Biology*. 48(6):1015-1030.
- Emmrich M, Pédrón S, Brucet S, Winfield IJ, Jeppesen E, Volta P, Argillier C, Lauridsen TL, Holmgren K, Hesthagen T. 2014. Geographical patterns in the body-size structure of European lake fish assemblages along abiotic and biotic gradients. *Journal of Biogeography*. 41(12):2221-2233.
- Ersoy Z, Scharfenberger U, Baho DL, Buçak T, Feldmann T, Hejzlar J, Levi EE, Mahdy A, Nöges T, Papastergiadou E et al. 2020. Impact of nutrients and water level changes on submerged macrophytes along a temperature gradient: A pan-European mesocosm experiment. *Global Change Biology*. 26(12):6831-6851.
- Feng L, Dai Y, Hou X, Xu Y, Liu J, Zheng C. 2021. Concerns about phytoplankton bloom trends in global lakes. *Nature*. 590(7846):35-47.
- Feuchtmayr H, Moran R, Hatton K, Connor L, Heyes T, Moss B, Harvey I, Atkinson D. 2009. Global warming and eutrophication: effects on water chemistry and autotrophic communities in experimental hypertrophic shallow lake mesocosms. *Journal of Applied Ecology*. 46(3):713-723.
- Figueiredo BR, Calvo C, López-Rodríguez A, Mormul RP, Teixeira-de Mello F, Benedito E, Meerhoff M. 2019. Short-term interactive effects of experimental heat waves and turbidity pulses on the foraging success of a subtropical invertivorous fish. *Water*. 11(10):2109.
- Folke C. 2016. Resilience (republished). *Ecology and Society*. 21(4).
- Fox AD, Jørgensen HE, Jeppesen E, Lauridsen TL, Søndergaard M, Fugl K, Myssen P, Balsby TJ, Clausen P. 2020. Relationships between breeding waterbird abundance, diversity, and clear water status after the restoration of two shallow nutrient-rich Danish lakes. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 30(2):237-245.
- Freeman EC, Creed IF, Jones B, Bergström AK. 2020. Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes. *Global Change Biology*. 26(9):4966-4987.
- García-Palacios P, Gross N, Gaitán J, Maestre FT. 2018. Climate mediates the biodiversity–ecosystem stability relationship globally. *Proceedings of the National Academy of Sciences*. 115(33):8400-8405.
- Geerts A, Vanoverbeke J, Vanschoenwinkel B, Van Doorslaer W, Feuchtmayr H, Atkinson D, Moss B, Davidson TA, Sayer CD, De Meester L. 2015. Rapid evolution of thermal tolerance in the water flea *Daphnia*. *Nature Climate Change*. 5(7):665-668.

- Gianuca AT, Engelen J, Brans KI, Hanashiro FTT, Vanhamel M, van den Berg EM, Souffreau C, Meester LD. 2018. Taxonomic, functional and phylogenetic metacommunity ecology of cladoceran zooplankton along urbanization gradients. *Ecography*. 41(1):183-194.
- Gillefalk M, Mooij WM, Teurlincx S, Janssen AB, Janse JH, Chang M, Köhler J, Hilt S. 2019. Modelling induced bank filtration effects on freshwater ecosystems to ensure sustainable drinking water production. *Water Research*. 157:19-29.
- González-Bergonzoni I, Jeppesen E, Vidal N, Teixeira-de Mello F, Goyenola G, López-Rodríguez A, Meerhoff M. 2016. Potential drivers of seasonal shifts in fish omnivory in a subtropical stream. *Hydrobiologia*. 768(1):183-196.
- González-Bergonzoni I, Meerhoff M, Davidson TA, Teixeira-de Mello F, Baattrup-Pedersen A, Jeppesen E. 2012. Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. *Ecosystems*. 15(3):492-503.
- Govaert L, Pantel JH, De Meester L. 2016. Eco-evolutionary partitioning metrics: Assessing the importance of ecological and evolutionary contributions to population and community change. *Ecology Letters*. 19(8):839-853.
- Goyenola G, Graeber D, Meerhoff M, Jeppesen E, Teixeira-de Mello F, Vidal N, Fosalba C, Ovesen NB, Gelbrecht J, Mazzeo N et al. 2020. Influence of farming intensity and climate on lowland stream nitrogen. *Water*. 12(4):1021.
- Goyenola G, Meerhoff M, Teixeira-de Mello F, González-Bergonzoni I, Graeber D, Fosalba C, Vidal N, Mazzeo N, Ovesen N, Jeppesen E et al. 2015. Monitoring strategies of stream phosphorus under contrasting climate-driven flow regimes. *Hydrology and Earth System Sciences*. 19(10):4099-4111.
- Graeber D, Boëchat IG, Encina-Montoya F, Esse C, Gelbrecht J, Goyenola G, Gücker B, Heinz M, Kronvang B, Meerhoff M et al. 2015. Global effects of agriculture on fluvial dissolved organic matter. *Scientific Reports*. 5(1):1-8.
- Green AJ, Alcorlo P, Peeters ET, Morris EP, Espinar JL, Bravo-Utrera MA, Bustamante J, Díaz-Delgado R, Koelmans AA, Mateo R et al. 2017. Creating a safe operating space for wetlands in a changing climate. *Frontiers in Ecology and the Environment*. 15(2):99-107.
- Guo C, Zhu G, Qin B, Zhang Y, Zhu M, Xu H, Chen Y, Paerl HW. 2019. Climate exerts a greater modulating effect on the phytoplankton community after 2007 in eutrophic Lake Taihu, China: Evidence from 25 years of recordings. *Ecological Indicators*. 105:82-91.
- Gyllström M, Hansson LA, Jeppesen E, Criado FG, Gross E, Irvine K, Kairesalo T, Kornijów R, Miracle MR, Nykänen M. 2005. The role of climate in shaping zooplankton communities of shallow lakes. *Limnology and Oceanography*. 50(6):2008-2021.
- Hamilton DP, Salmaso N, Paerl HW. 2016. Mitigating harmful cyanobacterial blooms: strategies for control of nitrogen and phosphorus loads. *Aquatic Ecology*. 50(3):351-366.
- Hansson L-A, Nicolle A, Granéli W, Hallgren P, Kritzberg E, Persson A, Björk J, Nilsson PA, Brönmark C. 2013. Food-chain length alters community responses to global change in aquatic systems. *Nature Climate Change*. 3(3):228-233.
- Harper AR, Santin C, Doerr SH, Froyd CA, Albini D, Otero XL, Viñas L, Pérez-Fernández B. 2019. Chemical composition of wildfire ash produced in contrasting ecosystems and its toxicity to *Daphnia magna*. *International Journal of Wildland Fire*. 28(10):726-737.
- Havens K, Paerl H, Philips E, Zhu M, Beaver J, Srifa A. 2016. Extreme weather events and climate variability provide a lens to how shallow lakes may respond to climate change. *Water*. 8(6):229.

- Havens KE, Elia AC, Taticchi MI, Fulton III RS. 2009. Zooplankton–phytoplankton relationships in shallow subtropical versus temperate lakes Apopka (Florida, USA) and Trasimeno (Umbria, Italy). *Hydrobiologia*.
- Hayes NM, Haig HA, Simpson GL, Leavitt PR. 2020. Effects of lake warming on the seasonal risk of toxic cyanobacteria exposure. *Limnology and Oceanography Letters*. 5(6):393-402.
- Heino J, Alahuhta J, Bini LM, Cai Y, Heiskanen AS, Hellsten S, Kortelainen P, Kotamäki N, Tolonen KT, Vihervaara P. 2021. Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. *Biological Reviews*. 96(1):89-106.
- Heino J, Melo AS, Bini LM. 2015. Reconceptualising the beta diversity–environmental heterogeneity relationship in running water systems. *Freshwater Biology*. 60(2):223-235.
- Hidding B, Bakker ES, Hootsmans MJ, Hilt S. 2016. Synergy between shading and herbivory triggers macrophyte loss and regime shifts in aquatic systems. *Oikos*. 125(10):1489-1495.
- Hillebrand H, Donohue I, Harpole WS, Hodapp D, Kucera M, Lewandowska AM, Merder J, Montoya JM, Freund JA. 2020. Thresholds for ecological responses to global change do not emerge from empirical data. *Nature Ecology & Evolution*. 4(11):1502-1509.
- Hilt S, Brothers S, Jeppesen E, Veraart AJ, Kosten S. 2017. Translating regime shifts in shallow lakes into changes in ecosystem functions and services. *BioScience*. 67(10):928-936.
- Ho JC, Michalak AM, Pahlevan N. 2019. Widespread global increase in intense lake phytoplankton blooms since the 1980s. *Nature*. 574(7780):667-70.
- Holgerson MA, Raymond PA. 2016. Large contribution to inland water CO₂ and CH₄ emissions from very small ponds. *Nature Geoscience*, 9(3):222-226.
- Horváth Z, Ptacnik R, Vad CF, Chase JM. 2019. Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. *Ecology Letters*. 22(6):1019-1027.
- Huisman J, Codd GA, Paerl HW, Ibelings BW, Verspagen JM, Visser PM. 2018. Cyanobacterial blooms. *Nature Reviews Microbiology*. 16(8):471-483.
- Huser BJ, Futter MN, Wang R, Fölster J. 2018. Persistent and widespread long-term phosphorus declines in Boreal lakes in Sweden. *Science of the Total Environment*. 613:240-9.
- Iglesias C, Meerhoff M, Johansson LS, González-Bergonzoni I, Mazzeo N, Pacheco JP, Teixeira-de Mello F, Goyenola G, Lauridsen TL, Søndergaard M. 2017. Stable isotope analysis confirms substantial differences between subtropical and temperate shallow lake food webs. *Hydrobiologia*. 784(1):111-123.
- IPCC, 2021: Summary for Policymakers. In: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu and B. Zhou (eds.)]. Cambridge University Press. In Press.
- Janssen AB, Hilt S, Kosten S, de Klein JJ, Paerl HW, Van de Waal DB. 2021. Shifting states, shifting services: Linking regime shifts to changes in ecosystem services of shallow lakes. *Freshwater Biology*. 66(1):1-12.
- Jeppesen E, Canfield DE, Bachmann RW, Søndergaard M, Havens KE, Johansson LS, Lauridsen TL, Sh T, Rutter RP, Warren G. 2020. Toward predicting climate change effects on lakes: a comparison of 1656 shallow lakes from Florida and Denmark reveals substantial differences

- in nutrient dynamics, metabolism, trophic structure, and top-down control. *Inland Waters*. 10(2):197-211.
- Jeppesen E, Kronvang B, Meerhoff M, Søndergaard M, Hansen KM, Andersen HE, Lauridsen TL, Liboriussen L, Beklioglu M, Özen A et al. 2009. Climate change effects on runoff, catchment phosphorus loading and lake ecological state, and potential adaptations. *Journal of Environmental Quality*. 38(5):1930-1941.
- Jeppesen E, Kronvang B, Olesen J, Audet J, Søndergaard M, Hoffmann C, Andersen H, Lauridsen TL, Liboriussen L, Larsen S et al. 2011. Climate change effects on nitrogen loading from cultivated catchments in Europe: implications for nitrogen retention, ecological state of lakes and adaptation. *Hydrobiologia*. 663(1):1-21.
- Jeppesen E, Lauridsen TL, Kairesalo T, Perrow M. 1997. Impact of submerged macrophytes on fish-zooplankton interactions in lakes. In: Jeppesen E, Søndergaard M, Søndergaard M et al., editors. *The structuring role of submerged macrophytes in lakes* New York: Springer Verlag; p. 91-114.
- Jeppesen E, Meerhoff M, Davidson TA, Trolle D, Søndergaard M, Lauridsen TL, Beklioglu M, Brucet Balmaña S, Volta P, González-Bergonzoni I. 2014. Climate change impacts on lakes: an integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes.
- Jeppesen E, Meerhoff M, Holmgren K, González-Bergonzoni I, Teixeira-de Mello F, Declerck SA, De Meester L, Søndergaard M, Lauridsen TL, Bjerring R et al. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia*. 646(1):73-90.
- Jeppesen E, Meerhoff M, Jacobsen B, Hansen R, Søndergaard M, Jensen J, Lauridsen T, Mazzeo N, Branco C. 2007. Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia*. 581(1):269-285.
- Jeppesen E, Søndergaard M, Lauridsen TL, Davidson TA, Liu Z, Mazzeo N, Trochine C, Özkan K, Jensen HS, Trolle D et al. 2012. Biomanipulation as a restoration tool to combat eutrophication: recent advances and future challenges. *Advances in Ecological Research*. 47:411-488.
- Jeppesen E, Trolle D, Davidson TA, Bjerring R, Søndergaard M, Johansson LS, Lauridsen TL, Nielsen A, Larsen SE, Meerhoff M. 2016. Major changes in CO₂ efflux when shallow lakes shift from a turbid to a clear water state. *Hydrobiologia*. 778(1):33-44.
- Jöhnk KD, Huisman J, Sharples J, Sommeijer BEN, Visser PM, Stroom JM. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology*. 14(3):495-512.
- Kahru M, Leppanen J-M, Rud O. 1993. Cyanobacterial blooms cause heating of the sea surface. *Marine Ecology Progress Series*. 1-7.
- Kakouei K, Kraemer BM, Anneville O, Carvalho L, Feuchtmayr H, Graham JL, Higgins S, Pomati F, Rudstam LG, Stockwell JD, Thackeray SJ. 2021. Phytoplankton and cyanobacteria abundances in mid-21st century lakes depend strongly on future land use and climate projections. *Global Change Biology*. 27, 6409–6422.
- Kazanjian G, Flury S, Attermeyer K, Kalettka T, Kleeberg A, Premke K, Köhler J, Hilt S. 2018. Primary production in nutrient-rich kettle holes and consequences for nutrient and carbon cycling. *Hydrobiologia*. 806(1):77-93.

- Keller PS, Catalán N, von Schiller D, Grossart H-P, Koschorreck M, Obrador B, Frassl MA, Karakaya N, Barros N, Howitt J. 2020. Global CO₂ emissions from dry inland waters share common drivers across ecosystems. *Nature communications*. 11(1):1-8.
- Kosten S, Huszar VL, Bécares E, Costa LS, van Donk E, Hansson LA, Jeppesen E, Kruk C, Lacerot G, Mazzeo N et al. 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*. 18(1):118-126.
- Kosten S, Piñeiro M, de Goede E, de Klein J, Lamers LP, Ettwig K. 2016. Fate of methane in aquatic systems dominated by free-floating plants. *Water Research*. 104:200-207.
- Kosten S, Roland F, Da Motta Marques DM, Van Nes EH, Mazzeo N, Sternberg LdS, Scheffer M, Cole JJ. 2010. Climate-dependent CO₂ emissions from lakes. *Global Biogeochemical Cycles*. 24(2).
- Kosten S, van den Berg S, Mendonça R, Paranaíba JR, Roland F, Sobek S, Van Den Hoek J, Barros N. 2018. Extreme drought boosts CO₂ and CH₄ emissions from reservoir drawdown areas. *Inland Waters*. 8(3):329-340.
- Kraemer BM, Mehner T, Adrian R. 2017. Reconciling the opposing effects of warming on phytoplankton biomass in 188 large lakes. *Scientific Reports*. 7(1):1-7.
- Kratina P, Greig HS, Thompson PL, Carvalho-Pereira TS, Shurin JB. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*. 93(6):1421-1430.
- Lauridsen TL, Mønster T, Raundrup K, Nymand J, Olesen B. 2020. Macrophyte performance in a low arctic lake: effects of temperature, light and nutrients on growth and depth distribution. *Aquatic Sciences*. 82(1):1-14.
- Ledger ME, Brown LE, Edwards FK, Milner AM, Woodward G. 2013. Drought alters the structure and functioning of complex food webs. *Nature Climate Change*. 3(3):223-227.
- Lefevre S, McKenzie DJ, Nilsson GE. 2017. Models projecting the fate of fish populations under climate change need to be based on valid physiological mechanisms. *Global Change Biology*. 23(9):3449-3459.
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*. 7(7):601-613.
- Li Y, Shang J, Zhang C, Zhang W, Niu L, Wang L, Zhang H. 2021. The role of freshwater eutrophication in greenhouse gas emissions: A review. *Science of The Total Environment*. 144582.
- Li Z, He L, Zhang H, Urrutia-Cordero P, Ekvall MK, Hollander J, Hansson LA. 2017. Climate warming and heat waves affect reproductive strategies and interactions between submerged macrophytes. *Global Change Biology*. 23(1):108-116.
- Liu Z, Hu J, Zhong P, Zhang X, Ning J, Larsen SE, Chen D, Gao Y, He H, Jeppesen E. 2018. Successful restoration of a tropical shallow eutrophic lake: strong bottom-up but weak top-down effects recorded. *Water Research*. 146:88-97.
- Loreau M, Mouquet N, Gonzalez A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences*. 100(22):12765-12770.
- Lürling M, Mackay E, Reitzel K, Spears BM. 2016. Editorial-a critical perspective on geo-engineering for eutrophication management in lakes. *Water Research*. 97:1-10.
- Lürling M, van Oosterhout F, de Senerpont Domis L, Marinho MM. 2018. Response of natural cyanobacteria and algae assemblages to a nutrient pulse and elevated temperature. *Frontiers in Microbiology*. 9:1851.

- Mahdy A, Hilt S, Filiz N, Beklioğlu M, Hejzlar J, Özkundakci D, Papastergiadou E, Scharfenberger U, Šorf M, Stefanidis K et al. 2015. Effects of water temperature on summer periphyton biomass in shallow lakes: a pan-European mesocosm experiment. *Aquatic Sciences*. 77(3):499-510.
- Mantzouki E, Lüring M, Fastner J, de Senerpont Domis L, Wilk-Woźniak E, Koreivienė J, Seelen L, Teurlincx S, Verstijnen Y, Krztoń W. 2018. Temperature effects explain continental scale distribution of cyanobacterial toxins. *Toxins*. 10(4):156.
- Meerhoff M, Clemente JM, Teixeira-de Mello F, Iglesias C, Pedersen AR, Jeppesen E. 2007. Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes? *Global Change Biology*. 13:1888-1897.
- Meerhoff M, Iglesias C, Teixeira-de Mello F, Clemente JM, Jensen E, Lauridsen TL, Jeppesen E. 2007. Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology*. 52(6):1009-1021.
- Meerhoff M, Teixeira-de Mello F, Kruk C, Alonso C, Gonzalez-Bergonzoni I, Pacheco JP, Lacerot G, Arim M, Beklioğlu M, Brucet S et al. 2012. Environmental warming in shallow lakes: a review of potential changes in community structure as evidenced from space-for-time substitution approaches. *Advances in Ecological Research*. 46:259-349.
- Moi DA, Alves DC, Antiqueira PAP, Thomaz SM, Teixeira-de Mello F, Bonecker CC, Rodrigues LC, Garcia-Rios R, Mormul RP. 2021. Ecosystem shift from submerged to floating plants simplifying the food web in a tropical shallow lake. *Ecosystems*. 24(3):628-639.
- Montoya JM, Donohue I, Pimm SL. 2018. Planetary boundaries for biodiversity: implausible science, pernicious policies. *Trends in Ecology and Evolution*. 33(2):71-73.
- Moss B. 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia*. 200/201:367-377.
- Moss B, Kosten S, Meerhoff M, Battarbee RW, Jeppesen E, Mazzeo N, Havens K, Lacerot G, Liu Z, De Meester L et al. 2011. Allied attack: climate change and eutrophication. *Inland Waters*. 1(2):101-105.
- Moss B, Madgwick J, Phillips G. 1996. A guide to the restoration of nutrient-enriched shallow lakes. Norwich: Environment Agency (CE).
- Motelica-Wagenaar AM, Pelsma TA, Moria L, Kosten S. 2020. The potential impact of measures taken by water authorities on greenhouse gas emissions. *Proceedings of the International Association of Hydrological Sciences*. 382:635-642.
- Mölter T, Schindler D, Albrecht AT, Kohnle U. Review on the projections of future storminess over the North Atlantic European region. 2016. *Atmosphere*. 7(4):60.
- Naiman RJ, Decamps H. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*. 28(1):621-658.
- Netten JJ, Arts GH, Gylstra R, van Nes EH, Scheffer M, Roijackers RM. 2010. Effect of temperature and nutrients on the competition between free-floating *Salvinia natans* and submerged *Elodea nuttallii* in mesocosms. *Fundamental and Applied Limnology*. 177(2):125.
- Netten JJ, Van Zuidam J, Kosten S, Peeters ET. 2011. Differential response to climatic variation of free-floating and submerged macrophytes in ditches. *Freshwater Biology*. 56(9):1761-1768.

- Ockenden MC, Hollaway MJ, Beven KJ, Collins A, Evans R, Falloon P, Forber KJ, Hiscock K, Kahana R, Macleod C. 2017. Major agricultural changes required to mitigate phosphorus losses under climate change. *Nature Communications*. 8(1):1-9.
- Olesen JE, Carter TR, Diaz-Ambrona C, Fronzek S, Heidmann T, Hickler T, Holt T, Minguéz MI, Morales P, Palutikof JP. 2007. Uncertainties in projected impacts of climate change on European agriculture and terrestrial ecosystems based on scenarios from regional climate models. *Climatic Change*. 81(1):123-143.
- Oliveira Junior ES, Temmink RJ, Buhler BF, Souza RM, Resende N, Spanings T, Muniz CC, Lamers LP, Kosten S. 2019. Benthivorous fish bioturbation reduces methane emissions, but increases total greenhouse gas emissions. *Freshwater Biology*. 64(1):197-207.
- Özen A, Karapınar B, Kucuk I, Jeppesen E, Beklioglu M. 2010. Drought-induced changes in nutrient concentrations and retention in two shallow Mediterranean lakes subjected to different degrees of management. *Hydrobiologia*. 646(1):61-72.
- Paerl HW, Hall NS, Hounshell AG, Luettich RA, Rossignol KL, Osburn CL, Bales J. 2019. Recent increase in catastrophic tropical cyclone flooding in coastal North Carolina, USA: Long-term observations suggest a regime shift. *Scientific Reports*. 9(1):1-9.
- Paerl HW, Hall NS, Hounshell AG, Rossignol KL, Barnard MA, Luettich RA, Rudolph JC, Osburn CL, Bales J, Harding LW. 2020. Recent increases of rainfall and flooding from tropical cyclones (TCs) in North Carolina (USA): implications for organic matter and nutrient cycling in coastal watersheds. *Biogeochemistry*. 150(2):197-216.
- Paerl HW, Havens KE, Hall NS, Otten TG, Zhu M, Xu H, Zhu G, Qin B. 2020. Mitigating a global expansion of toxic cyanobacterial blooms: confounding effects and challenges posed by climate change. *Marine and Freshwater Research*. 71(5):579-592.
- Paerl HW, Huisman J. 2008. Blooms like it hot. *Science*. 320:57-58.
- Paerl HW, Paul VJ. 2012. Climate change: links to global expansion of harmful cyanobacteria. *Water Research*. 46(5):1349-1363.
- Peacock M, Audet J, Bastviken D, Cook S, Evans CD, Grinham A, Holgerson MA, Högbom L, Pickard AE, Zieliński P, Futter MN. 2021. Small artificial waterbodies are widespread and persistent emitters of methane and carbon dioxide. *Global Change Biology*. 27(20):5109-23.
- Peeters ETM, van Zuidam JP, van Zuidam BG, Van Nes EH, Kosten S, Heuts PG, Roijackers RM, Netten JJ, Scheffer M. 2013. Changing weather conditions and floating plants in temperate drainage ditches. *Journal of Applied Ecology*. 50(3):585-593.
- Peixoto R, Marotta H, Bastviken D, Enrich-Prast A. 2016. Floating aquatic macrophytes can substantially offset open water CO₂ emissions from tropical floodplain lake ecosystems. *Ecosystems*. 19(4):724-736.
- Pimm SL, Donohue I, Montoya JM, Loreau M. 2019. Measuring resilience is essential to understand it. *Nature Sustainability*. 2(10):895-897.
- Pinay G, Bernal S, Abbott BW, Lupon A, Marti E, Sabater F, Krause S. 2018. Riparian corridors: A new conceptual framework for assessing nitrogen buffering across biomes. *Frontiers in Environmental Science*. 6:47.
- Planas D, Desrosiers M, Groulx S-R, Paquet S, Carignan R. 2000. Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. *Canadian Journal of Fisheries and Aquatic Sciences*. 57(S2):136-145.
- Rockström J, Steffen W, Noone K, Persson Å, Chapin FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ. 2009. A safe operating space for humanity. *Nature*. 461(7263):472-475.

- Romero GQ, Marino NA, MacDonald AAM, Céréghino R, Trzcinski MK, Mercado DA, Leroy C, Corbara B, Farjalla VF, Barberis IM. 2020. Extreme rainfall events alter the trophic structure in bromeliad tanks across the Neotropics. *Nature Communications*. 11(1):1-8.
- Rosentreter JA, Borges AV, Deemer BR, Holgerson MA, Liu S, Song C, Melack J, Raymond PA, Duarte CM, Allen GH et al. 2021. Half of global methane emissions come from highly variable aquatic ecosystem sources. *Nature Geoscience*. 14:225-230.
- Scharfenberger U, Jeppesen E, Beklioglu M, Søndergaard M, Angeler DG, Çakiroğlu Aİ, Drakare S, Hejzlar J, Mahdy A, Papastergiadou E et al. 2019. Effects of trophic status, water level, and temperature on shallow lake metabolism and metabolic balance: A standardized pan-European mesocosm experiment. *Limnology and Oceanography*. 64(2):616-631.
- Scheffer M, Barrett S, Carpenter S, Folke C, Green AJ, Holmgren M, Hughes T, Kosten S, Van de Leemput I, Nepstad D. 2015. Creating a safe operating space for iconic ecosystems. *Science*. 347(6228):1317-1319.
- Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, Van Nes EH, Rietkerk M, Sugihara G. 2009. Early-warning signals for critical transitions. *Nature*. 461(7260):53-59.
- Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock WA, Dakos V, Van de Koppel J, Van de Leemput IA, Levin SA, Van Nes EH. 2012. Anticipating critical transitions. *Science*. 338(6105):344-348.
- Scheffer M, Hosper HS, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*. 8(8):275-279.
- Scheffer M, van Nes EH. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. *Hydrobiologia*. 584:455-466.
- Sepulveda-Jauregui A, Hoyos-Santillan J, Martinez-Cruz K, Anthony KMW, Casper P, Belmonte-Izquierdo Y, Thalasso F. 2018. Eutrophication exacerbates the impact of climate warming on lake methane emission. *Science of the Total Environment*. 636:411-419.
- Silva LG, Doyle KE, Duffy D, Humphries P, Horta A, Baumgartner LJ. 2020. Mortality events resulting from Australia's catastrophic fires threaten aquatic biota. *Global Change Biology*. 26(10):5345-5350.
- Silva V, Pereira JL, Campos I, Keizer JJ, Gonçalves F, Abrantes N. 2015. Toxicity assessment of aqueous extracts of ash from forest fires. *Catena*. 135:401-408.
- Søndergaard M, Bjerring R, Jeppesen E. 2013. Persistent internal phosphorus loading during summer in shallow eutrophic lakes. *Hydrobiologia*. 710(1):95-107.
- Søndergaard M, Jensen JP, Jeppesen E. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia*. 506(1-3):135-145.
- Steffen W, Rockström J, Richardson K, Lenton TM, Folke C, Liverman D, Summerhayes CP, Barnosky AD, Cornell SE, Crucifix M et al. 2018. Trajectories of the Earth System in the Anthropocene. *Proceedings of the National Academy of Sciences*. 115(33):8252-8259.
- Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT. 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecology letters*. 21(2):243-252.
- Suding KN, Gross KL, Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution*. 19(1):46-53.
- Swartz TM, Miller JR. 2021. The American Pond Belt: an untold story of conservation challenges and opportunities. *Frontiers in Ecology and the Environment*.

- Taranu ZE, Gregory-Eaves I, Leavitt PR, Bunting L, Buchaca T, Catalan J, Domaizon I, Guilizzoni P, Lami A, McGowan S. 2015. Acceleration of cyanobacterial dominance in north temperate-subarctic lakes during the Anthropocene. *Ecology Letters*. 18(4):375-384.
- Taylor S, Gilbert PJ, Cooke DA, Deary ME, Jeffries MJ. 2019. High carbon burial rates by small ponds in the landscape. *Frontiers in Ecology and the Environment*. 17(1):25-31.
- Teixeira-de Mello F, Meerhoff M, Pekcan-Hekim Z, Jeppesen E. 2009. Littoral fish community structure and dynamics in subtropical and temperate shallow lakes: potential implications for temperate lakes under climate warming. *Freshwater Biology*. On line.
- Thompson PL, Guzman LM, De Meester L, Horváth Z, Ptasnik R, Vanschoenwinkel B, Viana DS, Chase JM. 2020. A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters*. 23(9):1314-1329.
- Trenberth KE, Dai A, Van Der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J. 2014. Global warming and changes in drought. *Nature Climate Change*. 4(1):17-22.
- Trochine C, Guerrieri M, Liboriussen L, Meerhoff M, Lauridsen TL, Soendergaard M, Jeppesen E. 2011. Filamentous green algae inhibit phytoplankton with enhanced effects when lakes get warmer. *Freshwater Biology*. 56(3):541-553.
- Trolle D, Hamilton DP, Pilditch CA, Duggan IC, Jeppesen E. 2011. Predicting the effects of climate change on trophic status of three morphologically varying lakes: Implications for lake restoration and management. *Environmental Modelling & Software*. 26:354-370.
- Urrutia-Cordero P, Ekvall MK, Hansson L-A. 2016. Local food web management increases resilience and buffers against global change effects on freshwaters. *Scientific Reports*. 6(1):1-9.
- Vadeboncoeur Y, Moore MV, Stewart SD, Chandra S, Atkins KS, Baron JS, Bouma-Gregson K, Brothers S, Francoeur SN, Genzoli L, Higgins SN, Hilt S, Katona LR, Kelly D, Oleksy IA, Ozersky T, Power ME, Roberts D, Smits AP, Tromboni F, Vander Zanden MJ, Volkova, EA, Waters AS, Wood SA, Yamamuro M. 2021. Blue waters, green bottoms: Benthic filamentous algal blooms are an emerging threat to clear lakes worldwide. *BioScience*. 71(10):1011-27.
- Van Doorslaer W, Vanoverbeke J, Duvivier C, Rousseaux S, Jansen M, Jansen B, Feuchtmayr H, Atkinson D, Moss B, Stoks R. 2009. Local adaptation to higher temperatures reduces immigration success of genotypes from a warmer region in the water flea *Daphnia*. *Global Change Biology*. 15(12):3046-3055.
- Velthuis M, Kosten S, Aben R, Kazanjian G, Hilt S, Peeters ET, van Donk E, Bakker ES. 2018. Warming enhances sedimentation and decomposition of organic carbon in shallow macrophyte-dominated systems with zero net effect on carbon burial. *Global Change Biology*. 24(11):5231-5242.
- Velthuis M, van Deelen E, van Donk E, Zhang P, Bakker ES. 2017. Impact of temperature and nutrients on carbon: nutrient tissue stoichiometry of submerged aquatic plants: an experiment and meta-analysis. *Frontiers in Plant Science*. 8:655.
- Veraart AJ, De Klein JJ, Scheffer M. 2011. Warming can boost denitrification disproportionately due to altered oxygen dynamics. *PLoS One*. 6(3):e18508.
- Vidal N, Yu J, Gutierrez MF, Teixeira-de Mello F, Tavşanoğlu ÜN, Çakiroğlu AI, He H, Meerhoff M, Brucet S, Liu Z et al. 2021. Salinity shapes food webs of lakes in semiarid climate zones: a stable isotope approach. *Inland Waters*. 1-16.
- Vidon P, Allan C, Burns D, Duval TP, Gurwick N, Inamdar S, Lowrance R, Okay J, Scott D, Sebestyen S. 2010. Hot spots and hot moments in riparian zones: potential for improved

- water quality management 1. *Journal of the American Water Resources Association*. 46(2):278-298.
- Wagner C, Adrian R. 2009. Cyanobacteria dominance: quantifying the effects of climate change. *Limnology and Oceanography*. 54:2460-2468.
- Wang H, Wang W, Yin C, Wang Y, Lu J. 2006. Littoral zones as the “hotspots” of nitrous oxide (N₂O) emission in a hyper-eutrophic lake in China. *Atmospheric Environment*. 40(28):5522-5527.
- Wang R, Dearing JA, Langdon PG, Zhang E, Yang X, Dakos V, Scheffer M. 2012. Flickering gives early warning signals of a critical transition to a eutrophic lake state. *Nature*. 492(7429):419-422.
- Weyhenmeyer GA, Kosten S, Wallin MB, Tranvik LJ, Jeppesen E, Roland F. 2015. Significant fraction of CO₂ emissions from boreal lakes derived from hydrologic inorganic carbon inputs. *Nature Geoscience*. 8(12):933-936.
- Woolway RI, Merchant CJ, Van Den Hoek J, Azorin-Molina C, Nöges P, Laas A, Mackay EB, Jones ID. 2019. Northern Hemisphere atmospheric stilling accelerates lake thermal responses to a warming world. *Geophysical Research Letters*. 46(21):11983-92.
- Wurtsbaugh WA, Paerl HW, Dodds WK. 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *Wiley Interdisciplinary Reviews: Water*. 6(5):e1373.
- Yan X, Xu X, Wang M, Wang G, Wu S, Li Z, Sun H, Shi A, Yang Y. 2017. Climate warming and cyanobacteria blooms: Looks at their relationships from a new perspective. *Water Research*. 125:449-457.
- Yılmaz G, Çolak MA, Özgencil İK, Metin M, Korkmaz M, Ertuğrul S, Soyluer M, Bucak T, Tavşanoğlu ÜN, Özkan K et al. 2021. Decadal changes in size, salinity and biota in lakes in Konya Closed Basin, Turkey, subjected to increasing water abstraction for agriculture and climate change. *Inland Waters*. in press.
- Yvon-Durocher G, Jones JI, Trimmer M, Woodward G, Montoya JM. 2010. Warming alters the metabolic balance of ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 365:2117-2126.
- Zhang P, Grutters B, Van Leeuwen CH, Xu J, Petruzzella A, van den Berg RF, Bakker ES. 2019. Effects of rising temperature on the growth, stoichiometry, and palatability of aquatic plants. *Frontiers in Plant Science*. 9:1947.
- Zhang X, Zhen W, Jensen HS, Reitzel K, Jeppesen E, Liu Z. 2021. The combined effects of macrophytes (*Vallisneria spiralis*) and a lanthanum-modified bentonite on water quality of shallow eutrophic lakes: A mesocosm study. *Environmental Pollution*. 277:116720.
- Zhou Y, Zhou L, Zhang Y, de Souza JG, Podgorski DC, Spencer RG, Jeppesen E, Davidson TA. 2019. Autochthonous dissolved organic matter potentially fuels methane ebullition from experimental lakes. *Water Research*. 166:115048.

Figure legends

Fig. 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, as explained in section 2. 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 at the right-hand side.

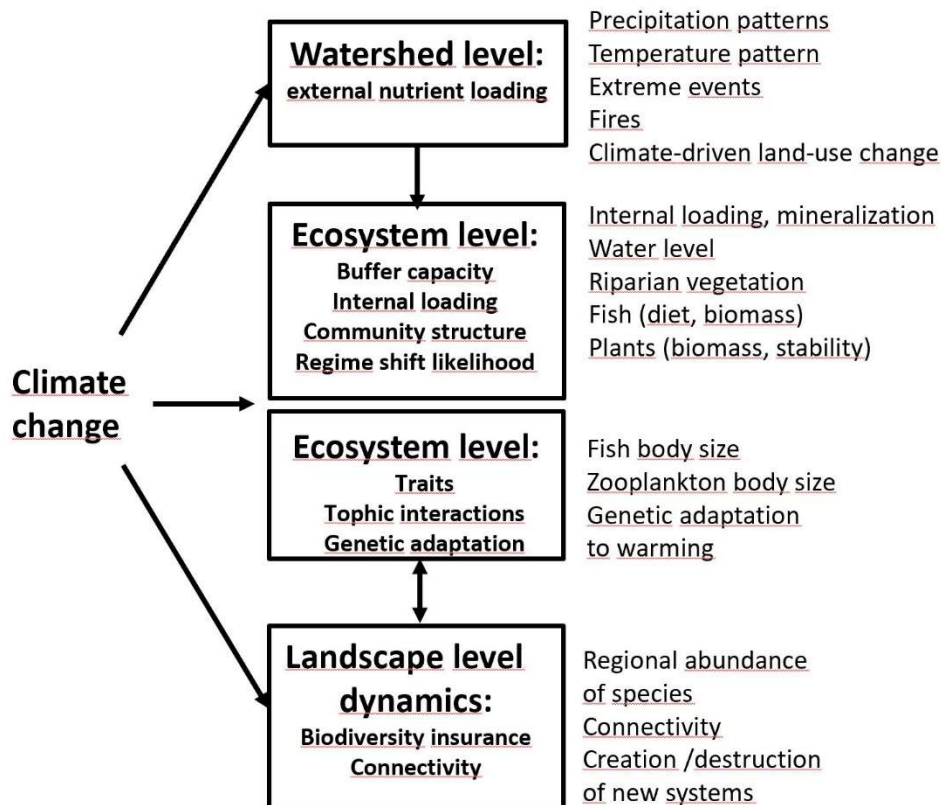
Fig. 2. Schematic view of main feedback effects of climate change on eutrophication and its symptoms. Dashed line indicates that changes in precipitation regimes may either lead to higher or lower nutrient and organic carbon loading, depending on local and regional circumstances. Warming intensifies 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 water body also depends on landscape processes, including other anthropogenic impacts, such as fragmentation and 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).

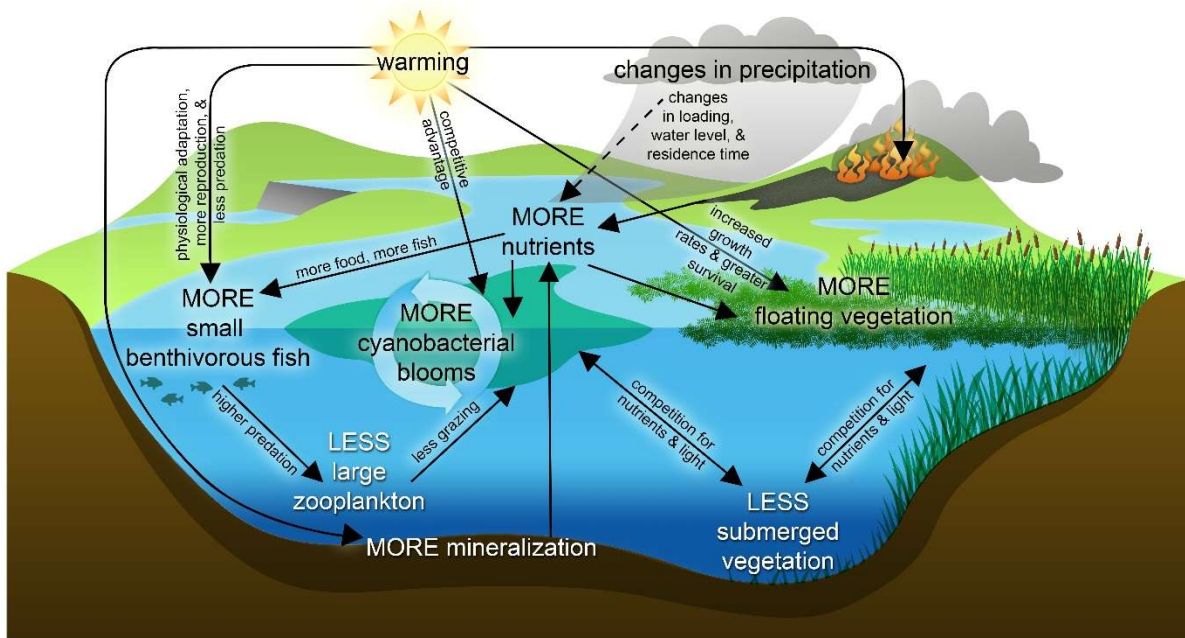
Fig. 3. Current understanding of main feedback effects of eutrophication on climate change. The blue arrow indicates carbon sequestration; red arrows indicate carbon emission routes; black arrows indicate other type of effects. The dashed line indicates that changes in precipitation regimes may either 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 feedbacks with climate change. Warming and eutrophication may increase both CO₂ uptake and release and thus net CO₂ balance is unclear, whereas potential effects on other GHG and particularly CH₄ are evident. Strong fluctuations in water level due to changes in precipitation may lead to cycles of drying-rewetting of sediments, promoting CO₂ release. GHG are produced and released by diffusion across different lake compartments, and CH₄ also by ebullition (bubbles). The role on GHG emissions of key communities, such as macrophytes, fish and macroinvertebrates, are subject of intense research. Drawing by Alan R. Joyner, based on Fig. 2 in Moss et al. (2011).

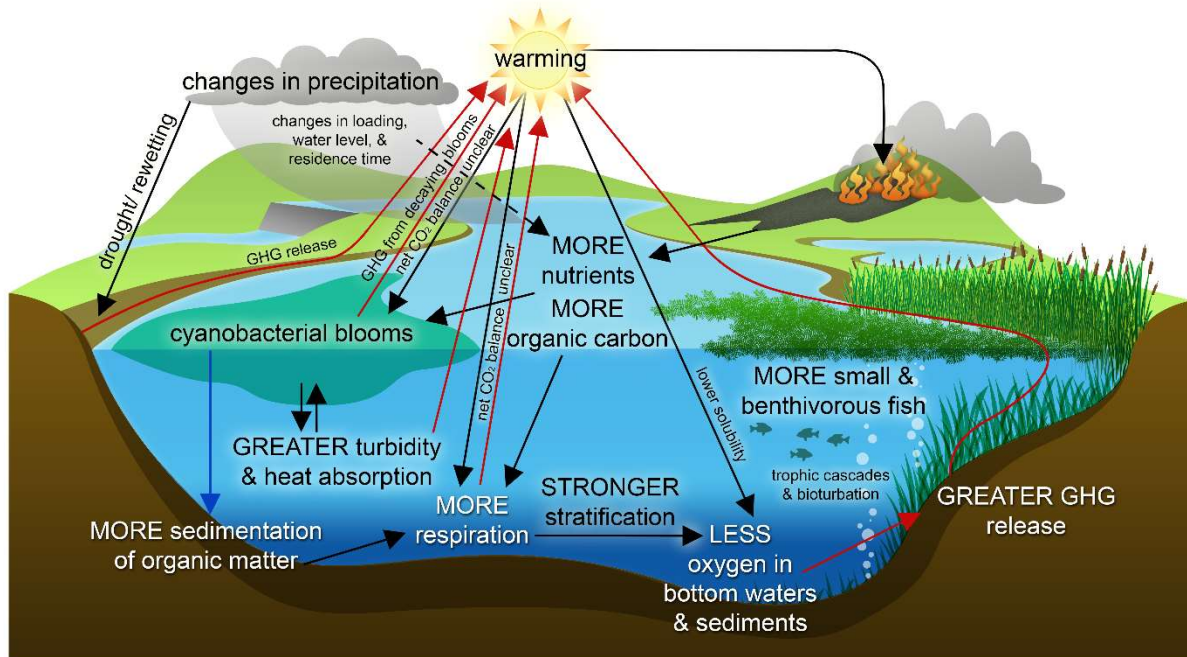
Fig. 4. Synergy between climate warming and eutrophication, highlighting some of the feedbacks including effects through changes in the hydrological dynamics. To restore or keep lakes and ponds in a state of high biodiversity, clear water, and a low carbon footprint (illustrated as the grey space), as climate change progresses a major reduction in nutrient loading and eutrophication symptoms are required. That often needs measures at the landscape and lake levels to maintain, strengthen, or recover resilient mechanisms. See the text for the elaboration on drivers and feedbacks 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). Painting by Tone Bjordam.



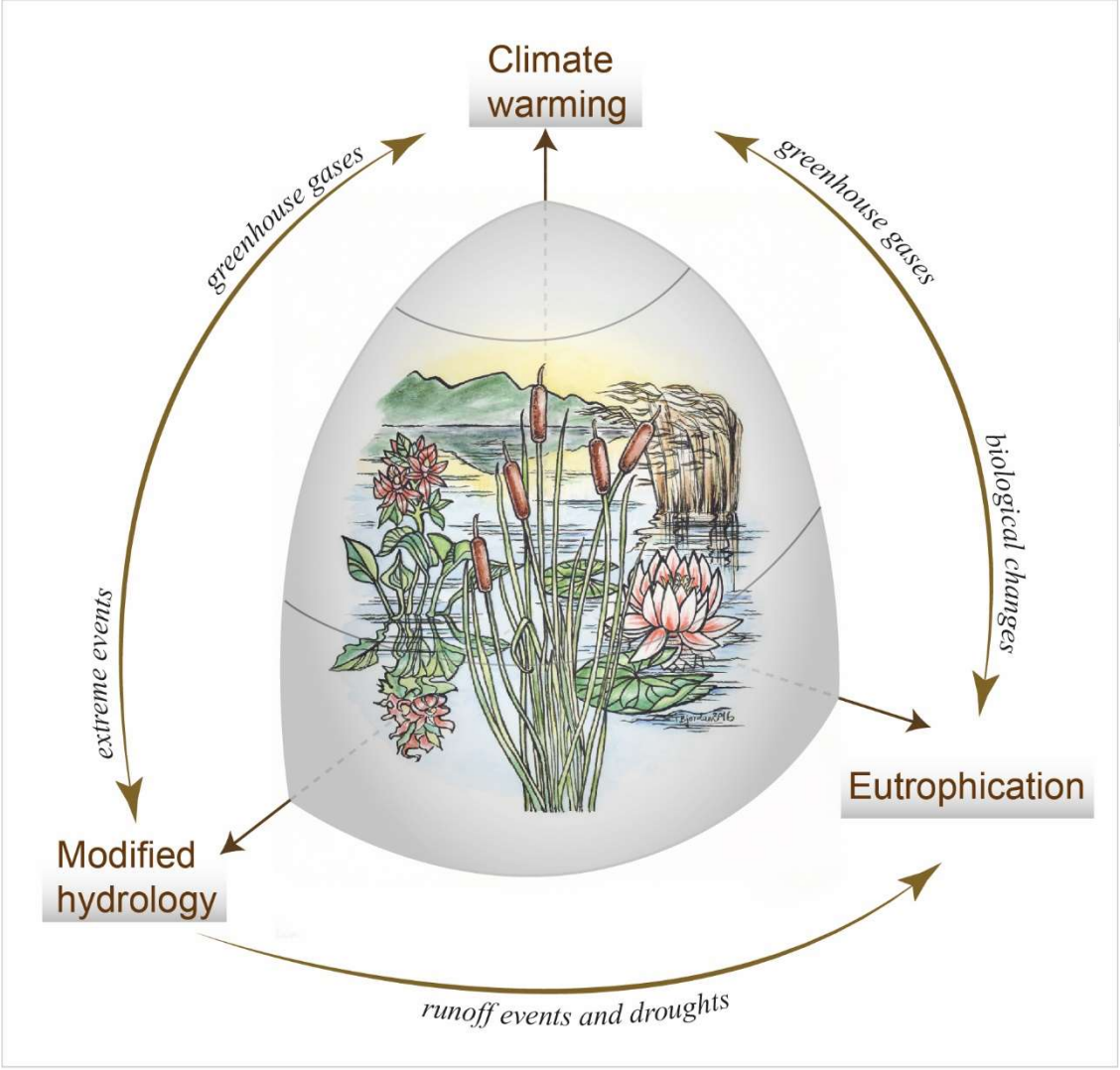
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