

Translating Regime Shifts in Shallow Lakes into Changes in Ecosystem Functions and Services

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Shallow lakes, the most prevalent type of freshwater ecosystems, can shift between clear states with macrophyte dominance and turbid, phytoplankton-dominated states. Such transformations, commonly termed regime shifts, have gained increasing attention in recent decades. Of 1084 studies documenting regime shifts, only 28% investigated the consequences for ecosystem functions and services such as habitat (13%), carbon processing (4%), or nutrient retention (4%). Although there is general consensus that a clear macrophyte state supports a higher diversity of aquatic organisms than a turbid one, the effects of shifts on primary production, carbon burial, greenhouse-gas emissions, and nutrient retention remain ambiguous. Shifts between the two states also affect drinking-water quality and the recreational value of lakes, leading to conflicting management measures and potentially deteriorating natural functions. We call for more comprehensive studies on the effects of regime shifts on ecosystem functions in shallow lakes to guide their sustainable management.

Keywords: alternative states, biodiversity, eutrophication, greenhouse-gas emissions, nutrient retention

Shallow lakes and ponds are the most abundant freshwater ecosystems on Earth (Verpoorter et al. 2014). They provide many economically valuable services and long-term benefits to society, such as drinking-water supply, and are often used for different types of recreation, such as swimming, boating, and angling (Baron et al. 2002). In addition to their utility for urban, agricultural, and industrial activities, the natural ecosystem functions of shallow lakes include the provision of habitat for aquatic flora and fauna, regional carbon (C) processing mediated by aquatic primary production, C burial in sediments and the emission of natural greenhouse gases (GHG), and watershed nutrient retention (Williamson et al. 2008). However, human pressures on ecosystems are increasing, whether by altering the abiotic environment (e.g., through eutrophication and climate change) or by direct changes to biota (e.g., species introductions). It is therefore crucially important to understand how ecosystem functions will respond to anthropogenic perturbations.

Shallow lakes and ponds can exhibit alternative states, a characteristic that they share with other ecosystems such as coral reefs and grasslands (Scheffer et al. 1993, 2001). In their pristine state, many shallow lakes are characterized by clear waters and abundant submerged vegetation. These macrophytes stabilize clear-water conditions during their vegetative period by reducing resuspension, increasing sedimentation within macrophyte stands, providing habitat for piscivorous fish, providing refuge for zooplankton from

fish predation, and suppressing phytoplankton growth via competition for nutrients and the excretion of allelochemicals (Scheffer et al. 1993). In turn, clear-water conditions support submerged macrophytes. This positive feedback between water clarity and macrophyte abundance results in a certain resistance of shallow lakes and ponds, with their water remaining clear despite sudden or gradual increases in external stressors such as nutrient loading. Passing a critical threshold level of nutrient loading, however, results in the complete loss of submerged vegetation and a shift to turbid conditions. Other perturbations such as storm events can also precipitate regime shifts. Once a lake has shifted, macrophytes often do not return in subsequent years because of a reduced light availability via suspended and attached algae, as well as sediment disturbance produced by waves and benthivorous fish (Scheffer et al. 1993, Jeppesen et al. 1998, Phillips et al. 2016). The resulting turbid state is thus also resistant to decreases in external stressors. A return to the pristine, clear state requires nutrient-loading reductions to below a threshold level that at least theoretically is lower than the threshold level at which the lake shifted from clear to turbid. The response of shallow lakes to gradual changes of external stressors such as nutrient loading can be sudden and hysteretic, although gradual changes often occur (Jeppesen et al. 2007), making predictions of shifts and subsequent restoration measures challenging. Lake managers are in crucial need for predictive tools that incorporate

key variables to identify combinations of factors and conditions, along with thresholds, that portend regime shifts. Knowledge on the ecological resilience of lakes is important for the understanding of why lake management strategies frequently fail to achieve their anticipated outcomes and why lake improvements are sometimes short lived.

Beyond being difficult to predict and reverse, regime shifts are also believed to have consequences for ecosystem functions and services (Scheffer et al. 2001). Carpenter and Lodge (1986) reviewed the effects of submerged macrophytes on the physical, chemical, and biological environment of lakes. They predicted that modifications in macrophyte composition or biomass could significantly change ecosystem structure and productivity. However, they also concluded that controlled, whole-lake manipulations of macrophytes would be needed to elucidate the impact of changes in macrophyte presence on ecosystem processes. Since this early review, numerous studies have been conducted on regime shifts in shallow lakes and ponds. Different approaches have been applied, such as paleolimnological studies of sediment layers from periods experiencing different states, analyses of long-term data sets on lakes undergoing shifts in states, and comparisons of data sets from different habitats within lakes or from lakes exhibiting different states (including remote sensing, mesocosm- and full-scale biomanipulation experiments, and modeling; supplemental table S1). We hypothesized that the majority of these studies have focused on factors stabilizing the regimes, drivers of shifts, or methods to predict, prevent, or reverse shifts rather than on the consequences of regime shifts for ecosystem functions and services, although knowledge on the latter is vital for the proper management of shallow lakes.

To test this hypothesis, we searched literature from the past 30 years on the Web of Science (WoS) using combinations of the search terms *shallow lake** (*truncation for retrieval of plurals and variant spellings), *pond**, *alternative stable state**, *alternate stable state**, *regime shift**, *clear water state*, *bistability*, and *macrophyte dominance*. We also searched all articles that cite the key papers by Phillips and colleagues (1978) and Scheffer and colleagues (1993). We focused on freshwater systems and thus excluded marine and brackish systems.

On the basis of the article titles and/or abstracts, we first selected all papers in which researchers examined regime shifts in shallow freshwater ponds and lakes, and subsequently among those, we selected all studies focusing on any ecosystem function or service. We then divided all studies on regime shifts affecting ecosystem functions or services into five major groups: (1) provision of habitats for a diverse flora and fauna; (2) landscape C processing; (3) nutrient removal and retention; (4) recreation, as well as food and drinking-water supply; and (5) other functions, such as resilience to invasive species, energy transfer in the food web, and changes in trophic links. For groups 1–3, we evaluated whether lakes with macrophyte dominance have higher, equal, or lower values of biodiversity separately for seven different aquatic organism groups, primary production,

greenhouse-gas (GHG) emissions, C burial, phosphorus (P) and nitrogen (N) retention, and denitrification. On the basis of this selection, we briefly discuss the state of knowledge regarding the effects of ecosystem state shifts on habitat provision, landscape C balance, and nutrient retention as three major natural ecosystem functions of shallow lakes. In addition, we discuss how regime shifts may impair the use of shallow lakes for drinking water and recreation.

Alternative states and ecosystem functions and services in shallow lakes

In total, 1084 studies were found with the appropriate search criteria and that dealt with regime shifts in shallow lakes and ponds within the past 30 years (WoS, 1977–March 2016). Currently, almost 100 such studies are published per year, and the existing studies annually receive approximately 5500 citations (2015). As we hypothesized, most of these studies focused on the detection of regime shifts, on factors stabilizing the different states, perturbations that lead to regime shifts, early warning signals, or restoration measures that can reverse shifts to the turbid state.

Only about 28% of the 1084 studies focused on the effects of regime shifts in ponds and shallow lakes on ecosystem functions and services (figure 1). These include articles on the effects of regime shifts (i.e., the effect of the act of change), as well as those on the effects associated with alternative dominant states (i.e., the effect of one condition versus another) in one or more systems (e.g., lakes, ponds, and/or mesocosms) or model scenarios.

About half of these 300 articles reported changes in habitat provision for a range of aquatic organisms, including waterfowl, macrozoobenthos, zooplankton, aquatic macrophytes, algae (phytoplankton and periphyton), and bacteria. Fewer studies revealed the consequences of regime shifts in shallow lakes and ponds on landscape C processing, despite the recently increasing interest in the role of inland waters for global C turnover (Cole et al. 2007). The same holds true when considering the effects of regime shifts on nutrient retention at the scale of both the lake and the watershed (figure 1). Other ecological functions and services on which the effects of shallow-lake regime shifts were examined included resilience to invasive species, ecological energy-transfer efficiencies in the food web, and trophic links.

Many reported regime shifts were preceded by an increase in nutrient loading. As a consequence, differences in nutrient loading complicate the comparison of ecosystem functions between clear and turbid lakes in those studies. Regime shifts without changes in nutrient loading are often a consequence of major disturbances such as biomanipulation, fish kills, water-level changes, or major changes in sediment loading or resuspension events (e.g., heavy storms or hurricanes) that may destroy macrophyte communities. Differences between ecosystem functions in shallow lakes and ponds with either macrophyte or phytoplankton dominance are thus often difficult to disentangle from the influence of the driver(s) that triggered the shift.

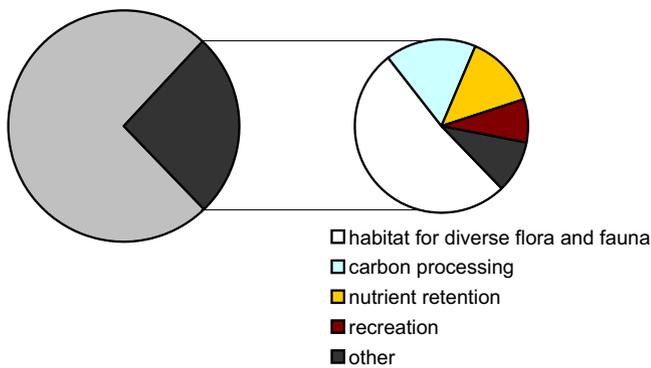


Figure 1. The share of studies on ecosystem functions and services among 1084 studies focusing on regime shifts between macrophyte- and phytoplankton-dominated states in shallow lakes and ponds (left; gray: studies on reported regime shifts not mentioning ecosystem functions and services; black: regime-shift studies including effects on ecosystem functions and/or services) and the share of different ecosystem functions and services considered (right).

Observational scale and potential biases

The majority of the studies (250) dealing with the effects of regime shifts on ecosystem functions and services were performed in lakes, 19 studies were performed in small- or large-scale experiments, 3 were modeling studies, and 6 were meta-analyses. In this article, all studies were given equal weight. Publication bias toward studies reporting significant differences between macrophyte-dominated (M) and phytoplankton-dominated (P) states is possible, but for this article, the bias is believed to be small because the comparison of ecosystem functions between the different regimes was often a by-product rather than the focus of many papers. Although the inclusion of meta-analyses may in theory increase the weight of certain studies (because of duplication), their relative contribution to our analysis is minor. By combining the outcomes of the different types of studies, we hoped to strengthen rather than weaken the results of our analyses. However, we recognize that grouping different studies introduced additional problems, such as different nutrient loading between states and variation in the statistics used, which may interfere with a proper comparison of ecosystem functions.

Regime shifts affect the provision of habitats for diverse aquatic communities

In total, 143 studies documented habitat provision for seven aquatic organism groups (waterfowl, fish, macrozoobenthos, zooplankton, aquatic plants, phytoplankton or periphyton, and bacteria) in macrophyte- and phytoplankton-dominated shallow lakes (some included data on several groups; table S1).

Most studies focused on zooplankton, whereas a few focused on fish (figure 2a). Most studies described a positive relationship between submerged macrophyte presence and the diversity and/or abundance of waterfowl, fish,

macrozoobenthos, and zooplankton (figures 2a, 3a, 3b; table S1). In addition to a greater faunal diversity (table S1; Jeppesen et al. 2000), macrophyte diversity itself is also higher in the clear-water state than under turbid conditions (figure 2a). The situation for phytoplankton and bacteria is less clear, with studies suggesting that clear and turbid states differ significantly in community composition but not necessarily in total diversity (figure 2a; table S1). Declerck and colleagues (2005) further noted that conservation practices designed to increase the richness of one group of organisms may decrease the richness of other organism groups in shallow lakes.

Recent work has highlighted that regime shifts may also affect the genetic diversity of different species groups as well as the ability of organisms to adapt to the conditions associated with each state. A shift from turbid to clear conditions, for instance, resulted in a low genetic diversity in the recovered dominant macrophyte species compared with that in other lakes in the clear state that have not undergone recent regime shifts (Hilt et al. 2013). Algae were found to genetically adapt to the presence or absence of macrophytes, as well as changing zooplankton grazing pressures (Vanormelingen et al. 2009). However, localized genetic adaptations by phytoplankton (e.g., toward macrophyte allelochemicals) did not always occur (Eigemann et al. 2013).

Considerable knowledge gaps exist regarding the effects of regime shifts in shallow lakes on the abundance and diversity of parasites, viruses, and pathogens. There is also limited knowledge regarding the effects of regime shifts on the ability of nonindigenous species to invade shallow lakes, even though invasive species can cause widespread problems in ecosystems. Vermonden and colleagues (2010) reported a greater abundance of nonindigenous macroinvertebrates under phytoplankton dominance than under macrophyte dominance. A lack of native macrophytes in many phytoplankton-dominated lakes was believed to contribute to the recent increase in the diversity and abundance of nonnative macrophyte species in Germany (Hussner et al. 2010).

Overall, the clear, macrophyte-dominated state may be regarded as beneficial for most aquatic organism groups, and a shift to turbid conditions therefore results in a loss of biodiversity in shallow lakes, particularly at higher trophic levels.

Consequences of regime shifts for landscape carbon processing

Among the available studies on the consequences of regime shifts in shallow lakes and ponds for landscape C processing, the most prominent topics are primary production, C burial, and GHG emissions. However, the results of the 43 analyzed studies (see “Landscape C processing” in table S1) were conflicting, with no agreed-on differences between the two regimes (figures 2b, 3c, 3d). This controversy may perhaps arise from the wide range of methodologies and assumptions adopted by the studies within this field.

Studies have reported primary productivity based on biomass, net primary production (Blindow et al. 2006), and

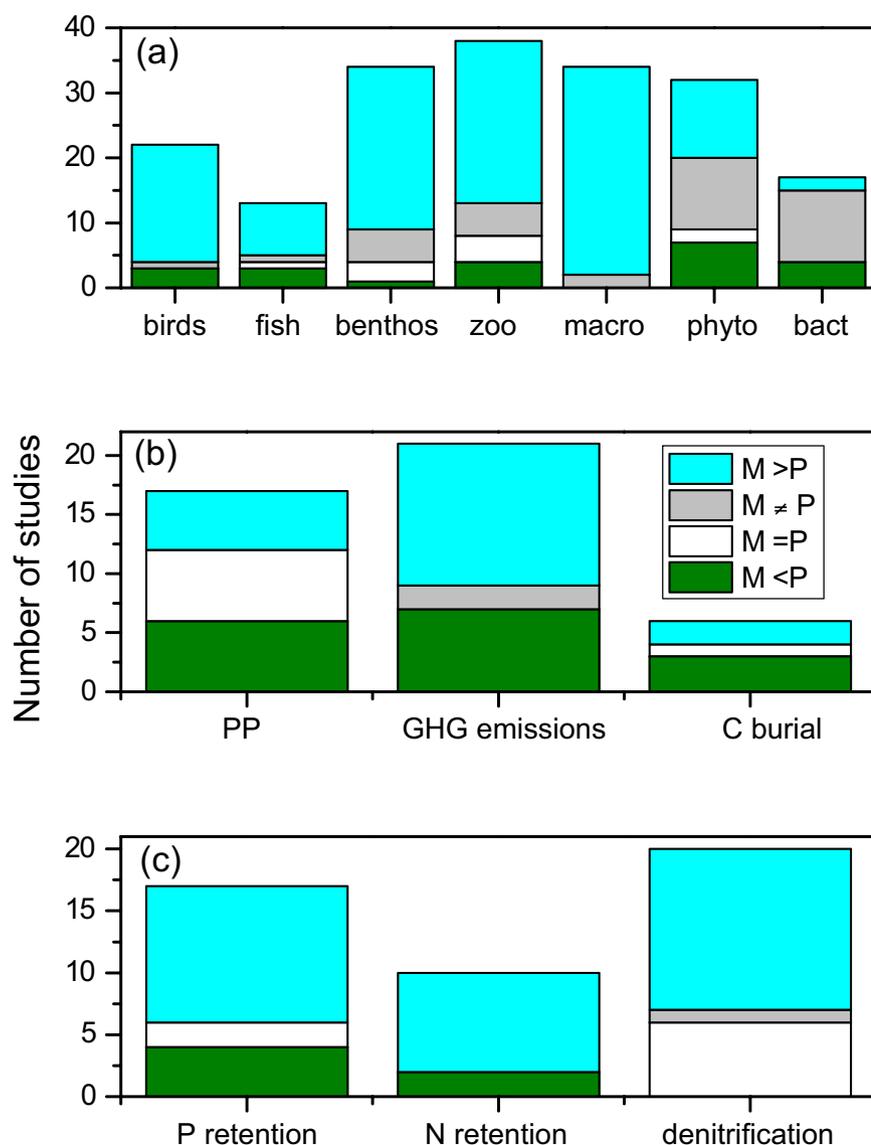


Figure 2. The number of studies reporting differences in important natural ecosystem functions between shallow lakes and ponds in the macrophyte-dominated (M) and those in the phytoplankton-dominated (P) state. (a) Habitat for flora and fauna, including birds, fish, macrozoobenthos (benthos), zooplankton (zoo), submerged plants (macro), phytoplankton (phyto), and bacteria (bact); (b) landscape carbon processing, including primary production (PP); greenhouse-gas (GHG) emissions; carbon burial, and (c) nutrient retention. $M > P$: macrophyte dominance provides higher biodiversity, PP, GHG emissions, carbon burial, or nutrient retention than phytoplankton dominance, $M \neq P$: difference between macrophyte and phytoplankton dominance but no clear trend; $M = P$: no difference between macrophyte and phytoplankton dominance; $M < P$: macrophyte dominance provides lower biodiversity, PP, GHG emissions, carbon burial, and nutrient retention than phytoplankton dominance.

gross primary production (Brothers et al. 2013). In many cases, periphyton (attached algae) production was entirely excluded from estimates (e.g., Blindow et al. 2006) or was considered to be represented by lake-center diel O_2 curves,

despite a high degree of spatial variability in such measurements (Zimmer et al. 2016) and a possibly poor methodological suitability for shallow lakes due to convective currents and microstratification (Brothers et al. 2017). Most primary production in eutrophic lakes is carried out by suspended or attached algae (Vadeboncoeur et al. 2008, Brothers et al. 2013), and a loss of phytoplankton production may be compensated by an increase in benthic (attached) algal production (Vadeboncoeur et al. 2008, Brothers et al. 2016). Carpenter and Lodge (1986) predicted that high macrophyte abundance would result in higher ecosystem productivity through enhanced P recycling from the sediments and a positive effect of macrophytes on fish abundance, resulting in increased predation on both littoral grazers and zooplankton. Although submerged macrophytes may play a key mechanistic role in establishing clear-water states (Phillips et al. 2016), their primary-productivity rates relative to algae can be minor, because macrophyte primary production depends on their size and morphology, as well as the depth and benthic slope of the lake (e.g., Jeppesen et al. 2012, Brothers et al. 2013). Simple models and calculations including multiple primary-producer groups across littoral and pelagic habitats within systems have indicated that the primary productivity of a clear-water system can be substantially higher than that under phytoplankton dominance (Brothers et al. 2013). However, comprehensive field studies including all primary-producer groups across climate regions are needed in order to make broad conclusions regarding the effects of regime shifts on primary productivity in shallow lakes.

Few studies documented the relationship between regime shifts and C burial (figure 2b), and we therefore did not discriminate between studies at different temporal scales. Oxygen exposure time and sediment source are both important factors controlling the burial efficiency of organic C (Sobek et al. 2009). Given that regime shifts appear to influence primary productivity and therefore oxygen production in lakes, it is possible that C burial and regime shifts are linked as well. Recent (within the past approximately 150 years) C burial rates

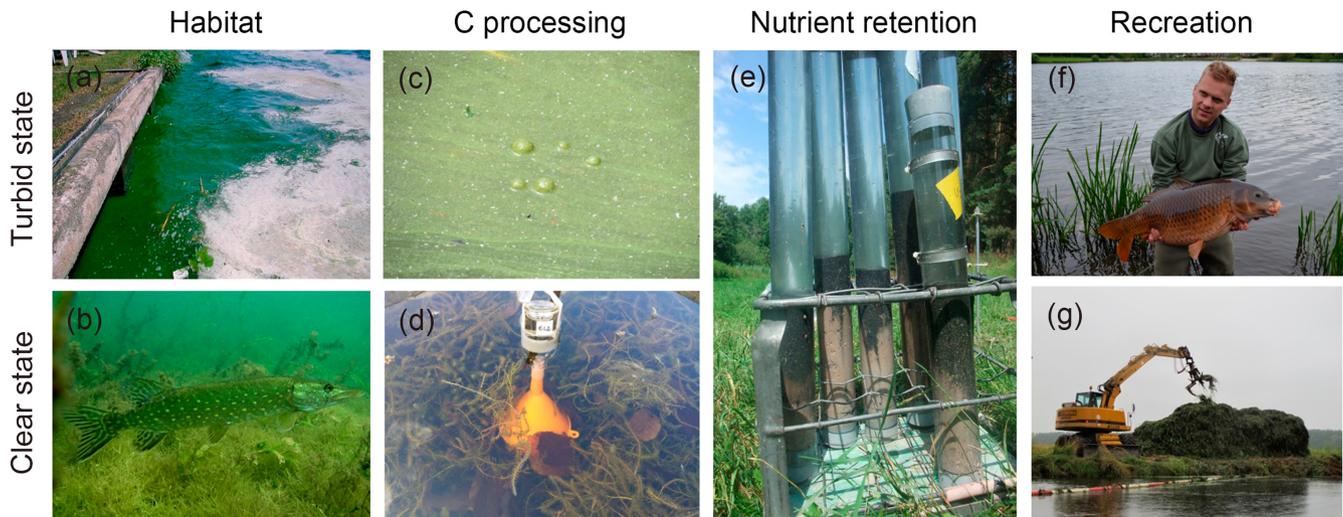


Figure 3. Regime shifts between turbid and clear states in shallow lakes and ponds influence important natural ecosystem functions, such as habitat provision for a high diversity of aquatic organisms, such as (a) a turbid lake with phytoplankton dominance and (b) a clear lake with macrophytes; landscape carbon (C) sequestration, including (c) the ebullition of greenhouse gases from a turbid lake and (d) the measurements of methane (CH_4) ebullition in a macrophyte-dominated system; and nutrient retention in the catchment, such as in (e) the sediment core from a shallow lake with upper dark layers formed after a shift from a macrophyte- to a phytoplankton-dominated state. Recreational use of shallow lakes, such as angling and carp stocking (f), may induce a shift to the turbid state or may require macrophyte harvesting (g). Photographs: Sabine Hilt (a, d, e); Klaus van de Weyer (b); Sarian Kosten (c); John Beijer (f); Jan Köhler (g).

calculated from dated sediment cores have increased in tandem with lake nutrient concentrations but not regime shifts *per se* (Heathcote and Downing 2012, Pacheco et al. 2013). However, a study focusing on alternate states (independently of nutrient availability) in a biomanipulated lake and 68 shallow regional lakes revealed no significant link between C burial rates and primary-producer dominance (Zimmer et al. 2016). In another study, researchers examined two lakes that exhibited alternative states at similar nutrient concentrations, identifying a significant increase in C burial rates in the turbid lake that temporally corresponded with its loss of submerged macrophytes (Brothers et al. 2013). This apparent discrepancy between studies may result from different methodologies used to distinguish alternative states (Zimmer and colleagues [2016] adopting a *k*-means cluster analysis with states sometimes being considered as lasting as briefly as 1 year) or by differences in macrophyte decay rates (Wang et al. 2016) or morphometry between study lakes.

Most lakes are net carbon dioxide (CO_2) sources to the atmosphere. Carbon-dioxide emissions from lakes are strongly regulated by inorganic C inflows in many lakes, but in nutrient-rich lakes, within-lake processes may play an important role as well (Wehenmeyer et al. 2015). In these systems, the above-mentioned changes in primary production caused by shifts in primary-producer composition have important implications for CO_2 fluxes. Partial CO_2 pressure, an important driver of CO_2 water-atmosphere fluxes, has been found to be systematically low in macrophyte-dominated lakes (Kosten et al. 2010), with emissions decreasing with macrophyte biomass (Xing et al. 2006, Davidson

et al. 2015). In contrast, lower benthic mineralization rates due to low hypolimnetic oxygen concentrations were believed to be responsible for lower CO_2 emissions from a phytoplankton-dominated lake compared with those from a macrophyte-dominated one (Brothers et al. 2013). A sudden shift from phytoplankton dominance to a clear-water state in lakes where macrophyte beds are not yet fully recovered may also lead to an increase in CO_2 emissions as a consequence of the decrease in primary production (Jeppesen et al. 2016). Time lags may thus play an important role in the evaluation of regime shift effects on ecosystem functions.

The impact of regime shifts on methane (CH_4) emissions is also not straightforward, because primary producers influence CH_4 emissions in multiple ways. Macrophytes may both stimulate and reduce methanogenesis through the production of organic matter and the promotion of anoxic conditions (Veraart et al. 2011) and radial oxygen loss at the roots (Sand-Jensen et al. 1982), respectively. Furthermore, they may influence CH_4 oxidation by supplying oxygen and providing substrate for methanotrophic bacteria, and they may directly transport CH_4 from the sediments or water column to the atmosphere (Xing et al. 2006, Kosten et al. 2016 and the references therein). Consequently, both higher and lower CH_4 emissions have been reported in floating macrophyte beds relative to open water sites (reviewed by Kosten et al. 2016), and CH_4 emissions from submerged macrophyte beds may increase (Xing et al. 2006) or decrease (Davidson et al. 2015) with macrophyte biomass. However, most data only incorporate diffusive and macrophyte-mediated CH_4 fluxes. Data on CH_4 ebullition (the flux of

bubbles from the sediments to the atmosphere; figure 3b) are often absent or based on short-term (minutes) measurements that likely underestimate the ebullitive flux. In many lakes, ebullition contributes a large share to the total CH₄ emissions (Bastviken et al. 2008). A scarcity of reliable data therefore impedes conclusions about the impact of regime shifts on CH₄ emissions. This applies to the overall conclusion on how regime shifts relate to GHG emissions as well, because most of the available studies did not carry out a full analysis of CO₂, CH₄, and N₂O emissions (table S1).

Knowledge of regime-shift effects on nutrient retention remains scarce

Anthropogenic changes to global nutrient cycles are currently driving many ecosystems to the brink of collapse and are being identified as one of the most pressing threats to the stability of global ecosystems (Steffen et al. 2015). However, our knowledge of regime-shift effects on *nutrient retention* (here defined as the temporary removal of nutrients from the water column via storage in plant tissues, sediments, or binding agents) and permanent removal (e.g., via denitrification) in shallow lakes remains scarce (figure 1). This is surprising given that shifts between the two regimes are largely nutrient driven and that nutrient retention plays a key role in hysteretic effects within lakes (Scheffer et al. 1993). Nearly two-thirds of 31 studies dealing with the effects of regime shifts on N documented an increase in N retention or permanent removal when macrophytes were abundant, whereas 23% reported no effect, 7% showed different microbial N cycling communities between alternative states (without reporting effects on functioning), and only 7% reported negative effects. Numbers for P are similar, with 65% of 17 studies reporting an increase in P removal from the water and thus retention in lakes featuring macrophyte dominance, 24% showing the opposite effect, and 11% finding no difference between states (figure 2c).

There are various ways in which nitrogen (N) and phosphorus (P) cycling can be affected by shifts between the two regimes in lakes. Macrophytes and their epiphytic algae can contribute to nutrient retention by temporarily removing N and P from lake water by assimilation (e.g., Reddy and De Busk 1985, Van Donk et al. 1993, Kreiling et al. 2011, Veraart et al. 2011). In a biomanipulated lake, for instance, macrophytes stored 86% of the lake's N load in their tissue but released 30% of the stored N back into the water column after the growing season (Van Donk et al. 1993). Enhanced macrophyte-mediated N retention in that study lake contributed to phytoplankton N limitation, stabilizing the macrophyte-dominated state. Up to 96% of the total water column P in macrophyte-dominated lakes may be temporarily stored in macrophyte tissues (Canfield et al. 1983). However, most lakes receive a continuous input of nutrients, and unless macrophytes are harvested by migrating waterfowl or humans, there are limitations for the capacity of these plants to store nutrients derived from the catchment. However, long-term effects on P retention can

occur when oxygen release in the rhizosphere of rooted macrophytes produces oxic habitats in anoxic zones. This oxygen release leads to P immobilization by iron-coated macrophyte roots, and clear-water conditions promote benthic oxygen production, further reducing P release from the sediments (Zhang et al. 2013). Very dense macrophyte stands, however, may result in reduced redox potential at the sediment surface and enhanced P release from the sediments (Boros et al. 2011). Rooted macrophytes also physically stabilize the sediments and increase sediment-burial rates by reducing resuspension via reduced water-flow rates and shear stresses (Jeppesen et al. 1998). At the same time, they provide organic substrates and oxygen to the sediment microbial community, thus stimulating nitrification and denitrification (Eriksson and Weisner 1997). Beyond the mere presence of macrophytes, the type of macrophyte can be an important determinant affecting nutrient uptake and nitrification–denitrification capabilities. Microcosm studies have shown that floating vegetation can stimulate denitrification by reducing oxygen availability (Veraart et al. 2011), whereas the enhanced oxidation of sediments by macrophytes and benthic algae may stimulate a coupled nitrification–denitrification process, which can contribute considerably to N removal (Vila-Costa et al. 2016). Wang and colleagues (2016) reported differential responses of water nutrient stocks to the disappearance of macrophytes depending on their biomass and species-specific decomposition rates. Suspended and dissolved concentrations (i.e., the mobile pool) of P increased 2.0- to 4.3-fold after the shift, whereas N tended to decrease or remained unchanged.

The existing studies therefore suggest that N and P retention and coupled nitrification–denitrification processes are greater in the macrophyte-dominated state and furthermore help to stabilize this state and reduce nutrient transport to downstream aquatic ecosystems. However, it should be noted that although we here consider high nitrification–denitrification rates to be a beneficial ecosystem service, at high nitrate-loading rates, the denitrification process may become less efficient (Kreiling et al. 2011) and more frequently truncated, resulting in the release of reactive N₂O rather than inert N₂ (Van de Leemput et al. 2011). Emissions of this potent GHG should therefore be carefully monitored, in particular in those lakes that are at the beginning of the bioremediation process and where nutrient concentrations remain high.

Regime shifts may impair the use of shallow lakes for drinking water and recreation

Only 36 studies directly address the negative consequences of regime shifts for drinking-water quality and for recreational use of shallow lakes (supplemental table S2). The phytoplankton-dominated state is generally considered less suitable for drinking-water production and swimming because of algal fouling and the potential presence of toxic cyanobacteria blooms (O'Neil et al. 2012). These are linked with high P loading, especially at high water temperatures. Future climate warming is thus assumed to worsen this problem (Kosten

et al. 2012). Apart from measures to reduce external and internal P loading (Hupfer and Hilt 2008), the active planting of submerged macrophytes, and especially allelopathically active species, has been a proposed solution to mitigate cyanobacteria blooms (Hilt et al. 2006). However, this measure has not been tested, and the complex interactions between allelochemicals, cyanobacteria, and phytoplankton species might lead to counterintuitive results, facilitating the proliferation of cyanobacteria (Chang et al. 2012).

Lake-restoration projects typically aim to establish clear-water states because they represent pristine conditions in most cases, provide habitat for a more diverse flora and fauna (figure 2a), and are most desirable for swimming and drinking-water production. However, serious conflicts often arise with stakeholders such as anglers and boaters who may consider submerged vegetation to be a nuisance, especially when tall-growing or floating-leaved macrophytes prevail. Moreover, high macrophyte abundances may under certain circumstances increase the risk of “swimmer’s itch,” a skin rash caused by microscopic parasites (table S2).

Consequently, the nuisance growth of macrophytes, which has been reported for both native and invasive species (Hilt et al. 2006), has been combatted by various macrophyte removal measures such as cutting (figure 3g) or the introduction of herbivorous fish, although these are illegal in some regions. These measures may eventually produce a shift to turbid conditions (Kuiper et al. 2017), counteracting other restoration measures applied to improve lake water quality (Hilt et al. 2006). Comprehensive studies of thresholds for the minimum macrophyte coverage or volume infested needed for maintaining clear-water conditions are still missing. Low-growing macrophyte meadows may create ideal circumstances, maintaining a clear-water state without interfering with swimming or boating (Blindow et al. 2014). However, this will not be feasible in many systems because low-growing macrophyte meadows require low nutrient loading (Van Nes et al. 1999).

In addition to macrophyte cutting, recreational use can trigger regime shifts from clear-water to turbid states in eutrophic lakes. This can stem from the inhibitory effects of motorboats on submerged macrophytes (via chopping by motors and/or sediment resuspension), the removal of piscivorous fish by angling, and the stocking of macrophyte-feeding fish, such as grass carp (table S2; Wittmann et al. 2014), or of benthivorous fish, such as common carp, that can also destroy submerged vegetation (table S2; Villizzi et al. 2015). The stocking of carp (figure 3f) has become common practice across Europe and North America, resulting in an emerging conflict between nature-conservation interests and the requirements of competitive anglers (Williams et al. 2002). In addition, boat and campsite sanitary waste disposal, as well as the feeding and excretion of waterfowl (e.g., Kitchell et al. 1999), may cause an increase in nutrient loading, potentially triggering a regime shift (King and Mace 1974).

Lake-restoration measures aiming to establish clear-water states to allow for safe drinking-water supply and swimming

in waters without cyanobacteria blooms also support natural ecosystem functions of shallow lakes, such as the provision of habitats for a diverse flora and fauna, and potentially also higher nutrient retention. All human recreational uses that risk a shift to the turbid state or prevent a shift back to the clear state by negatively affecting submerged vegetation are thus not only at odds with the aims of lake restoration but may also affect additional natural ecosystem functions of shallow lakes to a yet-unknown extent. Sustainable compromises for the recreational use of shallow lakes must be found that consider the risk of regime shifts and potential consequences for natural ecosystem functions at the landscape scale.

Conclusions

Freshwater ecosystems are among the most affected ecosystems on Earth and are currently being severely altered or destroyed at a faster rate than at any other time in human history (NRC 1992 in Baron et al. 2002). Lakes integrate the effects of anthropogenic changes in their catchments (Williamson et al. 2008), and shallow lakes are especially vulnerable to stressors such as eutrophication, climate change, or water-level changes because of their large area-to-volume ratio, more variable or absent stratification (Mooij et al. 2007), and the greater structural and biological importance of submerged aquatic macrophytes. These macrophytes are the key to a unique characteristic of shallow lakes because of their stabilizing effect on water clarity. Extensive nutrient loading has triggered sudden losses of macrophytes in many shallow lakes, producing shifts from clear to turbid states.

Regime shifts may severely affect ecosystem functions and services. However, shallow-lake management strategies lack the modeling and decision-making tools necessary to predict regime shifts and quantify the effectiveness of management measures such as decreased nutrient loading, fish removal, or macrophyte planting to reverse them (Hupfer and Hilt 2008). Existing management strategies also remain generally uninformed as to the consequences of regime shifts for ecosystem functions and services. In addition, restoration toward a macrophyte-dominated state is often counterbalanced by certain types of recreational use or associated management actions that risk shifts to the turbid state or prevent shifts to the clear state.

At present, most measures of shallow-lake management are applied in response to concerns over the occurrence of cyanobacteria blooms in the turbid state and consequent restrictions in the use for drinking-water production and swimming or as wildlife habitat. The potential impacts of shifts between alternative states on other ecosystem functions and services are largely unknown. Our analyses indicated that five of seven analyzed aquatic organism groups featured a lower biodiversity under turbid states. They also point to a potentially lower nutrient retention under phytoplankton dominance, which may reinforce the turbid state, producing a positive feedback loop in lakes, or the higher export of riverine nutrients to downstream lakes and/or coastal waters. We conclude that most existing studies

associated macrophyte-dominated lakes with improved natural ecosystem functions and services, including biodiversity and nutrient retention, and a higher drinking- and swimming-water quality. However, knowledge gaps were greatest when considering the consequences of regime shifts for landscape C cycling. This is an especially important topic for future research, given that C cycling in aquatic environments plays a significant role in regulating the Earth's climate, even if the total estimated GHG emissions from shallow lakes are currently minor relative to anthropogenic emissions (Tranvik et al. 2009). Overall, a better understanding of these processes will allow future lake management strategies to target improvements in these key functions of shallow lakes along with various ecosystem services such as habitat quality and nutrient retention.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

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