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OPINION

Shifting states, shifting services: Linking regime shifts to changes in ecosystem services of shallow lakes

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Abstract

1. Shallow lakes can shift between stable states as a result of anthropogenic or natural drivers. Four common stable states differ in dominant groups of primary producers: submerged, floating, or emergent macrophytes or phytoplankton. Shifts in primary producer dominance affect key supporting, provisioning, regulating, and cultural ecosystem services supplied by lakes. However, links between states and services are often neglected or unknown in lake management, resulting in conflicts and additional costs.
2. Here, we identify major shallow lake ecosystem services and their links to Sustainable Development Goals (SDGs), compare service provisioning among the four ecosystem states and discuss potential trade-offs.
3. We identified 39 ecosystem services potentially provided by shallow lakes. Submerged macrophytes facilitate most of the supporting (86%) and cultural (63%) services, emergent macrophytes facilitate most regulating services (60%), and both emergent and floating macrophytes facilitate most provisioning services (63%). Phytoplankton dominance supports fewer ecosystem services, and contributes most to provisioning services (42%).
4. The shallow lake ecosystem services we identified could be linked to 10 different SDGs, notably zero hunger (SDG 2), clean water and sanitation (SDG 6), sustainable cities and communities (SDG 11), and climate action (SDG13).
5. We highlighted several trade-offs (1) among ecosystem services, (2) within ecosystem services, and (3) between ecosystem services across ecosystems. These trade-offs can have significant ecological and economic consequences that may be prevented by early identification in water quality management.
6. In conclusion, common stable states in shallow lakes provide a different and diverse set of ecosystem services with numerous links to the majority of SDGs. Conserving and restoring ecosystem states should account for potential trade-offs between ecosystem services and preserving the natural value of shallow lakes.

KEYWORDS
climate change, cyanobacteria, eutrophication, higher plants, restoration

1 | INTRODUCTION

Freshwater lakes and ponds are of great human importance by providing potable freshwater (Gleick, 1993; Van Vliet, Flörke, & Wada, 2017), and by supporting numerous ecosystem services, including the provisioning of fish, shellfish, and edible plants for hundreds of millions of people (McIntyre, Reidy Liermann, & Revenga, 2016). Driven by anthropogenic or natural changes such as excess nutrient input and climate change, many shallow lakes have shifted between stable states (Havens et al., 2016; Huisman et al., 2018; Zhang et al., 2017). A change in states is defined as a persistent change in the structure and function of a system, where shifts in the dominant primary producers are most apparent (Scheffer et al., 2003; Scheffer & Van Nes, 2007). In oligotrophic and mesotrophic states, shallow lakes are typically dominated by various submerged macrophyte species, whereas in more eutrophic states, either floating macrophytes, emergent macrophytes or phytoplankton may prevail (Figure 1; Hilt et al., 2018; Kuiper et al., 2017; Scheffer et al., 2003). Due to ecological feedback causing resistance to external drivers, these states are often stable for periods extending from years to decades (Scheffer & Van Nes, 2007).

Societies receive ecosystem services from lakes (Reynaud & Lanzanova, 2017; Rinke, Keller, Kong, Borchardt, & Weitere, 2019). Ecosystem services are defined as human benefits obtained from nature. Different classification systems of ecosystem services exist, including The Economics of Ecosystems and Biodiversity (TEEB; Kumar, 2010), the Common International Classification of Ecosystem Services (CICES; Haines-Young & Potschin, 2012), and the classification set by Millennium Ecosystem Assessment (MEA; MEA, 2005). Here, we follow the last, which categorises ecosystem services as

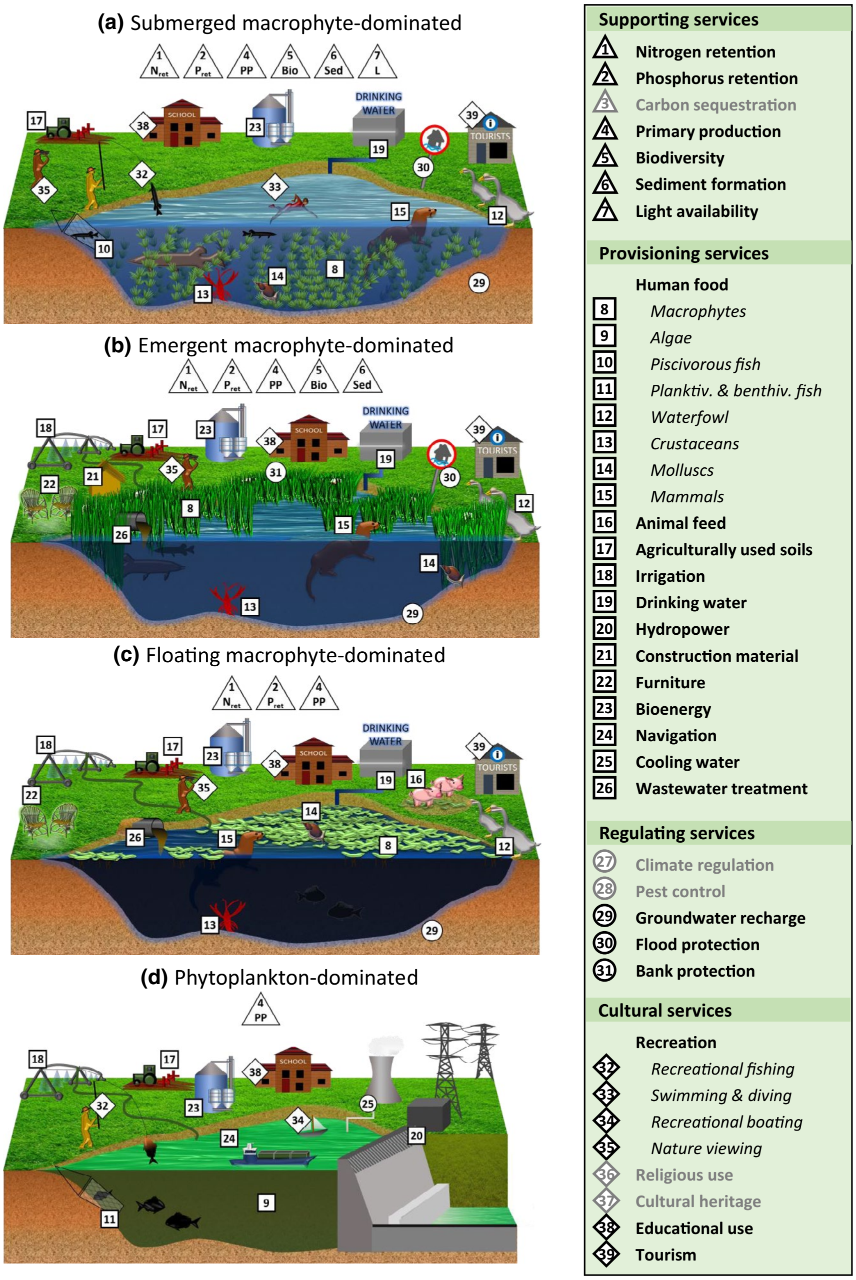

FIGURE 1 Examples of potential links between ecosystem services and the four shallow lake ecosystem states dominated by (a) submerged macrophytes, (b) emergent macrophytes, (c) floating macrophytes, and (d) phytoplankton. The ecosystem services in grey require further research and thus were not linked to a specific ecosystem state. Details regarding the allocation of services to ecosystem states are provided in Table 1 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Examples of potential links between ecosystem services and the four dominant groups of primary producers that are either dominated by submerged macrophytes, emergent macrophytes, floating macrophytes, or phytoplankton

SERVICE	MAIN SUSTAINABLE DEVELOPMENT GOALS (SDG) (see table S1)	SUBMERGED MACROPHYTE-DOMINATED	EMERGENT MACROPHYTE-DOMINATED	FLOATING MACROPHYTE-DOMINATED	PHYTOPLANKTON-DOMINATED	EXPLANATION*
Supporting services						
1. Nitrogen retention	SDG 6	•	•	•	○	Macrophyte dominance provides higher nitrogen retention than phytoplankton dominance[1]. In particular, the fast-growing emergent and floating species promote nitrogen retention[2; 3].
2. Phosphorus retention	SDG 6	•	•	•	○	Macrophyte dominance provides higher phosphorus retention than phytoplankton dominance[1]. In particular, the fast-growing emergent and floating species promote phosphorus retention[2; 3]. Low oxygen conditions that occur in phytoplankton-dominated and floating macrophyte-dominated systems may result in phosphorus release from sediments[3; 4].
3. Carbon sequestration	SDG 13	···	···	···	···	Due to contradictory processes that affect greenhouse gas uptake and production, the net effect on carbon sequestration for any of the systems is unclear[5].
4. Primary production	SDG 15	•	•	•	•	Primary production is generally higher in the more eutrophic systems, although exceptions are the cases when enrichment leads to destabilisation of the food web (cf. paradox of enrichment)[6; 7; 8]. Any of the four states can potentially reach high primary production.
5. Biodiversity	SDG 15	•	•	○	○	Biodiversity is generally lower in more eutrophic systems, but this depends on the species that contribute to biodiversity[9]. Submerged macrophyte dominance is associated with high biodiversity among macroinvertebrates and birds[5] followed by emergent macrophyte-dominated systems that are important habitats for various waterfowl[10].
6. Sediment stabilisation	SDG 15	•	•	○	○	Submerged and emergent macrophytes are rooted in the sediments, thereby stabilising sediments and protecting banks[11; 12]. As a result, systems dominated by either submerged or emergent macrophytes contribute to sediment formation.
7. Light availability	SDG 15	•	○	○	○	Phytoplankton and floating macrophytes strongly attenuate light in the water column. Also, emergent species shade the water column. In contrast, in submerged macrophyte-dominated systems light penetrates deeper[13; 14].
Provisioning services						
8. Macrophytes (Food)	SDG 2	•	•	•	○	Macrophyte-dominated systems can provide food such as stems, leaves, roots, rhizomes, flowers, and fruits. Common plant species used as human food include cattails (*Typha*), Chinese water chestnut (*Eleocharis dulcis*), Indian lotus (*Nelumbo nucifera*), water caltrop (*Trapa natans*), watercress (*Rorippa nasturtium-aquaticum*), water mimosa (*Neptunia oleracea*), water spinach (*Ipomoea aquatica*), wild rice (*Zizania spp.*), and wild taro (*Colocasia esculenta*)[15; 16].
9. Algae (Food)	SDG 2	○	○	○	•	Certain genera of filamentous cyanobacteria (e.g. *Spirulina* sp. and *Aphanizomenon flos-aquae*) are consumed in countries in Africa and Asia[17; 18]. For centuries, these species have been a significant source of high macro- and micronutrients, vitamins, and fibres. This makes some cyanobacterial species a healthy source of food or medicine[18].
10. Piscivorous fish (Food)	SDG 2	•	○	○	○	Clear, oligotrophic waters with sufficient oxygen commonly have a higher percentage of piscivorous fish than more turbid, eutrophic waters[9]. Therefore, most piscivorous fish can be found in systems dominated by submerged and emergent macrophyte[19], yet fisheries are least obstructed by plant material in systems dominated by submerged macrophytes[20]. Examples of piscivorous fish commonly found in clear waters are game fish species such as perch (*Perca fluviatilis*) and pike (*Esox lucius*)[21].
11. Planktivorous and benthivorous fish (Food)	SDG 2	○	○	○	•	Turbid waters commonly have the highest percentage of planktivorous and benthivorous fish[9]. Most planktivorous and benthivorous fish can be found in systems dominated by floating macrophytes or phytoplankton[9; 19], yet fisheries are least obstructed in systems dominated by phytoplankton. An example of fish commonly found in turbid waters is bream (*Abramis brama*).
12. Waterfowl (Food)	SDG 2	•	•	•	○	Macrophyte-dominated systems are important habitats for diverse waterfowl that provide meat[22].

(Contiues)

supporting, *provisioning*, *regulating*, and *cultural services* (MEA, 2005). *Supporting services* involve key ecosystem functions, such as primary production, nutrient cycling, and retention, as well as carbon sequestration. *Provisioning services* are outputs of nature directly obtained from ecosystems including human food, animal feed, and drinking water. *Regulating services* are benefits of processes such as climate regulation and pest control. Lastly, *cultural services* are non-material benefits (e.g. spiritual, aesthetic, and inspirational values) that facilitate activities such as recreation, social cohesion, and religious celebrations.

By providing ecosystem services, lakes contribute to the United Nations (UN) Sustainable Development Goals (SDGs). These goals are designed to achieve a better and more sustainable future for the global human population. Previous research showed a strong link between ecosystem services provided by various kinds of ecosystems and the SDGs, notably including the provision of food (SDG 2), water (SDG 6), sustainable cities (SDG 11), and carbon storage (SDG13; Wood et al., 2018). Lakes can play an important role in SDGs by providing a range of ecosystem services (Ho & Goethals, 2019; Steinman et al., 2017). These services, however, will also depend on the ecosystem state and dominant primary producer groups (Hilt, Brothers, Jeppesen, Veraart, & Kosten, 2017; Rinke et al., 2019). Changes in nutrient loading, weather extremes, or by management measures can alter lake processes such as the competitive advantage of one primary producer over another, which may result in a state shift toward dominance of a different group of primary producers. As a result, there might

TABLE 1 Continued

13. Crustaceans (Food)	SDG 2	●	●	●	○	Although being omnivorous and able to eat phytoplankton, most large crustacean species used for human consumption like crab (e.g. *Eriocheir sinensis*), crayfish (e.g. *Procambarus clarkii*) or shrimp (e.g. *Macrobrachium rosenbergii*), prefer to live in macrophyte-dominated systems[23; 24; 25]. These macrophyte-dominated systems may become turbid when the biomass of crustaceans becomes high.
14. Molluscs (Food)	SDG 2	●	●	●	○	Freshwater molluscs including snails serve as important protein sources in numerous countries, e.g., Mexico, Philippines, India, and China[26; 27]. At higher densities, however, they are detrimental to the clear-water state[28]. In phytoplankton-dominated systems, elevated cyanotoxins in molluscs may form a risk to human consumption[29].
15. Mammals (Food)	SDG 2	●	●	●	○	Although it is largely banned, mammals are hunted for human consumption. An example are nutria (*Myocastor coypus*) that is hunted for both meat and fur[30]. In the past, manatees (*Trichechus*) were hunted extensively[31; 32]. Both nutria and manatee feed on freshwater macrophytes[30; 31; 32; 33]. In phytoplankton-dominated systems, elevated cyanotoxins in mammals form a risk to human consumption[29].
16. Animal feed	SDG 12	○	○	●	○	Floating macrophytes such as duckweed and *Azolla* provide feed for domestic animals and are used in aquaculture[34].
17. Agriculturally used soils	SDG 12	●	●	●	●	Macrophyte biomass, as well as algal biomass, can be used to fertilise agricultural soils[35; 36]. For instance, the aquatic fern *Azolla* is used as a 'sister crop' in rice culture for natural nitrogen fertilisation[37]. Using aquatic plants and algae to fertilise soils has a health and safety risk through possible high concentrations of heavy metals or biotoxins[36].
18. Irrigation	SDG 12	○	●	●	●	The use of eutrophic systems for irrigation water is called fertigation since, eutrophic water is high in nutrient content. Note that phytoplankton-dominated systems may involve high cyanobacterial toxin concentrations that pose a putative human health risk[38]. By contrast, macrophyte-dominated systems have the risk of blocking irrigation canals. Treating these macrophytes with herbicides may result in unsuitable water for irrigation. Therefore, different irrigation systems are supported by different groups of primary producers[39].
19. Drinking water	SDG 6	●	●	●	○	Drinking water requires toxin-free and clear water which is potentially restricted in phytoplankton-dominated systems if toxic cyanobacterial biomass is high[40].
20. Hydropower	SDG 7	○	○	○	●	Hydropower benefits from low resistance, which can be reached when the waterway is free of potentially blocking macrophytes[41].
21. Construction material	SDG 11	○	●	○	○	Reed is an emergent macrophyte species often harvested for construction materials and roofing[42; 43].
22. Furniture	SDG 11	○	●	●	○	Emergent and floating macrophytes can be used for bio-based furniture[44]. Emergent species such as cattails (*Typha* sp.) can be used to produce fibre mats and composite panels for furniture indusries[44]. Moreover, rattan made of the floating species water hyacinth (*Eichhornia crassipes*) is patented[45].
23. Bioenergy	SDG 7	●	●	●	●	Bioenergy, including biofuel and biogas, can be produced from macrophytes and algae[46; 47].
24. Navigation	SDG 9	○	○	○	●	Macrophyte-dominated systems pose a high risk of blocking waterways for navigation[41; 48].
25. Cooling water	SDG 7	○	○	○	●	The use of cooling water benefits from low resistance, which can be reached when the waterway is free of potentially obstructing macrophytes[41].
26. Wastewater treatment	SDG 6	○	●	●	○	Floating and emergent macrophytes are known for their capacity to effectively remove nitrogen and phosphorus from the water, thereby providing wastewater treatment[49; 50; 51].
Regulating services						
27. Climate regulation	SDG 13	⋯	⋯	⋯	⋯	See ecosystem service No. 3.
28. Pest control	SDG 3	⋯	⋯	⋯	⋯	Each system has its related pests, such as swimmers itch in macrophyte-dominated systems[1] and diseases such as botulism during anoxic conditions in eutrophic waters[52]. Changing a dominant group may control one pest, but might lead to another one.
29. Groundwater recharge	SDG 6	●	●	●	○	Cyanobacterial toxins, potentially present in phytoplankton-dominated systems, can contaminate groundwater, making the groundwater unsuitable for human use[53].
30. Flood protection	SDG 15	●	●	⋯	⋯	Macrophytes function as 'natural weirs' by blocking the floodplain at periods of low water while bending to allow water discharge in periods of high flow[54].
31. Bank protection	SDG 15	○	●	○	○	Emergent macrophytes can provide a natural solution to bank erosion[55].
Cultural services						
32. Recreational fishing	SDG 11	●	○	○	●	See ecosystem service Nos. 9 and 10. Depending on the target species.
33. Swimming & diving	SDG 11	●	○	○	○	Swimmers prefer clear water which is supported by submerged macrophytes. However, swimmers experience structural nuisance when macrophytes become excessive. Moreover, swimmers' itch is also associated with macrophytes[1].
34. Recreational boating	SDG 11	○	○	○	●	Advantage of phytoplankton-dominated systems for recreational boating is the absence of structural nuisance[41], however, boating is possibly less attractive during toxic cyanobacterial blooms with malodours and poor aesthetics[56]. Macrophyte-dominated systems are seen as a nuisance as they physically obstruct the movement of boats or ships[41].
35. Nature viewing	SDG 11	●	●	●	○	Wildlife watching including bird watching is among the activities where people observe nature[22]. Due to malodours and low biodiversity, phytoplankton-dominated systems are usually less attractive for nature viewing[56].
36. Religious use	SDG 11	⋯	⋯	⋯	⋯	Depends on local customs.
37. Cultural heritage	SDG 11	⋯	⋯	⋯	⋯	Depends on cultural preferences.
38. Educational use	SDG 4	●	●	●	●	All systems provide educational opportunities to demonstrate what functions are appreciated or not. The educational value of each of the states depends on the goal of education.
39. Tourism (other than Nos. 32–38)	SDG 12	●	●	●	○	Due to malodours, low biodiversity and poor aesthetics, phytoplankton-dominated systems exhibiting algal blooms are usually not desirable for tourism[56].
In summary	**SDGs**	***n* (%)**	***n* (%)**	***n* (%)**	***n* (%)**	
Supporting services	6, 13, 15	6 (86%)	5 (71%)	3 (43%)	1 (14%)	out of 7 supporting services
Provisioning services	2, 6, 7, 9, 11, 12	9 (47%)	12 (63%)	12 (63%)	8 (42%)	out of 19 provisioning services
Regulating services	3, 6, 13, 15	2 (40%)	3 (60%)	1 (20%)	0 (0%)	out of 5 regulating services
Cultural services	4, 11,12	5 (63%)	3 (38%)	3 (38%)	3 (38%)	out of 8 cultural services
Total		22 (56%)	23 (59%)	19 (49%)	12 (31%)	out of 39 ecosystem services

Circles denote that primary producer dominance supports (•) or does not support (○) ecosystem services. In some cases, dominance by either of the four primary producers has contrasting implications for the ecosystem services, which we denote by dashed lines (⋯). We also explain why certain dominant primary producers support an ecosystem service or not. Specific cases may deviate from our examples. *References to the literature are indicated with superscript numbers and can be found in the reference list provided in Supporting Information.

also be a shift in ecosystem services provided by lakes, and there may be trade-offs between ecosystem services.

Here, we first provide a comprehensive overview of shallow freshwater lake ecosystem services for each of the four dominant groups of primary producers (submerged, floating, or emergent macrophytes, or phytoplankton) and link these services to the SDGs. Secondly, we discuss trade-offs between these services. Lastly, we argue that linking ecosystem states to distinct ecosystem services, and thereby SDGs, and identifying potential trade-offs may help in prioritising management strategies.

2 | PRIMARY PRODUCER GROUPS AND ECOSYSTEM SERVICES

In shallow lakes and ponds, multiple stable states are recognised, each characterised by a dominant group of primary producers (Scheffer et al., 2003; Scheffer & Van Nes, 2007). The four major groups are either dominated by submerged macrophytes, emergent macrophytes, floating (i.e. roots in the water), or floating-leaved (i.e. roots in the sediment) macrophytes and phytoplankton. While each dominant group of primary producers is comprised of a different species pool across biomes and/or continents (Mikheyeva, Parparov, Adamovich, Gal, & Lukyanova, 2017), the species within a dominant group share similar growth strategies (Verhofstad & Bakker, 2019). For each of the four dominant groups, we elaborate on how they contribute to various ecosystem services.

2.1 | Submerged macrophytes

Submerged macrophytes are commonly found in oligotrophic to mesotrophic systems (Figure 1a). Low-growing submerged vegetation such as Chara (*Charophyceae*) generally dominates in oligotrophic shallow lakes, while canopy-forming and tall-growing submerged vegetation dominates mesotrophic to eutrophic shallow lakes (Verhofstad et al., 2017). Submerged macrophytes support clear-water conditions in lakes, which is beneficial for numerous ecosystem services. Specifically, high water transparency by suppression of sediment resuspension (Vermaat, Santamaria, & Roos, 2000) as a *supporting service* is beneficial to *provisioning services* such as drinking water production (Gillefalk, Massmann, Nützmann, & Hilt, 2018), as well as to various *cultural services* including recreation, because bathers, swimmers, tourists, and lakeside property owners usually prefer clear water (Angradi, Ringold, & Hall, 2018). Macrophytes also provide several *cultural services* such as recreational fishing (Slagle & Allen, 2018) and hunting (Huber, Meldrum, & Richardson, 2018).

Submerged macrophytes have the potential for *provisioning services* through human food supply. For example, some freshwater submerged macrophytes are consumed by humans (Aasim, Bakhsh, Sameeullah, Karataş, & Khawar, 2018; Chai, Ooh, Quah, & Wong, 2015). Indirectly, submerged macrophytes provide a *supporting service* for human food by either providing habitat for game fish and invertebrates (Craig, 2008), or by serving as food for herbivores which—in turn—are consumed by humans. Examples of the latter are fish, waterfowl, crustaceans, molluscs, and mammals (Bakker et al., 2016).

Submerged macrophytes additionally provide *supporting services* through oxygen production (Caraco, Cole, Findlay, & Wigand, 2006), as well as nutrient retention and denitrification (Veraart, de Bruijne, de Klein, Peeters, & Scheffer, 2011), which reduces nutrient concentrations in the water column and suppresses phytoplankton dominance (Scheffer, Hosper, Meijer, Moss, & Jeppesen, 1993). They provide a huge surface for periphytic biofilm, in which nitrification and denitrification are coupled (Körner, 1999). These periphytic biofilms provide food for higher trophic levels, yet also hamper macrophyte growth by shading if they become abundant (Hilt et al., 2018). Oxygen loss from roots of submerged macrophytes (Wang, Hu, Xie, & Yang, 2018) mediates the formation of iron crusts in anaerobic sediment, leading to an enhanced phosphorus binding (Hupfer & Dollan, 2003). Submerged macrophytes also provide habitat for piscivorous fish and their prey (Jeppesen, Peder Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000), and give shelter for zooplankton (Hupfer & Dollan, 2003). Several submerged macrophyte species excrete allelopathic substances that inhibit phytoplankton growth (Hilt & Gross, 2008). For most aquatic organism groups, the dominance of submerged macrophytes provides habitat for a higher diversity of species (Hilt et al., 2017).

2.2 | Emergent macrophytes

Emergent macrophytes (Figure 1b) are rooted in the sediment and restricted to shallow water usually <1.5 m deep because of the energy required to extend shoots to the water surface (Grace, 1989), although exceptions exist (Cronk & Fennessy, 2009). Having the largest part of their biomass generally above the water surface, they are the most productive vegetation type as they have direct access to light, as well as nutrients from the sediment (Kazanjian et al., 2018). Typical emergent macrophyte species for temperate and tropical regions include common reed (*Phragmites australis*), cattail (*Typha* sp.), and papyrus (*Cyperus papyrus*). These species are often used in constructed wetlands as part of (waste) water treatment because of the important *regulating services* they provide. They take up dissolved nutrients from the sediment and the water column for their growth, which leads to nutrient removal if they are harvested (Meerburg et al., 2010). They also transfer oxygen into the rhizosphere (Wang et al., 2018) supporting nitrification and aerobic degradation of organic matter. Emergent macrophytes stabilise substrate, prevent constructed wetlands (planted filter beds that are drained at the bottom) from clogging, and provide a large surface for bacterial growth (Brix, 1994). Substantial amounts of carbon are sequestered in both the above- and below-ground biomass of emergent plants (De Klein & Van der Werf, 2014). *Regulating services* in lakes also include reduction of wave energy that may protect infrastructure at the banks from erosion damage (Coops, van den Brink,

& van der Velde, 1996). Emergent macrophytes, such as common reed (*Phragmites australis*) and papyrus (*Cyperus papyrus*), are often harvested for construction materials including roofing (Kipkemboi & van Dam, 2018; Köbbing, Thevs, & Zerbe, 2013). These species may also provide *cultural services* when they are used for cultural practices such as for weddings and witchcraft (Kakudidi, 2004; Van Dam, Kipkemboi, Rahman, & Gettel, 2013). Some emergent macrophyte parts are used for human consumption, including wild rice grains (Zhai, Tang, Jang, & Lorenz, 1996) and *Typha* roots and shoots, of which the latter was part of the European Paleolithic human diet, and is considered a potential protein-rich food source for the future (Morton, 1975; Revedin et al., 2010).

2.3 | Floating macrophytes

Floating or floating-leaved macrophytes (Figure 1c) often show high growth rates, with duckweeds (e.g. *Lemnaceae*) representing the most rapidly growing higher plants (Ziegler, Adelmann, Zimmer, Schmidt, & Appenroth, 2015). As a *supporting service*, they can form thick mats that block light penetration and prevent phytoplankton growth, including toxic cyanobacterial bloom formation. Unlike submerged macrophytes, they release most of the photosynthetically produced oxygen into the air, while waters below floating macrophytes therefore often turn anoxic. Consequently, oxygen-sensitive biochemical transformations such as denitrification, methane formation, and release of iron-bound phosphorus from sediments are facilitated. The facilitation of iron-bound phosphorus, in turn, results in a positive feedback between phosphorus concentrations and floating macrophyte dominance (Kazanjian et al., 2018; Scheffer et al., 2003). A large proportion of the methane produced becomes oxidised below floating macrophytes with a decreased diffusive water–atmosphere flux, entrapment, and methane-oxidising bacteria in the aerobic rhizosphere (Kosten et al., 2016). Floating macrophytes have both negative (facilitating methane production) and positive (reducing methane diffusion) *regulating services* with regard to impacts on climate (Ávila et al., 2019; Kosten et al., 2016).

Under increasingly anoxic conditions, aquatic biodiversity in water bodies dominated by floating plants can be restricted to a few species insensitive to low oxygen concentrations (Saari, Wang, & Brooks, 2018). By contrast, like submerged macrophytes, floating macrophytes also provide habitat and food for invertebrates, birds, and mammals (Bakker et al., 2016). Their disappearance can have a cascading effect on other trophic levels. The dragonfly *Aeshna viridis* became rare as a consequence of the decline of water soldier (*Stratiotes aloides*), which provides a substrate for their eggs and protection for larvae (Rantala, Ilmonen, Koskimäki, Suhonen, & Tynkkynen, 2004). Such macrophyte-dependent changes in insect abundances have potential consequences for numerous services in which insects are involved. These include *supporting services* such as decomposition and nutrient recycling, and *provisioning services* such as food for higher aquatic trophic levels, terrestrial animal feed, and human food (Macadam & Stockan, 2017). Due to its attractive flowers, the floating water hyacinth (*Eichhornia crassipes*), native to South America, has spread globally since the late 1800s through the ornamental plant trade (Coetzee, Hill, Ruiz-Téllez, Starfinger, & Brunel, 2017). However, the excessive growth of this floating macrophyte species in response to eutrophication is linked to mosquito plagues (Crossetti et al., 2019). Today, water hyacinth is also called the *Terror of Bengal* as extensive growth may block shipping lanes and clog water intake for industries (Güereña, Neufeldt, Berazneva, & Duby, 2015; Ogutu-Ohwayo & Balirwa, 2006). Substantial financial resources are invested to manage and limit their proliferation (Wainger et al., 2018).

Floating macrophytes, including duckweed, also directly sustain *provisioning services* such as a high-protein food resource for humans, feed for domestic animals and fish (Appenroth et al., 2017), and biofuel production (Cui & Cheng, 2015). Lastly, floating macrophytes are capable of effectively removing nitrogen and phosphorus from the water, because they use dissolved nutrients for their growth. As such, they support sustainable nutrient recycling from wastewater through regular harvesting of the plants that can be subsequently used as fodder (Körner, Vermaat, & Veenstra, 2003). Additional benefits are realised in *provisioning services* like restoring soil and water quality for agriculture (Güereña et al., 2015). The harvested biomass of water hyacinth is used to produce furniture (Opande, Onyango, & Wagai, 2004).

2.4 | Phytoplankton

The proliferation of phytoplankton (Figure 1d) reduces water transparencywhich restricts light availability for submerged macrophytes, potentially leading to a shift from a macrophyte- to phytoplankton-dominated state (Sand-Jensen & Søndergaard, 1981; Scheffer, 1990; Scheffer & Carpenter, 2003). Phytoplankton growth and biomass production are *supporting services* that sustain higher trophic levels in aquatic food webs (e.g. zooplankton, planktivorous fish, piscivores). Dense phytoplankton blooms are often associated with the provisioning of fisheries with planktivorous or benthivorous fish such as shad, bream, and carp (Jeppesen et al., 1997; Weber & Brown, 2009). In contrast, dense phytoplankton blooms may suppress piscivorous game fish species such as pike due to impaired visibility for these visual predators (Turesson & Brönmark, 2007), while eutrophication of Lake Victoria led to increases in the production of the piscivorous Nile perch (*Lates nolitica*), which is a valuable export species (Downing et al., 2014; Galafassi et al., 2017). Moreover, phytoplankton, including cyanobacteria, were shown to constitute a major part of the food for Nile tilapia (*Oreochromis niloticus*; Semyalo et al., 2011). These various fish species are valued for human consumption (Tacon & Metian, 2013). Phytoplankton may furthermore support the proliferation of macroinvertebrate species harvested for food (Cai, Gong, & Qin, 2012). In some phytoplankton-dominated lakes, cyanobacteria are harvested for food (e.g. *Spirulina* or *Arthrospira*; Habib, 2008), and phytoplankton-dominated lakes may provide a genetic resource for the synthesis of valuable biochemicals

(Mooij, Stouten, Tamis, van Loosdrecht, & Kleerebezem, 2013; Muys et al., 2019).

3 | LINKING ECOSYSTEM STATES TO ECOSYSTEM SERVICES

We identified 39 ecosystem services potentially provided by shallow lakes (Figure 1 and Table 1). Based on our annotations, all three macrophyte-dominated systems each support about half of the ecosystem services (49–59%). Each macrophyte-dominated state excels in a different set of ecosystem services. Submerged macrophyte-dominated systems facilitate a higher part of the *supporting* and *cultural services* (86 and 63%, respectively), while emergent macrophyte-dominated systems facilitate most to the *provisioning* and *regulating services* (63 and 60%, respectively). Phytoplankton-dominated systems generally support the least ecosystem services (31%). We could not find *regulating services* for systems that are phytoplankton-dominated, although these systems could play a role in carbon sequestration when their biomass ends up in carbon storage (Hilt et al., 2017).

Several ecosystem services, including carbon sequestration, climate regulation, pest control, religious use, and cultural heritage, require further investigation before they can be linked to a specific dominating group of primary producers. Lakes sequester carbon, emit greenhouse gases (Tranvik et al., 2009), and they can transmit waterborne diseases (Bonadonna & La Rosa, 2019); yet the net effect of each of the dominant groups of primary producers on these ecosystem services is currently unclear. Recent research on the role of religion and other cultural functions in lake management (Lowe, Jacobson, Anold, Mbonde, & Lorenzen, 2019; Semyalo et al., 2011; Steinman et al., 2017) suggests potential links between lake state and cultural use that also warrant further investigation.

By supporting 39 ecosystem services, shallow lakes and the respective dominant primary producer groups directly contribute to 10 of the 17 SDGs. When also accounting for secondary contributions, lakes support up to 13 out of 17 SDGs (Table S1). The *supporting services* mainly contribute to SDGs linked to the biosphere, including clean water (SDG 6), climate control (SDG 13), and life on land (SDG 15). *Provisioning services* contribute mainly to SDGs linked to resources, such as food (SDG 2), clean water (SDG 6), energy (SDG 7), and infrastructure (SDG 9), as well as the sustainable and responsible use of these resources through sustainable cities (SDG 11) and responsible consumption and production (SDG 12). *Regulating services* focus on SDGs linked to well-being such as health (SDG 3), clean water (SDG 6), and life on land (SDG 15). Lastly, *cultural services* contribute to SDGs that are linked with economy and society through education (SDG 4), sustainable cities (SDG 11), and responsible consumption (SDG 12). Although ecosystem services in lakes did not contribute directly to all 17 SDGs, lakes and their predominant group of primary producers are indirectly important to each of them. For instance, if lakes dominated by submerged macrophytes provide sufficient economic services such as food and water resources, they indirectly contribute to a reduction in poverty (SDG 1) and prevent resource-related conflicts (SDG 16).

4 | SHIFTING STATES, SHIFTING SERVICES

Shifts to a different group of dominant primary producers can be induced by different internal and external disturbances. Examples of disturbances include a change in nutrient loading, planned intervention (e.g. mowing or biomanipulation), changes in lake morphometric and hydrological characteristics (e.g. depth or residence time), other man-controlled processes (e.g. bank filtration for drinking water), and changes in climatic conditions (Gillefalk et al., 2019; Havens et al., 2016; Kong et al., 2016; Scheffer et al., 1993; Scheffer & Van Nes, 2007). These disturbances can alter lake processes leading to a competitive advantage of one primary producer over another, which may result in a state shift toward dominance of a different group of primary producers. This, in turn, will also lead to a shift in the ecosystem services provided by the lakes, and thereby to a different set of SDGs.

Lake management seeks to achieve and maintain a stable state, producing the desired combination of ecosystem services. More diverse ecosystems provide a wider range of ecosystem services (Oliver et al., 2015). Therefore, biodiversity is considered a key characteristic of a healthy ecosystem functioning and is associated with higher resilience and productivity (Cardinale et al., 2006; Ptacnik et al., 2008). This so-called *insurance effect* of biodiversity may secure ecosystem resilience and productivity, and is identified by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services as the most important but also most threatened *supporting service* for human life (IPBES, 2019). In shallow lakes, submerged macrophyte dominance tends to be associated with higher biodiversity in multiple taxa, including invertebrates and birds compared to phytoplankton-dominated systems (Hilt et al., 2018). We note, however, that enhanced diversity of one group of organisms can lead to reduced diversity of other groups (Declerck et al., 2005). For instance, emergent macrophyte-dominated systems are important habitats for different waterfowl, but macroinvertebrate diversity is lower than in submerged macrophyte-dominated systems (Weisner & Thiere, 2010).

Phytoplankton-dominated lakes support a different set of ecosystem functions from macrophyte-dominated lakes, and they only exhibit minor overlaps in function. These differences in ecosystem services between and within stable states may lead to trade-offs for lake water management (see also Figure 1 and Table 1).

4.1 | Trade-offs between ecosystem services

Some ecosystem services associated with certain ecosystem states show direct trade-offs with each other. For instance, macrophyte-dominated states provide beneficial feedbacks to overall water quality and thereby favour several *supporting services*. However, high macrophyte abundances in more eutrophic systems, particularly those containing vertical tall-growing or floating species, constrain some *provisioning services*, such as navigation and drinking water supply, as well as *cultural services* like recreation and fishing (Hilt et al., 2017; Verhofstad & Bakker, 2019; Villamagna, Murphy, & Trauger, 2010). Thus, although these services are provided through good water quality promoted by the macrophytes, the macrophytes themselves constrain other services. A compromise would be possible in a mesotrophic lake, by aiming for a low abundance of macrophytes combined with high water clarity, though this often seems challenging and difficult to achieve (Kuiper et al., 2017; Van Nes et al., 1999). Primary producer dominance may also vary spatially within lakes, whereby a single lake may provide multiple services (Janssen et al., 2017, 2019). For example, Lake Okeechobee has a clear water littoral zone dominated by *Chara* sp., while the open water is dominated by phytoplankton, including harmful cyanobacteria (Harwell & Sharfstein, 2009; Havens, Phlips, Cichra, & Li, 1998).

4.2 | Trade-offs within ecosystem services

Trade-offs may arise within the provisioning of specific ecosystem services. For example, climate control as *regulating service* by emergent macrophytes can involve carbon capture, as their carbon retention is high. However, they may also enhance the emission of the potent greenhouse gas methane, as the stem may act as chimneys transporting methane from sediments to the atmosphere (Bodelier, Stomp, Santamaria, Klaassen, & Laanbroek, 2006; De Klein & Van der Werf, 2014; Laanbroek, 2009). Another example is the enhanced phosphorus removal from the lake water through harvesting of floating macrophytes. However abundant floating macrophytes may also lead to sediment anoxia that stimulates sediment phosphorus release, thereby increasing bioavailable phosphorus supplies in the water column.

4.3 | Trade-offs in ecosystem services across connected ecosystems

Intense use of lakes and the surrounding catchment for human benefit increases the pressure on lake resources and compromises a sustainable use of services they provide (Rinke et al., 2019; Teurlincx et al., 2019). For example, agricultural and industrial land use in catchments promotes food provisioning, and as such support SDG2 (Table S1). These human activities are also associated with eutrophication of lakes, and as such enhancing lake productivity (Beusen, Bouwman, Van Beek, Mogollón, & Middelburg, 2016). Although this could enhance food provisioning by lakes as well, it often leads to a proliferation of less desired primary producers such as harmful cyanobacteria or duckweed. As eutrophication also reduces water quality (Wetzel, 2001), it compromises access to clean water and use of water for sanitation, as indicated in SDG6, and reduces food provisioning by lakes, thereby negatively affecting SDG2 (Table 1 and Table S1). Increasing anthropogenic pressures on lake ecosystems linked to food production in surrounding catchments creates trade-offs with lake ecosystems services, including those related to food provisioning.

We propose that trade-offs in ecosystem services emerge within lakes, and also between lakes and their surrounding environment. Future shifts in states will also prompt shifts in ecosystem services supported and will lead to a change in trade-offs. The current scientific and public debate on the required ecosystem services provided by lakes would benefit from better recognition of these potential trade-offs. Indeed, leaving out the effect of potential trade-offs could lead to expensive *surprises* and the need for follow-up measures, for example mowing of dense macrophyte stands after biomanipulation (e.g. fish removal) of small eutrophic lakes used for swimming (Hussner, Gross, Van de Weyer, & Hilt, 2014; Kuiper et al., 2017). To support better inclusion of these trade-offs in the scientific and societal debate, we recommend management decisions to include factors such as the uniqueness of each lake embedded in its ecological characteristics, as well as its economic and cultural value, to prioritise among all ecosystem services and specific regional needs.

5 | CONCLUSIONS

Many lakes and ponds worldwide experience state shifts that have far-reaching consequences for ecosystem services that lakes provide. Institutions such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019), Food and Agriculture Organisation (FAO, 2019), and World Health Organisation (WHO, 2015) warn that ecosystems, including lakes, are no longer able to provide the desired ecosystem services due to a loss in biodiversity, thereby threatening human and ecosystem health and thus achieving the SDGs. We call for a scientific and public debate that includes the effect of potential trade-offs between the different stable states and their associated services, as there is no single state that provides all desirable ecosystem services. Submerged macrophyte-dominated shallow lakes provide the highest biodiversity, and support the greatest number of ecosystem services, as compared to the other stable states (Table 1). However, we still lack knowledge about the full set of shallow lake ecosystem services, their relative importance, and potential trade-offs between these services and associated SDGs (Table 1). Conserving and restoring ecosystem states should account for potential trade-offs between ecosystem services and preserving the natural value of shallow lakes.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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