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**REVIEW**

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

**Annette B. G. Janssen1**| **Sabine Hilt2**| **Sarian Kosten3**| **Jeroen J. M. de Klein4**| **Hans W. Paerl5**| **Dedmer B. Van de Waal6**

1Water Systems and Global Change Group, Wageningen University & Research, Wageningen, The Netherlands

2Department of Ecosystem Research, Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany

3Department of Aquatic Ecology and Environmental Biology, Institute for Water and Wetland Research, Radboud University, Nijmegen, The Netherlands

4Aquatic Ecology and Water Quality Management Group, Wageningen University & Research, Wageningen, The Netherlands

5Institute of Marine Sciences, The University of North Carolina at Chapel Hill, Morehead City, NC, U.S.A.

6Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

**Correspondence**

Annette B. G. Janssen, Water Systems and Global Change Group, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, The Netherlands. Email: [annette.janssen@wur.nl](mailto:annette.janssen@wur.nl)

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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 pro-ducer dominance affect key supporting, provisioning, regulating, and cultural ecosys-tem 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 con-tributes 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), sustain-able cities and communities (SDG 11), and climate action (SDG13).
5. We highlighted several trade-offs (1) among ecosystem services, (2) within eco-system 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



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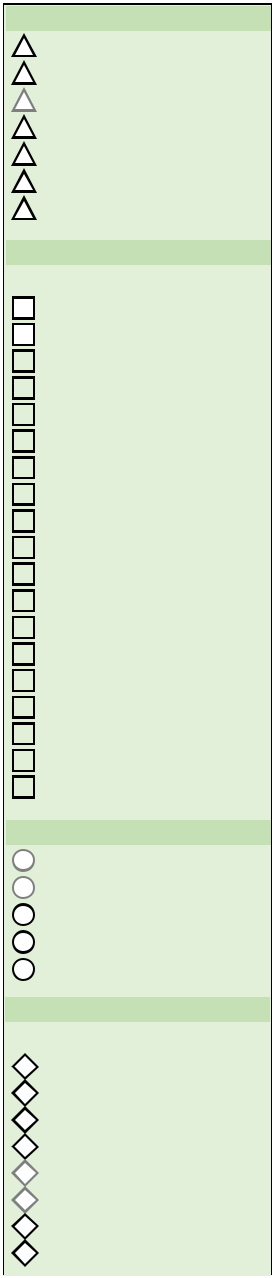


**1** | **INTRODUCTION**

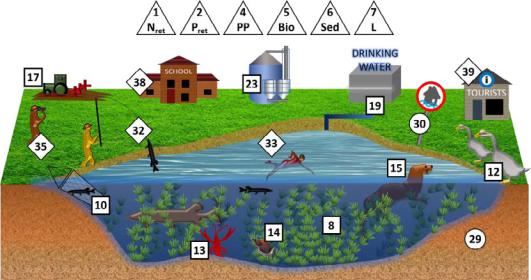
Freshwater lakes and ponds are of great human importance by providing potable freshwater (Gleick, 1993; Van Vliet, Flörke, & Wada, 2017), and by supporting numerous ecosystem services, including the provisioning of fish, shellfish, and edible plants for hundreds of millions of people (McIntyre, Reidy 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 phy-toplankton 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 extend-ing from years to decades (Scheffer & Van Nes, 2007).

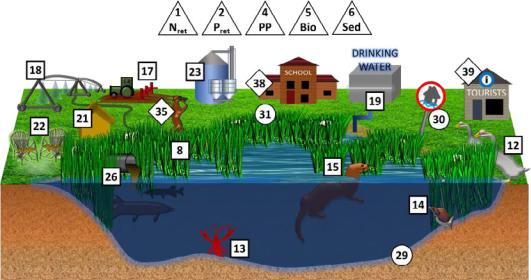
Societies receive ecosystem services from lakes (Reynaud & Lanzanova, 2017; Rinke, Keller, Kong, Borchardt, & Weitere, 2019). Ecosystem services are defined as human benefits obtained from nature. Different classification systems of ecosystem services exist, including The Economics of Ecosystems and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



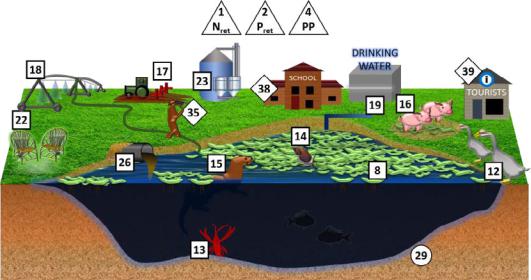
1. Submerged macrophyte-dominated



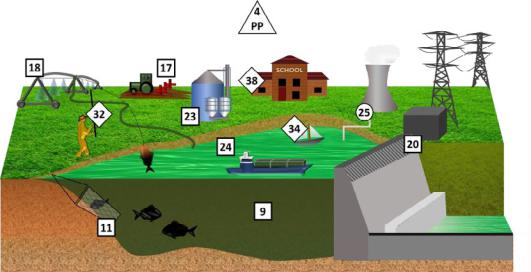
1. Emergent macrophyte-dominated



1. Floa**** macrophyte-dominated



1. Phytoplankton-dominated



**Suppor****ng services**

1. **Nitrogen retenon**
2. **Phosphorus retenon**
3. **Carbon sequestraon**
4. **Primary producon**
5. **Biodiversity**
6. **Sediment formaon**
7. **Light availability**

**Provisioning services**

**Human food**

1. *Macrophytes*
2. *Algae*
3. *Piscivorous fish*
4. *Plan******. & benthiv. fish*
5. *Waterfowl*
6. *Crustaceans*
7. *Molluscs*
8. *Mammals*
9. **Animal feed**
10. **Agriculturally used soils**
11. **Irrigaon**
12. **Drinking water**
13. **Hydropower**
14. **Construcon material**
15. **Furniture**
16. **Bioenergy**
17. **Navigaon**
18. **Cooling water**
19. **Wastewater treatment**

**Regula****ng services**

1. **Climate regula****on**
2. **Pest control**
3. **Groundwater recharge**
4. **Flood protecon**
5. **Bank protecon**

**Cultural services**

**Recrea****on**

1. *****nal fishing*
2. *Swimming & diving*
3. *****nal boa*****
4. *Nature viewing*
5. **Religious use**
6. **Cultural heritage**
7. **Educaonal use**
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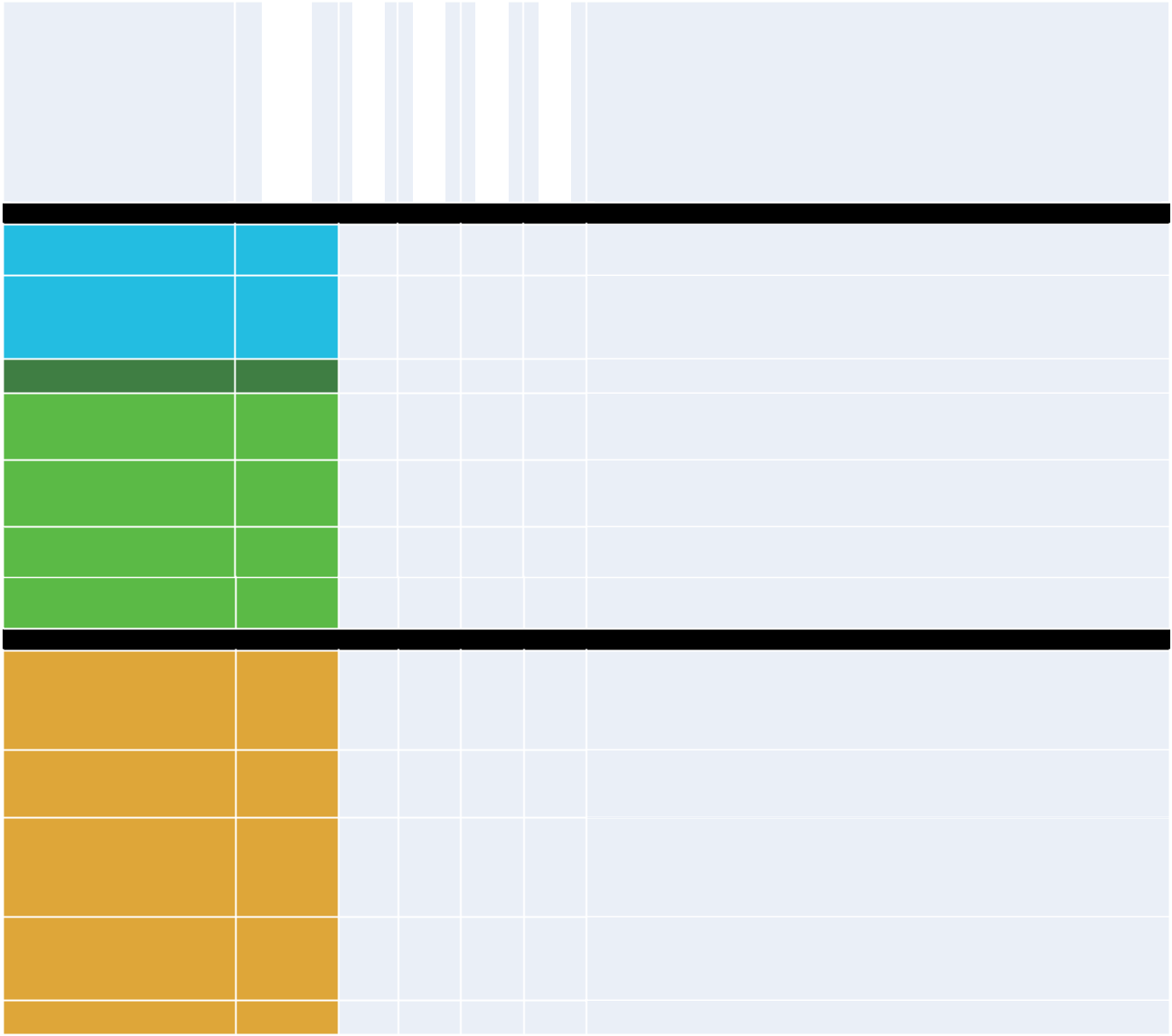
**FI G U R E 1** Examples of potentiallinks between ecosystem services and the four shallow lake ecosystem states dominated by (a) submerged macrophytes,

1. 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

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**TA B L E 1** Examples of potential links between ecosystem services and the four dominant groups of primary producers that are eitherdominated by submerged macrophytes, emergent macrophytes, floating macrophytes, or phytoplankton



SERVICE

Supporting services

1. Nitrogen retention
2. Phosphorus retention
3. Carbon sequestration
4. Primary production
5. Biodiversity
6. Sediment stabilisation
7. Light availability Provisioning services
8. Macrophytes (Food)
9. Algae (Food)
10. Piscivorous fish (Food)
11. Planktivorous and benthivorous fish (Food)
12. Waterfowl (Food)

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|  |  | MAIN SUSTAINABLEDEVELOPMENTGOALS(SDG)(seetableS1) |  |  |  |  |  |  | SUBMERGED | MACROPHYTE-DOMINATED |  |  |  |  |  |  | EMERGENTMACROPHYTE-DOMINATED |  |  |  |  |  | FLOATINGMACROPHYTE-DOMINATED |  |  |  |  |  |  | PHYTOPLANKTON- | DOMINATED |  |  |
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EXPLANATION\*

Macrophyte dominance provides higher nitrogen retention than phytoplankton dominance1. In particular, the fast-growing emergent and floating species promote nitrogen retention2; 3.

Macrophyte dominance provides higher phosphorus retention than phytoplankton dominance1. In particular, the fast-growing emergent and floating species promote phosphorus retention2; 3. Low oxygen conditions that occur in phytoplankton-dominated and floating macrophyte-dominated systems may result in phosphorus release from sediments3; 4.

Due to contradictory processes that affect greenhouse gas uptake and production, the net effect on carbon sequestration for any of the systems is unclear5.

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.

Biodiversity is generally lower in more eutrophic systems, but this depends on the species that contribute to biodiversity9. Submerged macrophyte dominance is associated with high biodiversity among macroinvertebrates and birds5 followed by emergent macrophyte-dominated systems that are important habitats for various waterfowl10.

Submerged and emergent macrophytes are rooted in the sediments, thereby stabilising sediments and protecting banks11; 12. As a result, systems dominated by either submerged or emergent macrophytes contribute to sediment formation.

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 deeper13; 14.

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.

Certain genera of filamentous cyanobacteria (e.g. *Spirulina* sp. and *Aphanizomenon flos-aquae*) are consumed in countries in Africa and Asia17; 18. For centuries, these specieshave been a significant source of high macro- and micronutrients, vitamins, and fibres. This makes some cyanobacterial species a healthy source of food or medicine18.

Clear, oligotrophic waters with sufficient oxygen commonly have a higher percentage of piscivorous fish than more turbid, eutrophic waters9 . Therefore, most piscivorous fish can be found in systems dominated by submerged and emergent macrophyte19, yet fisheries are least obstructed by plant material in systems dominated by submerged macrophytes20. Examples of piscivorous fish commonly found in clear waters are game fish species such as perch (*Perca fluviatilis*) and pike (*Esox lucius*)21.

Turbid waters commonly have the highest percentage of planktivorous and benthivorous fish9. Most planktivorous and benthivorous fish can be found in systems dominated by floating macrophytes or phytoplankton9; 19, yet fisheries are least obstructed in systems dominated by phytoplankton. An example of fish commonly found in turbid waters is bream (*Abramis brama*).

Macrophyte-dominated systems are important habitats for diverse waterfowl that provide meat22.

(Contiues)

*supporting*, *provisioning*, *regulating*, and *cultural services* (MEA, 2005). *Supporting services* involve key ecosystem functions, such as primaryproduction, nutrient cycling, and retention, as well as carbon seques-tration. *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-mate-rial 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 sustain-able future for the global human population. Previous research

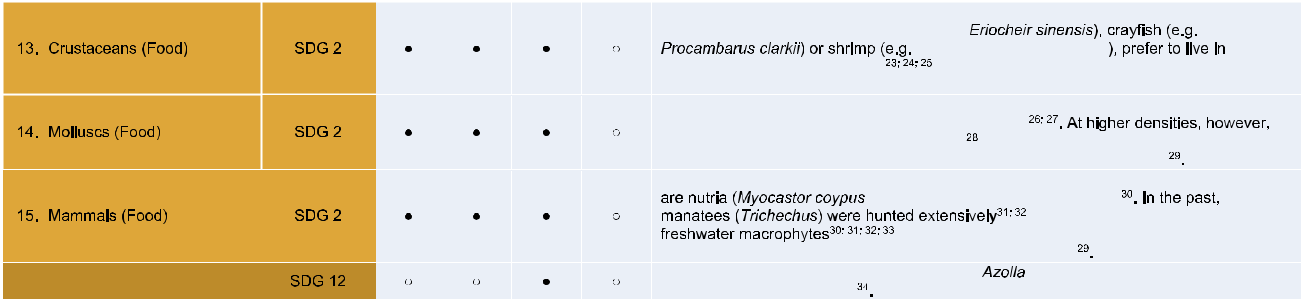
showed a strong link between ecosystem services provided by various kinds of ecosystems and the SDGs, notably including the provision of food (SDG 2), water (SDG 6), sustainable cities (SDG 11), and carbon storage (SDG13; Wood et al., 2018). Lakes can play an important role in SDGs by providing a range of ecosystem services (Ho & Goethals, 2019; Steinman et al., 2017). These ser-vices, however, will also depend on the ecosystem state and dom-inant 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 pro-cesses 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

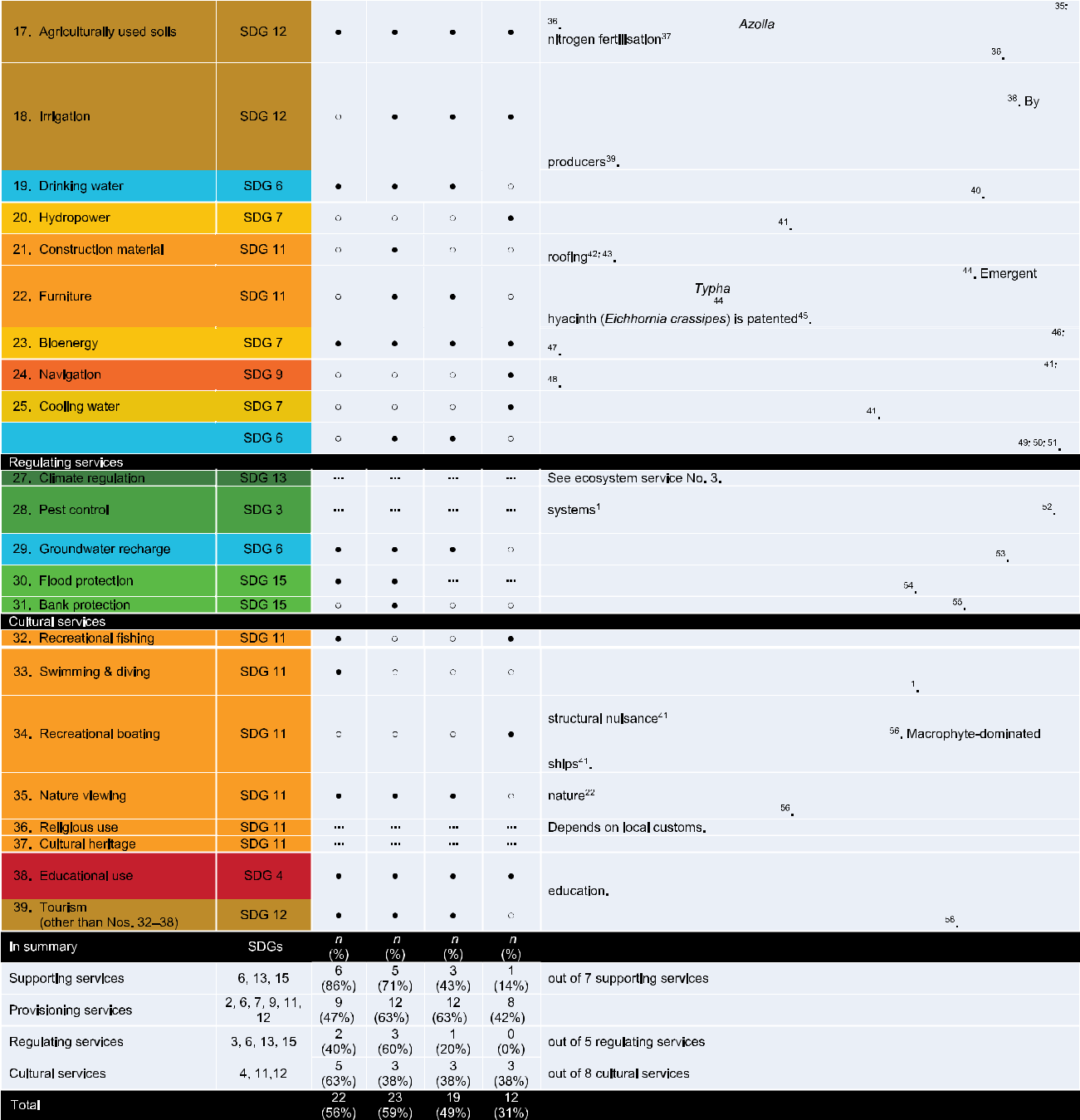
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**TA B L E 1** Continued



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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.

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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 mac-rophytes, 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.

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 concen-trations in the water column and suppresses phytoplankton dom-inance (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 bio-films provide food for higher trophic levels, yet also hamper macro-phyte 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 pi-scivorous fish and their prey (Jeppesen, Peder Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000), and give shelter for zooplankton (Hupfer & Dollan, 2003). Several submerged macrophyte species ex-crete 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).

**2.1**|**Submerged macrophytes**

Submerged macrophytes are commonly found in oligotrophic to mesotrophic systems (Figure 1a). Low-growing submerged vegeta-tion 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 ecosys-tem 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 drink-ing 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 freshwa-ter submerged macrophytes are consumed by humans (Aasim, Bakhsh, Sameeullah, Karataş, & Khawar, 2018; Chai, Ooh, Quah, & Wong, 2015). Indirectly, submerged macrophytes provide a *support-ing service* for human food by either providing habitat for game fish

**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 en-ergy 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 treat-ment 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 har-vested (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 sub-strate, 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 emer-gent plants (De Klein & Van der Werf, 2014). *Regulating services* in lakes also include reduction of wave energy that may protect infra-structure at the banks from erosion damage (Coops, van den Brink,

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* 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 mac-rophyte 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 sub-merged macrophytes, they release most of the photosynthetically produced oxygen into the air, while waters below floating macro-phytes therefore often turn anoxic. Consequently, oxygen-sensi-tive 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 bac-teria in the aerobic rhizosphere (Kosten et al., 2016). Floating mac-rophytes 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 sol-dier (*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 mac-rophyte 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 finan-cial 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 bio-fuel 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 ben-efits 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 mac-rophytes, potentially leading to a shift from a macrophyte- to phy-toplankton-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 sup-press piscivorous game fish species such as pike due to impaired vis-ibility 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 ex-port 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 con-sumption (Tacon & Metian, 2013). Phytoplankton may furthermore support the proliferation of macroinvertebrate species harvested for food (Cai, Gong, & Qin, 2012). In some phytoplankton-domi-nated lakes, cyanobacteria are harvested for food (e.g. *Spirulina* or *Arthrospira*; Habib, 2008), and phytoplankton-dominated lakes mayprovide a genetic resource for the synthesis of valuable biochemicals

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

resources, they indirectly contribute to a reduction in poverty (SDG 1) and prevent resource-related conflicts (SDG 16).

**3** | **LINKING ECOSYSTEM STATES TO ECOSYSTEM SERVICES**

We identified 39 ecosystem services potentially provided by shal-low 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 macro-phyte-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 phy-toplankton-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, cli-mate 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 ef-fect 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 re-spective dominant primary producer groups directly contribute to 10 of the 17 SDGs. When also accounting for secondary contribu-tions, lakes support up to 13 out of 17 SDGs (Table S1). The *sup-porting 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), en-ergy (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, *cul-tural services* contribute to SDGs that are linked with economy andsociety 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 macro-phytes provide sufficient economic services such as food and water

**4** | **SHIFTING STATES, SHIFTING SERVICES**

Shifts to a different group of dominant primary producers can be in-duced by different internal and external disturbances. Examples of disturbances include a change in nutrient loading, planned interven-tion (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 pri-mary 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 char-acteristic 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 se-cure 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, sub-merged macrophyte dominance tends to be associated with higher biodiversity in multiple taxa, including invertebrates and birds com-pared 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 import-ant habitats for different waterfowl, but macroinvertebrate diver-sity is lower than in submerged macrophyte-dominated systems (Weisner & Thiere, 2010).

Phytoplankton-dominated lakes support a different set of eco-system 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 ser-vices*. However, high macrophyte abundances in more eutrophic

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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 ser-vices* like recreation and fishing (Hilt et al., 2017; Verhofstad &Bakker, 2019; Villamagna, Murphy, & Trauger, 2010). Thus, al-though these services are provided through good water qual-ity 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 chal-lenging 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 cyano-bacteria (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 emer-gent macrophytes can involve carbon capture, as their carbon reten-tion 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 ben-efit increases the pressure on lake resources and compromises a sus-tainable 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 eutrophi-cation 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 cyano-bacteria 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 envi-ronment. Future shifts in states will also prompt shifts in ecosys-tem 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 po-tential 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 eutro-phic 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 achiev-ing 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 great-est 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 poten-tial trade-offs between these services and associated SDGs (Table 1). Conserving and restoring ecosystem states should account for poten-tial 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 cre-ated or analysed in this study.

**ORCID**

*Annette B. G. Janssen* <https://orcid.org/0000-0001-5000-7161>



*Sabine Hilt* <https://orcid.org/0000-0002-0585-2822>



*Sarian Kosten* <https://orcid.org/0000-0003-2031-0965>



*Jeroen J. M. de Klein* <https://orcid.org/0000-0003-0205-5171>



*Hans W. Paerl* <https://orcid.org/0000-0003-2211-1011>



*Dedmer B. Van de Waal* <https://orcid.org/0000-0001-8803-1247>

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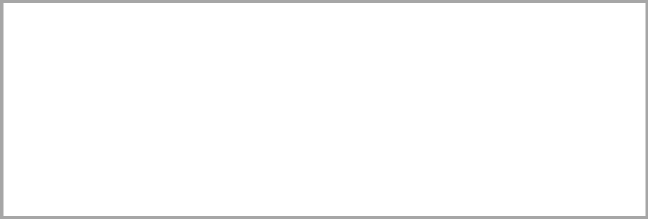
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Additional supporting information may be found online in the Supporting Information section.



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