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Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services

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ABSTRACT

The Anthropocene presents formidable threats to freshwater ecosystems. Lakes are especially vulnerable and important at the same time. They cover only a small area worldwide but harbour high levels of biodiversity and contribute disproportionately to ecosystem services. Lakes differ with respect to their general type (e.g. land-locked, drainage, floodplain and large lakes) and position in the landscape (e.g. highland *versus* lowland lakes), which contribute to the dynamics of these systems. Lakes should be generally viewed as 'meta-systems', whereby biodiversity is strongly affected by species dispersal, and ecosystem dynamics are contributed by the flow of matter and substances among locations in a broader waterscape context. Lake connectivity in the waterscape and position in the landscape determine the degree to which a lake is prone to invasion by non-native species and accumulation of harmful substances. Highly connected lakes low in the landscape accumulate nutrients and pollutants originating from ecosystems higher in the landscape. The monitoring and restoration of lake biodiversity and ecosystem services should consider the fact that a high degree of dynamism is present at local, regional and global scales. However, local and regional monitoring may be plagued by the unpredictability of ecological phenomena, hindering adaptive management of lakes. Although monitoring data are increasingly becoming available to study responses of lakes to global change, we still lack suitable integration of models for entire waterscapes. Research across disciplinary boundaries is needed to address the challenges that lakes face in the Anthropocene because they may play an increasingly important role in harbouring unique aquatic biota as well as providing ecosystem goods and services in the future.

Key words: biological diversity, ecosystem change, fresh waters, meta-system, monitoring, resilience, restoration

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I. INTRODUCTION

The Anthropocene witnesses the overwhelming impacts of humans on our planet's geology, climate, and ecosystems (Steffen *et al.*, 2011; Waters *et al.*, 2016). Indeed, the majority of ecosystems worldwide, including freshwater ecosystems, are threatened by multiple anthropogenic stressors (Vörösmarty *et al.*, 2010; McCluney *et al.*, 2014; Albert *et al.*, 2020; Birk *et al.*, 2020). Lakes are no exception, as they are threatened, *inter alia*, by climate change, land-use intensification, eutrophication, acidification, water abstraction, water-level regulation, morphological alteration, and invasive species (Dudgeon *et al.*, 2006; Smol, 2019). Understanding the resilience and recovery of lakes to environmental change has thus emerged as an important research program from the perspectives of biodiversity conservation and ecosystem services (Angeler & Drakare, 2013; Angeler *et al.*, 2015).

Biodiversity variation and ecosystem dynamics are affected by landscape connectivity, which facilitates organisms' movements and abiotic flows among locations (Mitchell, Bennett, & Gonzalez, 2013; Heino, 2013*b*). Therefore, understanding the effects of anthropogenic stressors on biodiversity and delivery of ecosystem services to humans requires lakes to be considered as integral parts of terrestrial–aquatic ecotones (e.g. Soininen *et al.*, 2015), parts of drainage systems (e.g. Soranno *et al.*, 1999), and as landscapes themselves (e.g. Vilmi *et al.*, 2016). The idea that lakes are not isolated from their surrounding terrestrial environments or other freshwater ecosystems dates back to Stephen Forbes (1887, p. 77) who wrote: "The fluviatile lakes, which are much more numerous and important, are appendages of the river systems of the State, being situated in the river bottoms and connected with the adjacent streams by periodical overflows. Their fauna is therefore substantially that of the rivers themselves, and the two should, of course, be studied together." This idea underscored the importance of considering lakes as parts of the drainage system by means of connections between riverine and lacustrine systems.

More than a century after the idea of Forbes (1887), the position of lakes in the landscape was further conceptually explored by Riera *et al.* (2000), who emphasized that lakes vary in the degree of connectedness to other ecosystems. They stated that the spatial organization of lake districts is largely a result of geomorphological history, which led them to introduce the concept of 'lake order' (Table 1). They and others showed that the landscape position of lakes (i.e. lake order) contributes to the understanding of several abiotic and biotic characteristics (Soranno *et al.*, 1999; Riera *et al.*, 2000). For instance, human settlements and species richness of various taxonomic groups typically increase with lake order (Kratz *et al.*, 1997; Lewis & Magnuson, 2000; Riera *et al.*, 2000). Moreover, highly connected lowland lakes are exceptionally vulnerable to various human activities in the surrounding areas, as human pressures generally increase with decreasing altitude (Solheim *et al.*, 2019). Consequently, the concept of lake order integrates societal and biological aspects, essentially reflecting that lakes are coupled socio-ecological systems (Schlüter *et al.*, 2012). The degree of connectivity to other aquatic systems along with the topographic position in the landscape further underlies these ideas. Lakes should thus be considered as parts of larger waterscapes (Soranno *et al.*, 2010), where the landscape of multiple lakes rather than individual lakes becomes the focal unit for ecosystem studies (Cumming, 2011). Such a view beyond traditional single-lake thinking can be very useful for understanding the stability of entire waterscapes in a changing world (Fried-Petersen *et al.*, 2020).

Lake landscape position and connectivity are largely determined by underlying geology and land forms. Thus, the concept of geodiversity, the diversity of Earth surface forms, materials and processes, may also be a useful concept to foster the understanding of lake biodiversity and ecosystem services (Brilha *et al.*, 2018; Schrodt *et al.*, 2019; Alahuhta, Toivanen, & Hjort, 2020). Positive relationships have been observed between biotic (biodiversity) or abiotic (geodiversity) attributes and ecosystem service supplies, suggesting that

Table 1. A glossary of key terms

Term	Definition
Dispersal limitation	A species cannot reach all suitable sites in a region because of large spatial distances or physical obstacles. At the local community level, dispersal limitation may result in the absence of many species that could be expected to occur based on prevailing environmental conditions (Heino *et al.*, 2015).
Drainage lake	A lake having surface water connections to other lakes *via* streams or rivers.
Dynamism	The tendency of environmental conditions and biological communities to vary in time and space (Datry, Bonada, & Heino, 2016).
Floodplain lake	A lake connected to the river by recurring flooding in the rainy season. Often lack connections to the river during the dry season.
Land-locked lake	A lake with no surface water connection by streams or rivers to other lakes in a drainage basin.
Lake	A standing water body with a surface area greater than two hectares (Williams *et al.*, 2004). Smaller standing water bodies are considered ponds and pools.
Lake order	Lake order is a measure of a lake's relative position in the landscape. It can be easily measured from maps, providing a proxy for connectivity and variation in physical, chemical and biological features of lakes in the landscape. Lake order varies from isolated lakes with no surface water connections (negative values) to drainage lakes with inlets and outlets (positive values). It is thus based on examination of hydrological inputs through groundwater, terrestrial inputs through surface waters, and among-lake connections *via* streams and rivers (Riera *et al.*, 2000).
Large lake system	A very large lake (more than 500 km^2 in surface area; Herdendorf, 1982), with often highly irregular shoreline and comprising a number of separate bays. Examples include Lake Saimaa in Finland, Lake Ladoga in Russia, Lake Taihu in China and the Great Lakes of North America.
Metacommunity	A set of local communities connected by the dispersal of species (Leibold *et al.*, 2004). For example, a set of lakes in a drainage basin equals a lake metacommunity.
Meta-ecosystem	A set of individual ecosystems connected by the movements of organisms and material between locations (Loreau, Mouquet, & Holt, 2003). A meta-ecosystem can comprise connected lakes in a watercourse or interactions between a lake and its riparian zone.
Non-stationarity	Posits that natural systems fluctuate within a changing envelope of variability (Milly *et al.*, 2008). Emphasizes non-linear change due to anthropogenic impacts. Challenges assumptions of attainment of historical reference conditions due to changing baselines.
Recovery	The tendency of a lake to return to its original (or at least to previous good) environmental and biological conditions after a disturbance. This view is rooted in the balance-of-nature view, traditionally embraced in ecological stability research (Allen *et al.*, 2019)
Resilience	The amount of disturbance needed to shift an ecosystem from one set of ecological structures, functions and feedbacks to another set (Holling, 1973). Inherent in this definition are thresholds, non-linear and often abrupt changes to alternative regimes from which a return to a previous regime is impossible due to stabilizing effects of feedbacks (Baho *et al.*, 2017).
Species sorting	In species sorting, sufficient dispersal allows species to track variation in local abiotic and biotic conditions, resulting in a good match between biological communities and the environment (Leibold *et al.*, 2004).
Watercourse lake	A lake connected to other lakes by streams or rivers.
Waterscape	A set of lacustrine and riverine sites in a regional setting, where physical, chemical, biological and societal factors determine both the regional and local dynamics underlying variation in biodiversity and ecosystem services.

enhancement of joint biodiversity and geodiversity conservation should improve production of ecosystem services (Nelson *et al.*, 2009; Cardinale *et al.*, 2012; Harrison *et al.*, 2014; Isbell *et al.*, 2017; Alahuhta *et al.*, 2018). This approach may also be useful for understanding biodiversity variation across freshwater ecosystems (Kärnä *et al.*, 2019; Toivanen *et al.*, 2019).

Lakes are not only biodiversity hotspots, but they also provide essential and valuable ecosystem services to human existence and economies (Sterner *et al.*, 2020). These services include raw water supplies (e.g. household drinking water, irrigation and industrial use), food (e.g. mussels, fish and waterfowl), hydropower, flood control, retention of pollutants and nutrients, climate regulation, recreation, tourism and aesthetic values, as well as waterways for inland water navigation and transport (Baron *et al.*, 2002; Tranvik *et al.*, 2009; Vilbaste *et al.*, 2016; Allan *et al.*, 2017). As multiple ecosystem services are largely sustained by biodiversity and associated ecosystem functions (Schröter *et al.*, 2014), the degree of connectivity of lakes should be given due attention (Mitchell *et al.*, 2013).

In this review, we focus on lakes as integral parts of drainage basins, which is the basic tenet of landscape limnology (Kling *et al.*, 2000). This idea has only recently received increasing interest (Fergus *et al.*, 2018; Soranno *et al.*, 2019), although understanding the broader waterscape context of lakes is imperative in a rapidly changing world. Broadening the perspective from individual lakes to entire waterscapes is also associated with two central concepts in ecology: metacommunities (Leibold *et al.*, 2004) and meta-ecosystems (Loreau *et al.*, 2003). Owing to different levels of connectivity, topography and other features, comparing sets of land-locked lakes, drainage lakes, floodplain lakes and large lake systems is deemed a suitable approach (Table 1). This approach facilitates 'waterscape thinking' in understanding and managing lake biodiversity and ecosystem services. Therefore, we first focus on physical connectivity and movements of organisms and matter among lakes in a waterscape. Second, we focus on lake ecosystem services, emphasizing how they can be associated with biodiversity and understood in a broader context of waterscapes. Third, we integrate waterscape thinking in the biodiversity monitoring and ecosystem management of lakes. Finally, we discuss key ideas for future studies and implications for the management of biodiversity and ecosystem services of lake ecosystems in the Anthropocene.

II. LAKES AS WATERSCAPES UNDERLYING THE MOVEMENT OF ORGANISMS AND MATERIAL

(1) The theoretical basis of metacommunity dynamics

When there is a strong potential for between-site exchanges of organisms, the set of local communities forms a 'metacommunity', an idea that integrates different local and regional processes affecting ecological communities (Leibold *et al*., 2004). In theory, local communities within a metacommunity can be structured by neutral processes and environmental filtering (Winegardner *et al*., 2012). The idea of neutral assembly is based on the hypothesis that all species are demographically identical on a *per capita* basis (Hubbell, 2001), and local communities are thus mainly structured by the vital rates of birth, death, dispersal, and speciation of species (Hubbell, 2006). Species traits have evolved to form self-similar clusters (Hubbell, 2005), which is considered in the context of the so-called 'emergent neutrality' (Holt, 2006). Conversely, environmental filtering may structure local ecological communities if different species have evolved distinct morphological and physiological traits that allow them to persist in certain environmental conditions only (Thakur & Wright, 2017).

The degree to which environmental filtering affects the assembly and maintenance of local communities is directly linked to dispersal rates. Dispersal may be limited, sufficient or very high (Winegardner *et al*., 2012). In theory, if dispersal is limited, local community structure tends to deviate from what could be expected based on local abiotic and biotic environmental conditions alone (Martiny *et al*., 2006). Sufficient dispersal, in turn, enables species to reach suitable habitat patches, leading to species sorting along environmental gradients (Leibold *et al*., 2004). Lastly, if dispersal rates are very high, the environmental signal in community composition tends to be masked, and species may occur in suboptimal habitats due to strong source–sink dynamics (Kneitel & Miller, 2003; Mouquet & Loreau, 2003). Rather than considering these three dispersal-related predictions as mutually exclusive, we should understand them as parts of a continuum of metacommunity organization (Heino *et al*., 2015; Brown *et al*., 2016).

Understanding the relative roles of spatial dynamics and environmental filtering has important implications for environmental change research, as was aptly put by Holt (2006, p. 533): "Niche and neutral perspectives have quite different implications for how one should manage natural resources and craft conservation strategies. A unified theory of communities that judiciously blends both perspectives is needed if ecologists are to understand the processes governing biodiversity at a fundamental level and then apply this understanding to the urgent problem of maintaining diversity in our rapidly changing world." In the remaining parts of this section and in Sections III and IV, we will focus on this idea for lake metacommunities and meta-ecosystems.

(2) Spatial dynamics and environmental filtering in lake metacommunities

Lakes are good model systems to study metacommunity ecology, as they are environmentally highly heterogeneous and biologically diverse (Cottenie *et al*., 2003; Soininen *et al*., 2011; Heino *et al*., 2017; Almeida-Gomes *et al*., 2020). They represent targets for moving organisms, surrounded by uninhabitable terrestrial habitats for many aquatic species. Consequently, different metacommunity dynamics may exist across different lake types, including land-locked lakes, drainage lakes, floodplain lakes, and large lake systems (Table 1). In the following, we will consider the main features of each lake ecosystem type in terms of understanding metacommunity (Fig. 1) and meta-ecosystem (Fig. 2) dynamics in waterscapes.

One can assume that land-locked lakes that are isolated from each other in the landscape (Fig. 1A), show limited exchange of aquatic organisms, and should exhibit high variation in community composition due to dispersal limitation (Heino *et al*., 2015). In addition, spatial variation in community composition may result from speciation events in the case of large ancient lakes (Martens, 1997). Interestingly, recent studies have shown that environmental filtering and biotic interactions are the main mechanisms structuring local communities across land-locked lakes (García-Girón *et al*., 2020), especially across those showing seasonal filling and drying (Castillo-Escrivà *et al*., 2016; Maloufi *et al*., 2016). In order to track spatial and temporal changes in environmental conditions among land-locked lakes, organisms have to be efficient dispersers (Bilton, Freeland, & Okamura, 2001). However, dispersal abilities vary among organismal groups (Beisner *et al*., 2006), and different groups may therefore show different metacommunity dynamics even across land-locked standing waters (De Bie *et al*., 2012). Environmental filtering may be prevalent for strong dispersers, whereas weak dispersers can be assumed to be more dispersal limited across sets of land-locked lakes (Heino, 2013*a*).

Compared to land-locked lakes, metacommunity organization should be different for drainage lakes connected to

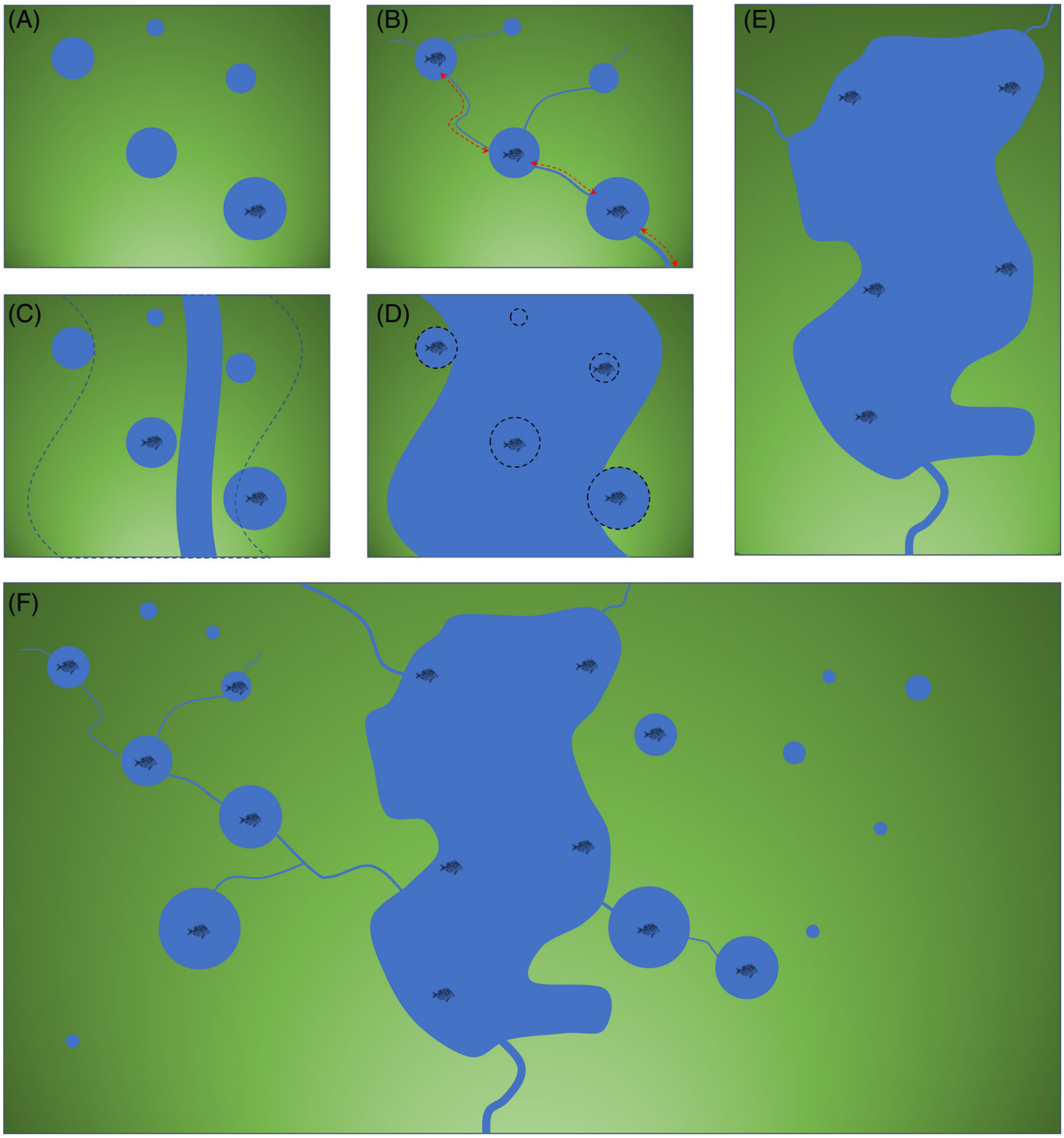

Fig 1. Likely occurrence of an obligatory aquatic species (e.g. a fish species) in different types of lakes assuming that the landscapes are close to a natural state. Increasing surface water connectivity leads to increasing probability of the hypothetical species occupying a given location in a metacommunity. (A) Land-locked lakes, (B) drainage lakes, (C) floodplain lakes in dry season, (D) floodplain lakes in rainy season, and (E) very large lake systems. (F) A waterscape where different types of lakes are intermingled and interconnected. In B, the red arrows refer to two-directional dispersal routes of fish through the watercourse.

the riverine network (Fig. 1B). In these drainage lakes, dispersal between localities may not be as limited as in land-locked lakes, and even obligatory aquatic organisms, such as fish, may be able to disperse from one lake to another through connecting rivers and streams (Tonn & Magnuson, 1982; Olden, Jackson, & Peres-Neto, 2001). Such increased connectivity may dictate that dispersal is an important mechanism in the assembly of drainage lake communities, which can be observed as rapid recolonizations of denuded lakes after physical (e.g. winterkill) or biotic (e.g. predation) disturbances (Tonn & Magnuson, 1982; Magnuson *et al.*, 1998). However, previous research has shown that ecological communities in drainage lakes are also mainly structured by environmental filtering (Cottenie *et al.*, 2003; Alahuhta *et al.*, 2015).

Floodplain lakes are good examples of waterscapes where temporally changing hydrological conditions and connectivity to the riverine system (Fig. 1C, D) drive local community dynamics (Junk, Bayley, & Sparks, 1989; Thomaz, Bini, & Bozelli, 2007). For example, during the flood period with

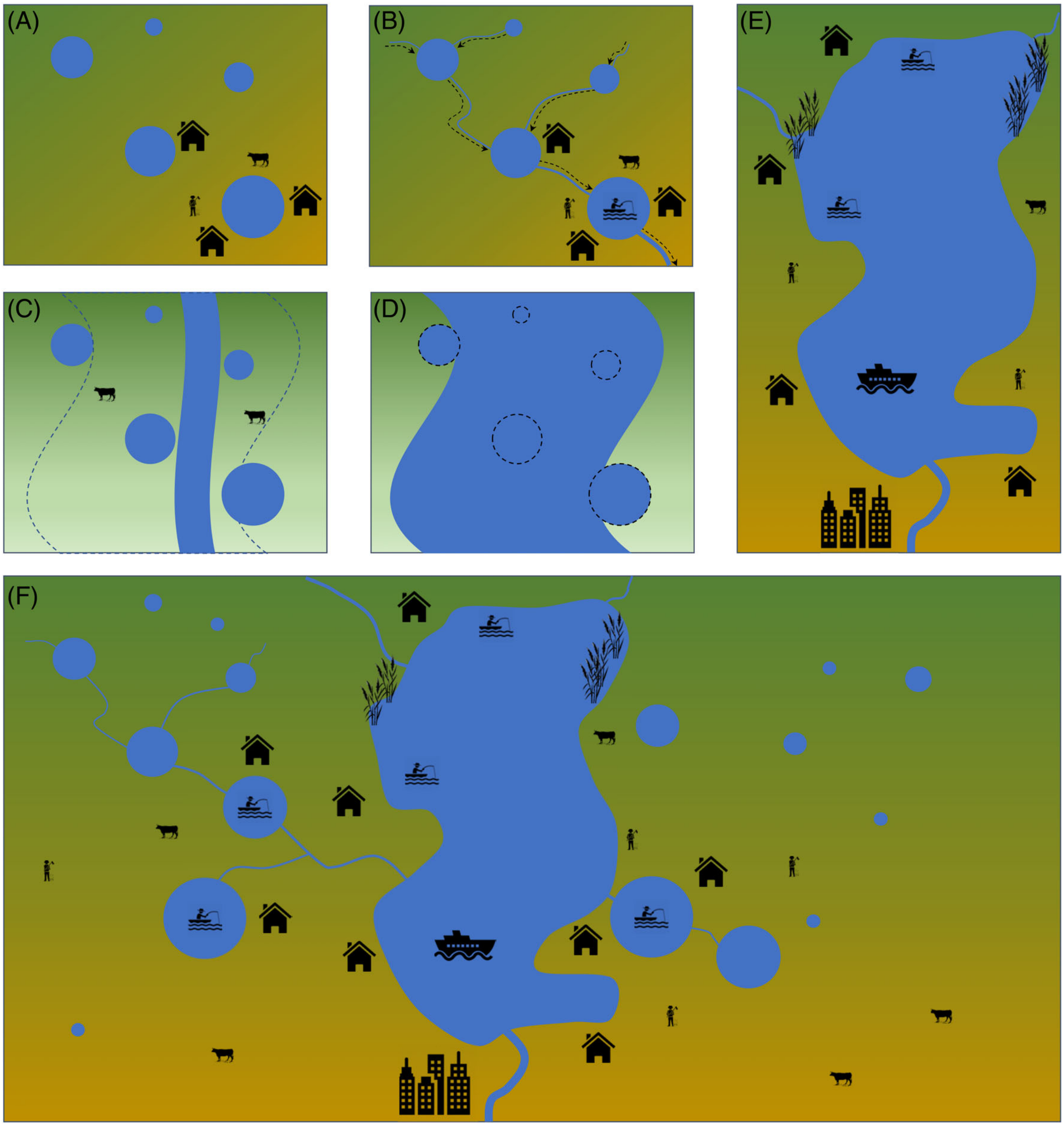

Fig 2. Variation in potential human impacts on different types of lakes (A–E) and on lakes in different landscape positions (A, B). Green colour refers to natural and forested areas, whereas light brown colour refers to agricultural and urban areas. The probability of the occurrence of fishermen, boating, housing, farm animals and farmers are shown by the symbols. Fresh waters are shown by blue colour. (A) Land-locked lakes, (B) drainage lakes, (C) floodplain lakes during dry seasons, (D) floodplain lakes during rainy season, and (E) very large lake systems. (F) A waterscape where different types of lakes are intermingled and interconnected. In B, the black arrows refer to the main downstream direction of nutrient and contaminant flow in the watercourse.

increasing connectivity, floodplain lakes may be affected by high dispersal rates (Thomaz *et al.*, 2007; Bozelli *et al.*, 2015), while environmental filtering (e.g. Simões *et al.*, 2013) and dispersal limitation may be more important during the dry phase (e.g. Petsch, Pinha, & Takeda, 2016). This is because the local communities become continuously more and more disconnected from the riverine systems with extended dry periods, which affects the assembly mechanisms of local communities (e.g. Fernandes *et al.*, 2014). The role of hydrological connectivity on local communities of floodplain lakes is emphasized because spatial variation in community composition may be higher during low-water than during high-water periods (Fernandes *et al.*, 2014; Padial *et al.*, 2014). However, opposite patterns have also been detected (Angeler *et al.*, 2010), which highlights the complexity that underpins community assembly in highly dynamic freshwater ecosystems (Datry *et al.*, 2016).

Large lake systems (Fig. 1E), including the world's largest lakes (Herdendorf, 1982), are even more physically connected systems than floodplain lakes. Within large lakes, dispersal rates between localities may be so high that they override the influences of local habitat conditions, thus profoundly affecting local community dynamics. In such situations, the importance of environmental filtering may be reduced to a large extent, resulting in local communities being possibly at least partly homogenized by efficient dispersal (Vilmi *et al.*, 2016; Cai *et al.*, 2017, 2019; Tolonen *et al.*, 2017). This is because high dispersal rates mediated by currents and wind in an environment with no apparent physical barriers should attain a more influential role than environmental filtering in large lake systems.

Despite the fact that considering different lake types separately may be a good starting point for understanding spatial dynamics and environmental filtering in lake metacommunities, they often occur in the same waterscape (Fig. 1F). In such heterogeneous waterscapes, it is not possible to consider differences between lake types as binary contrasts: the degree of connectedness varies greatly from perfectly land-locked lakes to large lake systems that may be connected to a large number of smaller drainage lakes by river networks. Therefore, sets of lakes should be understood as being connected in unique waterscapes, making the understanding of metacommunity organization context dependent and highly challenging. Recent findings in macrosystems ecology (Fergus *et al.*, 2018; Soranno *et al.*, 2019) and metacommunity ecology (García-Girón *et al.*, 2020; Lindholm *et al.*, 2020) have increased knowledge on the spatial and temporal variability of physical, chemical, and biological features of lakes, which has further consequences for understanding a set of lakes as a meta-ecosystem.

(3) Spatial dynamics of lake meta-ecosystems

Similar to metacommunities, a set of different types of lakes may also act as a meta-ecosystem (Loreau *et al.*, 2003) or as a terrestrial–aquatic ecotone (Soininen *et al.*, 2015). For example, lakes exchange organisms (e.g. emerging aquatic insects) and matter (e.g. riparian-based leaf litter inputs to lakes) with terrestrial ecosystems, which affect the dynamics of both ecosystems (Scharnweber *et al.*, 2014; Soininen *et al.*, 2015). This idea is also broadly related to catchment geodiversity, whereby the features of a catchment affect physical, chemical and biological features (Fergus *et al.*, 2018; Soranno *et al.*, 2019), and may further act as a surrogate for biodiversity in lakes (Iversen *et al.*, 2019; Toivanen *et al.*, 2019). In addition, exchanges of organisms and material occur between riverine and lacustrine ecosystems, which may be important for supplying and replenishing resources and biological communities in lakes (Tockner *et al.*, 1999; Ward, Tockner, & Schiemer, 1999). This is typical, for example, in riverine floodplain systems in tropical and subtropical areas (e.g. Junk *et al.*, 1989).

In a very broad spatial context, fresh waters act as transmitters of the movement of organisms and matter across the terrestrial–marine continuum. Riverine systems discharge carbon and nutrients from catchments and lakes into seas by water flow (Cole *et al.*, 2007; Ludwig *et al.*, 2009), whereas bidirectional transfers of organisms, energy and nutrients between terrestrial, freshwater and marine systems result from animal migrations, including those of diadromous fish species (Naiman *et al.*, 2002; Jonsson & Jonsson, 2003; Petticrew, Rex, & Albers, 2011). For example, contaminants biomagnifying into migrating salmon in the sea may be a dominant source of organic pollutant contamination in lakes (Ewald *et al.*, 1998; Krümmel *et al.*, 2005).

Finally, besides natural matter and organisms that are typically distributed between ecosystems, different lakes also exchange anthropogenically derived materials from the catchment (Fig. 2). For example, strong winds may contribute to toxic algal blooms in large lakes (e.g. Wu *et al.*, 2015) and distribute large amounts of microplastics in lake surface waters (e.g. Fischer *et al.*, 2016). Also, the hydrological conditions may affect the distributions of drug concentrations in lakes (e.g. Metcalfe *et al.*, 2003). In addition, movements of humans in waterscapes (e.g. boating, canoeing and fishing) are known to distribute invasive species among lakes, which may have drastic effects on biodiversity (Johnson, Ricciardi, & Carlton, 2001; Cambray, 2003; Rahel, 2007; Kelly *et al.*, 2013). The distributions and routes of contaminants, pollutants and invasive species are fundamental abiotic and biotic agents of global change and thus require more attention from a meta-ecosystem perspective. Therefore, considering lakes as parts of waterscapes rather than focussing on each lake separately would increase our understanding of major local and regional phenomena that underlie lake ecosystem services and anthropogenic stressors impacting lakes (see Section III).

III. LAKE ECOSYSTEM SERVICES AND DISSERVICES: SOCIO-ECONOMIC VALUES AND THREATS TO THEIR SUPPLIES IN WATERSCAPES

Nature's contributions to people are increasingly considered equivalent to 'ecosystem services' (Millenium Ecosystem Assessment, 2005), although they comprise more than proposed by the original ecosystem services framework (Díaz *et al.*, 2018). The idea of nature's contributions to people emphasizes the important role that culture plays in determining links between people and nature and highlights the role of indigenous and local knowledge in understanding the value of nature (Heino *et al.*, 2020). However, this idea has not frequently been considered in the context of freshwater ecosystems, although they are among the most important ecosystems for human well-being.

Mapping and socio-economic valuation of freshwater ecosystem services have so far been scarce compared to terrestrial systems. The review of Egoh *et al.* (2012) revealed that less than 5% of ecosystem service indicators apply to

Table 2. Selected examples of studies focussing on the ecosystem services provided by freshwater ecosystems

Example	Description
Monetary value	The average monetary value of the ecosystem services provided by lakes has been estimated to be \$4267 ha^{-1} $year^{-1}$ (de Groot *et al.*, 2012). This estimate was based on a very low number of case studies with poor spatial coverage (15 studies in total, 2–8 case studies for values of each ecosystem service). Therefore, these monetary value estimates of lake ecosystem services should be used with caution because they are statistically and spatially unrepresentative at present.
Recreational fisheries	Recreational fisheries have locally high relative importance in providing employment. For example, the fishery of the Spey catchment in Scotland contributes £11.6 million annually to the local economy and supports 401 full-time jobs (Butler *et al.*, 2009), whereas freshwater anglers spend over £1.114 billion in the UK (Winfield, 2016).
Outdoor activities	Outdoor activities, such as swimming, canoeing, wind surfing, boating, cruise-tourism, birdwatching, and holidaying, are considered important for human well-being and enhance local and regional economies. As an example, this was shown in an assessment of coastal ecosystem services in the Nordic countries which had a marine focus but also included case studies from rivers and lakes (https://www.norden.org/fi/node/7618).
Climate regulation	Holocene lake sediments have been estimated to contain 820 Pg buried organic carbon worldwide (Tranvik *et al.*, 2009). This concentration is almost twice as high as the shorter-term carbon sink comprising terrestrial plant biomass (~460 Pg; Cole *et al.*, 2007), but lower than carbon storage of terrestrial soils (~1395 Pg). In Finland, lakes contain the second largest areal C stocks (19 kg C m^{-2}) after peatlands (72 kg C m^{-2}), and exceed by significant amounts stocks in the forest soil (uppermost 75 cm; 7.2 kg C m^{-2}) and woody biomass (3.4 kg C m^{-2}) (Kortelainen *et al.*, 2004). Relative organic carbon burial capacity is especially high for small lakes and for lakes with large catchments (Downing *et al.*, 2008). Despite their relatively small surface area (~3% of the Earth's surface; Downing *et al.*, 2006), freshwater lakes have also been estimated to contribute from 6 to 24% of global methane release, a highly potent greenhouse gas (Bastviken *et al.*, 2004, 2011).

freshwater ecosystems. Furthermore, Van der Ploeg & de Groot (Van der Ploeg & Groot, 2010) estimated that less than 1% of ecosystem service data sets were from lakes and rivers. Therefore, mapping and valuing of freshwater ecosystem services comprises a research gap to be filled in the future, especially in the context of waterscape thinking (https://ipbes.net/global-assessment). In the following, we discuss several examples that emphasize different lake ecosystem services. Although these examples are not exhaustive, they present a common thread that links together lake biodiversity, ecosystem services and human impacts that affect waterscapes directly and indirectly. They are also simultaneously linked to context-dependent management challenges across waterscapes (see Section IV).

(1) Lake fisheries

An important ecosystem service provided by lakes is related to fisheries (Sterner *et al.*, 2020). Catches in freshwater systems are continuously increasing, especially in Asia and Africa (Welcomme *et al.*, 2010; Jia, Zhang, & Liu, 2013), while marine fish stocks and catches are declining (Coll *et al.*, 2008; Pauly & Zeller, 2016). Commercial, domestic and recreational fisheries significantly contribute to food security, employment, nature-related enjoyment and economies around the world (Butler *et al.*, 2009; EU, 2011; McIntyre, Liermann, & Revenga, 2016). Therefore, freshwater fisheries are economically significant from local to global scales (Table 2). Recreational fisheries are important to human well-being, as well as to local and national economies (Cowx, Arlinghaus, & Cooke, 2010; Melstrom & Lupi, 2013; Pope, Allen, & Angeler, 2014). Future sustainability of freshwater fisheries is, however, threatened by many human impacts that include climate change (Ficke, Myrick, & Hansen, 2007; Comte *et al.*, 2013), eutrophication (Diekmann *et al.*, 2005; Dodds *et al.*, 2009), pollution, introduced species, parasites, diseases (FAO, 2018; Reid *et al.*, 2019) and overfishing (Allan *et al.*, 2005; Carpenter, Stanley, & Vander Zanden, 2011). Given that fish movements are interrupted by various man-made obstacles (Januchowski-Hartley *et al.*, 2013; Grill *et al.*, 2019), lake fisheries should move from a focus on single lakes to that of entire waterscapes. This is because the fish yield provided by a single lake may be dependent on the movement and recovery of a target fish species from other lakes after a disturbance event (Tonn & Magnuson, 1982; Magnuson *et al.*, 1998).

(2) Recreational activities associated with lakes

Many recreational outdoor activities are associated with lakes (Table 2). These outdoor activities, including swimming, canoeing, wind surfing, boating, cruise-tourism, angling, birdwatching and holidaying, are important for human well-being and economies (Xie, 2012; Sport and Recreation Alliance, 2017; Mackintosh, Griggs, & Tate, 2019). However, eutrophication, pollution, climate change, spread of invasive species, and their undesirable side effects (e.g. increased prevalence of harmful algal blooms) are diminishing recreational and lakefront property values (Pretty *et al.*, 2003; Dodds *et al.*, 2009). For instance, cyanotoxins pose serious threats to human health (Caller *et al.*, 2009) and aquatic food webs (Ferrão-Filho & Kozlowsky-Suzuki, 2011; Taipale *et al.*, 2019). Similarly, the increasing incidence and magnitude of blooms of raphidophycean flagellates (*Gonyostomum semen*) has several socio-ecological repercussions, including skin irritation in swimmers and drinking water quality degradation (Angeler, Allen, & Johnson, 2012). This is also true for algal blooms in general (Heisler *et al.*, 2008).

Along with the positive effects of recreational activities on humans, there are also potential harmful impacts on lakes. For example, canoeing, boating and cruise-tourism are likely to spread invasive species when moving from one lake to another or between distant locations in a large lake system (Johnson & Padilla, 1996; Johnson *et al.*, 2001). Although these harmful impacts may be difficult to prevent, they should be considered when planning a focus on lakes where those recreational activities are freely allowed. In a waterscape context, it would be desirable to preserve parts of large lake systems or certain individual lakes where recreational activities are limited. These locations could act as havens of biodiversity from which colonization of more human-influenced lakes is possible.

(3) Water as a resource

Lakes are crucial supplies of drinking and household water for millions of people worldwide (Delpla *et al.*, 2009; Qin *et al.*, 2010). However, the quality, quantity and availability of these resources are threatened for various reasons. Climate change is predicted to increase temporal and regional variation in precipitation, causing regional scarcity (or increase) of water resources for industry, agriculture and households (Bangash *et al.*, 2013; Donnelly *et al.*, 2017). The quality and quantity of water supplies for human use are already being harmed by climate change, pollution, eutrophication and overuse of lake water for agricultural irrigation (Delpla *et al.*, 2009; Whitehead *et al.*, 2009; Qin *et al.*, 2010; Rodell *et al.*, 2018). Poor water quality increases the costs of water treatment and may even prevent the use of water by humans (Pretty *et al.*, 2003; Qin *et al.*, 2010). Sewage water treatment plants are also now facing novel challenges, as improved detection and analysis techniques indicate that aquatic systems receive a variety of pollutants. For instance, traces of micropollutants, medicines and illicit drugs appear in water samples taken from lakes that receive high amounts of treated waste-waters (Metcalfe *et al.*, 2003; Berset, Brenneisen, & Mathieu, 2010; Guo *et al.*, 2014). Furthermore, an increasing body of evidence shows that, in addition to oceans, lakes also are receiving notable amounts of microplastic pollution (Fischer *et al.*, 2016; Mason *et al.*, 2016). Microplastic particles eventually accumulate in the food web through ingestion by animals (Browne *et al.*, 2008; Setälä, Fleming-Lehtinen, & Lehtiniemi, 2014; Redondo-Hasselerharm *et al.*, 2020). Again, considering lakes as integral parts of waterscapes would help in tracing and predicting the potential sources and impacts of pollution at the level of an individual lake and beyond.

(4) Hydropower production

Dams built for providing hydropower are increasingly being planned all over the world (Lees *et al.*, 2016). Hydropower production has strong negative trade-offs with other ecosystem services through decreased connectivity, thereby threatening freshwater biodiversity and fisheries (Ziv *et al.*, 2012; Wieser, 2019). The social and ecological impacts of hydroelectric dams on upper and lower reaches of rivers have been recognized for a long time (Baxter, 1977; Hellsten *et al.*, 1996). However, these impacts can be even more detrimental in tropical, near-pristine floodplain–river systems (Lees *et al.*, 2016; Anderson *et al.*, 2018). The impacts on floodplain lakes upstream from dams are sharp and unequivocal because these environments are permanently flooded by the impoundment. Downstream impacts are also severe because flow regulation disturbs the seasonal flood pulse, a key process maintaining biodiversity and ecosystem services in floodplain systems (Arantes *et al.*, 2019). This is also a prime example of meta-ecosystem thinking, in this specific example related to the river–floodplain linkages disrupted by damming in a broader waterscape.

(5) Regulating services associated with lakes

The relative importance of lakes (per unit area) in climate regulation has been classified as high (Millenium Ecosystem Assessment, 2005; Downing, 2010). Indeed, important roles of lakes in climate regulation have been supported by several studies (Downing *et al.*, 2008; Tranvik *et al.*, 2009; Williamson *et al.*, 2009; Le Quéré *et al.*, 2015). For example, most of the displaced organic carbon (C) from terrestrial systems is buried in the sediments of freshwater lakes and coastal systems, representing short-term to long-term sequestration of atmospheric CO_2, whereas the significance of open ocean sediments in carbon burial is much lower (Downing *et al.*, 2008; Tranvik *et al.*, 2009; Le Quéré *et al.*, 2015).

Lakes modify terrestrially fixed carbon transport to the coast by both evading CO_2 to the atmosphere and sequestering C in the sediments. Thus, both areal C evasion and C burial are larger in small lakes compared to large ones (Kortelainen *et al.*, 2004, 2006; Cole *et al.*, 2007). At the landscape scale, the role of small lakes has been emphasized in net C accumulation, whereas the role of large lowland lakes in releasing CO_2 to the atmosphere may be pronounced (e.g. Einola *et al.*, 2011). However, the role of lakes in landscape-scale C cycling in a changing climate is still highly uncertain.

Lakes emit methane through several pathways, including bubble flux from the sediments, diffusive emissions and plant-mediated emissions through emergent macrophytes (Bastviken *et al.*, 2004; Beaulieu, Del Sontro, & Downing, 2019). CH_4 emissions from hydroelectric reservoirs may also be significant because methane is released during water passage through turbines (Kemenes, Forsberg, & Melack, 2007; Barros *et al.*, 2011). Even though methane leakage is augmented by emergent macrophytes, CH_4 release from lakes is also biologically controlled by methanotrophic bacteria (Schubert *et al.*, 2010; Borrel *et al.*, 2011; Oswald *et al.*, 2016). All these studies indicate a prominent role of lakes in global carbon budgets, especially considering their small coverage of the earth surface (Table 2). Lakes can be considered both sinks and sources of greenhouse gases, yet their role in the carbon cycle depends on their own characteristics, catchment features and local climate conditions (Bastviken *et al.*, 2004; Downing *et al.*, 2008; Tranvik *et al.*, 2009; Einola *et al.*, 2011).

The Millennium Ecosystem Assessment (2005) emphasised that regulating ecosystem services may be the most valuable ones (Sutherland *et al.*, 2018; Vaughn, 2018). The control capacity of lakes and buffering effects of lake-margin wetlands through retention and sedimentation of nutrients and pollutants is an important regulating ecosystem service (Simonit & Perrings, 2011; Vilbaste *et al.*, 2016). In the lake littoral zone, pollution control capacity and nutrient retention are generally boosted by aquatic macrophyte beds and periphyton growth (Petticrew & Kalff, 1992; Dodds, 2003). The balance between nutrient retention and internal loading in lakes is affected by trophic status, whereas nutrient balance is dominated by retention in oligotrophic lakes and by internal loading in eutrophic lakes (Søndergaard, Jensen, & Jeppesen, 2001).

IV. MANAGING LAKES IN THE WATERSCAPE CONTEXT IN A NON-STATIONARY WORLD

Environmental factors, habitat connectivity, and movements of organisms and material are major factors shaping lake communities and ecosystems in waterscapes (see Section II). However, it is becoming increasingly evident that global environmental change fundamentally alters disturbance regimes that can alter ecological communities (e.g. species invasions and extinctions) and abiotic templates (e.g. habitat fragmentation, ecotone boundaries, and the magnitude, frequency and duration of floods and droughts), and ultimately ecosystem service provisioning (https://ipbes.net/global-assessment; Albert *et al.*, 2020). Also, 'boom–bust dynamics', especially for invasive species, further complicate understanding regime shifts when the population of an invasive species rises to outbreak levels followed by a dramatic decline (Strayer *et al.*, 2017). Because many of these factors extend beyond individual lakes, the management, restoration and conservation of lakes need to embrace a wider waterscape perspective (Soranno *et al.*, 2010; Heino, 2013*b*; Teurlincx *et al.*, 2019; Fried-Petersen *et al.*, 2020). In this section, we focus on several challenges to the management of lakes in a waterscape context. We particularly embrace the resilience perspective (Holling, 1973; Table 2). This perspective refers to tipping points, alternative system regimes and non-stationary changes (Baho *et al.*, 2017), which complicate adaptive and transformative management of lakes in a rapidly changing world. Lakes are perhaps among the best-studied ecosystems regarding the phenomena of biological resilience and alternative regimes (Scheffer *et al.*, 1993), providing opportunities to extend the discussion from the local lake ecosystem level to that of entire waterscapes (Fig. 3). This approach is thus associated with resilience thinking in a spatially explicit way (Allen *et al.*, 2016; Sundstrom *et al.*, 2017).

The capacity of ecosystems to absorb disturbances is limited, and they can thus undergo profound abiotic and biotic changes once a disturbance threshold is passed. There are many examples of lakes that have changed from a desired clear-water regime to an undesired algal-dominated regime due to eutrophication (Carpenter, 2003; Bicudo *et al.*, 2007). Inherent in such shifts is the loss of recreational values (e.g. fisheries, swimming and boating) and biodiversity change (Hilt *et al.*, 2017). Once stabilized in degraded regimes, lakes will not return to the clear-water state in the absence of significant, long-lasting and costly management. In this context, higher temperatures induced by climate warming are also often associated with increasingly eutrophic conditions. Furthermore, new system regimes are often hysteretic, meaning that the energy required to return them to a previous regime is substantially higher than the energy that pushed the system into its alternative regime. This hysteresis often makes it difficult to break the feedbacks of a degraded system, which hinders their return to the previous regime (Suding, Gross, & Houseman, 2004). There is a large body of lake biomanipulation studies documenting restoration failures due to this difficulty (Gulati, Pires, & Van Donk, 2008).

At least two fundamental implications arise from lake resilience research that are crucial to our understanding and management of lakes as parts of waterscapes. First, regime shifts in lakes contrast with the assumption that ecosystems recover after disturbances have ceased, eventually reaching pre-disturbance equilibrium or approaching arbitrarily defined reference conditions if given enough time. This assumption is rooted in classical ecological stability research, which considers a balanced (i.e. ecosystems recover their balance after disturbances) rather than a discontinuous (i.e. non-linear regime changes) view of ecosystems (Allen *et al.*, 2019). Second, defining biological reference conditions *per se* is problematic because even reference states change, locally and regionally, as well as in time, which complicates assessments of ecosystem recovery (Duarte *et al.*, 2009). This was exemplified by McCrackin *et al.* (2017) who estimated that, depending on the biological group (e.g. algae, submerged macrophytes, invertebrates or vertebrates) or ecosystem function (e.g. nitrogen, phosphorus or carbon cycling), recovery times after control of nutrient inputs ranged from less than a year to approximately a century. However, assuming recovery at the scale of centuries can be erroneous because changing ecological baselines due to anthropogenic environmental change often manifest at decadal timescales. More specifically, rapid environmental change may outpace the attainment of recovery targets, which thus become obsolete. Such a phenomenon is again indicative of non-stationary change (Table 1), which can be further demonstrated with the current debate concerning recovery of surface waters from acidification. Scientists and managers frequently embraced a stationary view that lake ecosystems have not had enough time to recover biologically since the implementation of acidification mitigation measures in the 1970s and

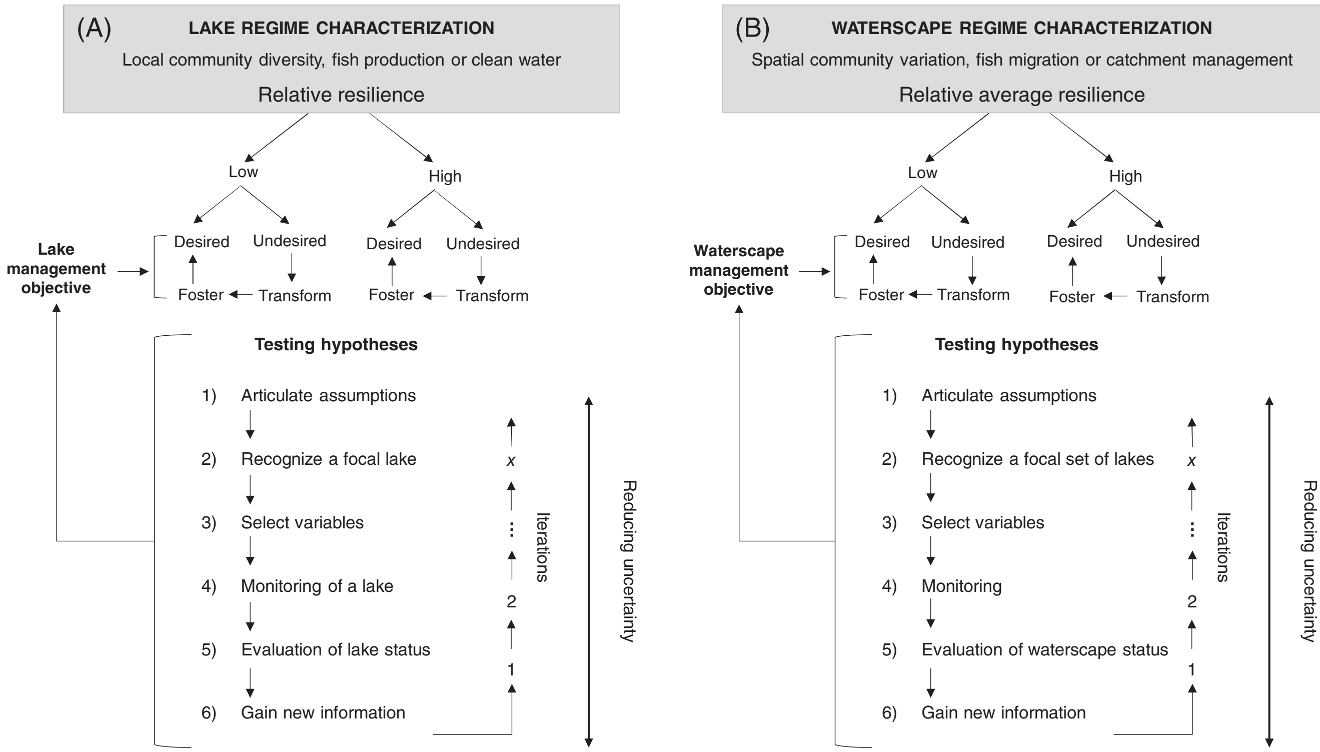

Fig 3. Adaptive management, inference and modelling framework that reiteratively tests, re-calibrates, and refines resilience-based hypotheses to attain management goals for individual lakes (A) or the entire waterscape (B). Adaptive management objectives are different for individual lakes and entire waterscapes. Modified from the general ideas of Baho *et al.* (2017).

1980s. This contrasts with non-stationary viewpoints. Research has shown that recovery can be masked because of abiotic (e.g. decreased water transparency) and biotic (e.g. algal expansion and bloom formation) factors. These factors may not necessarily be directly related to acidification and may alter the ecological baselines of both acidified and reference lakes relatively fast (Angeler & Johnson, 2012). Such non-stationary interpretations are also echoed in hypotheses about acidified lakes comprising stable degraded regimes from which biotic and abiotic recovery to a circumneutral regime equivalent is unlikely (Baho *et al.*, 2014).

In the face of non-stationary change, managers often have to rely on mitigating the impacts when restoration is unfeasible. This can have crucial implications for sustainable management of lakes in the long term because the amount of management needed may vary strongly and potentially increase over time (Angeler *et al.*, 2020*b*). However, our ability to manage lakes locally, let alone in entire waterscapes, is inadequate. This suggests that long-term costs and benefits need to be carefully compared against the potential harm that can arise from management itself. For example, if lake management targets the optimization of specific ecosystem services (e.g. fisheries), the result may be loss of resilience (Holling & Meffe, 1996). Therefore, the management of waterscapes has a strong uncertainty component, meaning that many future challenges are unknown and cannot be envisioned in the context of current practices (Angeler, Allen, & Carnaval, 2020a).

Managing waterscapes for specific sets of ecosystem services may require deliberate transformations for a sustainable future. However, implementing such a management strategy is difficult owing to the scales and dimensions (e.g. ecological, social, economic, and legal) that need to be considered in a waterscape context. The implication is that despite exhaustive adaptive experimentation and knowledge acquisition, we are unlikely to know enough to intentionally create desired waterscapes that are self-organizing and self-maintaining in a rapidly changing world (Baho *et al.*, 2017). Also, a major limitation of such intended transformation is our lack of knowledge of what a novel, future, viable and self-organizing ecosystem should look like (Murcia *et al.*, 2014), although scenario planning could be useful for this purpose (Kok *et al.*, 2017). Given the reality of non-stationary change, management goals related to deliberate transformations of waterscapes to maintain biodiversity and ecosystem services may thus become unrealistic. Hence, there is a need for consistent management in the form of human-provided inputs to maintain feedbacks, although such waterscapes might potentially have low resilience and could potentially be exposed to unintended management side effects or indirect social dynamics (Angeler *et al.*, 2020*b*).

One complex example is lake liming, which has been implemented to counteract acidification effects and mimic conditions of circumneutral lakes in Northern Europe and North America (Henriksson & Brodin, 1995; Sandoy & Romunstad, 1995). Rather than restoring a circumneutral regime, liming only mimics such conditions. Specifically, liming forces the acidified regime to approximate lake conditions that are conducive to ecosystem service provisioning (e.g. recreational fishing and aquaculture). Liming is done to manage for the ghost of a past circumneutral lake regime (Angeler *et al.*, 2020*b*), that is a regime that is no longer maintainable without massive management. The fact that liming is a form of coercive management is manifested in the ultimate return of acidic conditions once liming is ceased (Clair & Hindar, 2005). In biodiversity conservation and restoration contexts, liming is increasingly viewed as detrimental due to its considerable alteration of biogeochemical and biological features of lakes (Angeler *et al.*, 2017). This example indicates that substantial negative side effects can arise when management is based on approaches aimed at maintaining a ghost of a past circumneutral regime. The liming example shows a fundamental challenge for the sustainable management of waterscapes in a rapidly changing world.

Finally, the degree to which fundamental science translates into the arena of environmental and sustainable development action will vary, highlighting complicated questions of who or what benefits from lake management and who or what is marginalized (Blythe *et al.*, 2018). These are critically important questions for addressing the need to manage waterscapes for desired human outcomes. Rather than relying on intended transformation of sets of lakes to desirable and self-organizing waterscapes, ever-increasing amounts of management are required to satisfy the growing demands of ecosystem services for a growing human population. The resilience of ecological systems that is based to a large degree on human-induced management is considered fragile owing to the lack of ecologically based self-reinforcing feedbacks (Rist *et al.*, 2014). Because management is contingent on environmental law, considerable policy implications arise from such uncertainty. Events from the past, such as the spread of agriculture, that led to regime shifts in lakes and required extensive management to mitigate human-caused eutrophication (Carpenter, 2005), may provide lessons for the future. Such lessons could form the cornerstone for novel thinking about the complexity associated with the sustainable management of lakes.

V. WHERE TO GO FROM HERE?

Based on the evidence and ideas summarized above, there are a number of important avenues for future research and management of lakes that should help to fill knowledge gaps. The following four key gaps should thus be addressed in studies that integrate current knowledge about local and regional factors that dictate the ecology of individual lakes and broader waterscapes. This will also entail a systemic understanding of their resilience and how this resilience influences biodiversity and ecosystem services.

(1) An assessment of regime shifts at local, regional and global scales

These evaluations should build on assessing early warning signals based on multiple lines of evidence (Wang *et al.*, 2012; Spanbauer *et al.*, 2014), and focus on the effects of climate warming, land-use change, increases of dissolved organic carbon, alien species invasions, and recovery from acidification on lake communities and ecosystems. These stressors may be acting individualistically or jointly (Birk *et al.*, 2020). One should also keep in mind that the effects of multiple stressors accumulate to low-lying and highly connected lakes (Solheim *et al.*, 2019), which are usually those with heavily populated shorelines (Fig. 2). Evaluations of the effects of these stressors on lakes should facilitate the identification of management priorities, including proactive and reactive interventions to mitigate stress. Here, understanding lakes as parts of waterscapes provides a more holistic perspective than narrower approaches focussing on single lakes. Specifically, to facilitate management, research could target the identification of specific lakes in a waterscape that may serve as havens of biodiversity and sentinels of ecological change for the entire waterscape.

(2) A need to include a spatial dimension to the measurement of lake ecosystem resilience

Much work on resilience in lakes has been inferred from temporal studies in individual lakes. However, such studies tell us little about the resilience of temporally highly dynamic systems that are part of a broader waterscape (Allen *et al.*, 2016). Spatial resilience and spatial regimes (Sundstrom *et al.*, 2017) are emergent concepts that can be useful to study broader waterscapes. This is exemplified by a recent avian study that could accurately reconstruct and predict how fast entire ecoregions move in the landscape in relation to environmental change (Roberts *et al.*, 2019*a*). It would be interesting to assess how regime shifts in the terrestrial matrix affect a waterscape, i.e. whether or not waterscape regimes change in response to terrestrial regime changes.

(3) Comparative studies of lake ecosystem resilience

Researchers need to assess the relevant spatio-temporal scales and ecological contexts (e.g. different lake types as defined above) objectively in comparative studies rather than being based on subjective definitions (e.g. defined by political boundaries, research-defined scales or limited ecological contexts). Surrogates of resilience have been developed, and an increasing amount of data is available that would allow such comparisons (Nash *et al.*, 2014; Angeler *et al.*, 2016). Comparison of resilience-based assessments with traditional biodiversity studies should be made because these

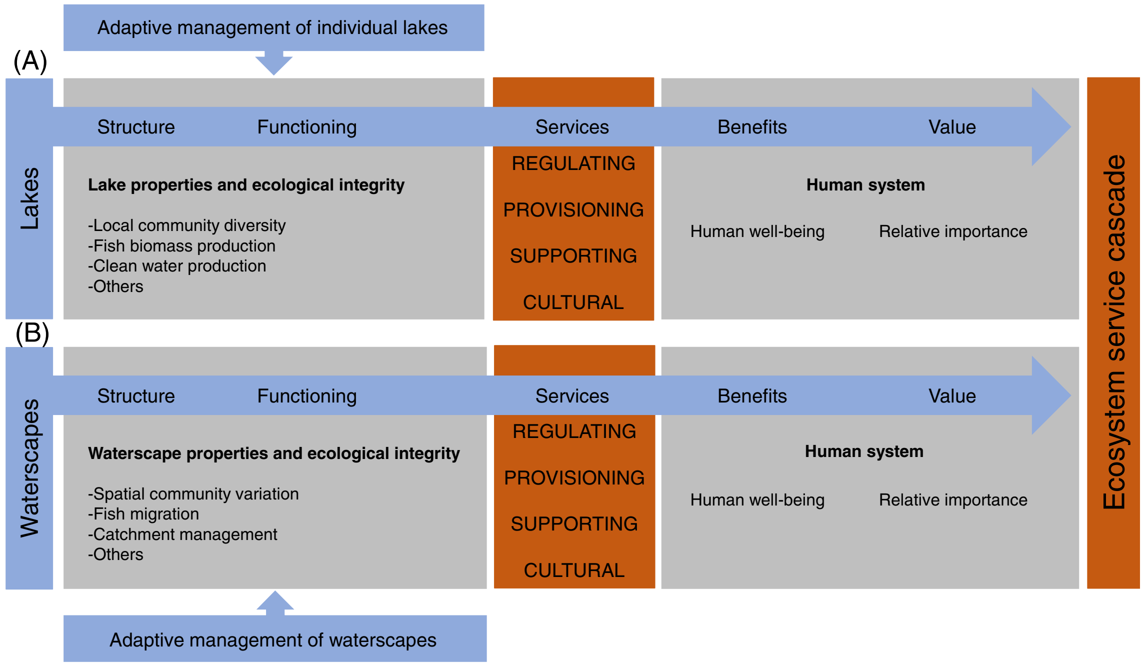

Fig 4. An approach for the adaptive management of individual lakes (A) and entire waterscapes (B), resulting in the ecosystem service cascade. Figure is modified following the ideas of Müller *et al.* (2010) and Giakoumis & Voulvoulis (2018).

approaches may not show congruent results (Roberts *et al.*, 2019*b*).

(4) A wrap-up with reality check

There is an ongoing discussion about what we must or should do, but economic, political, and practical realities are an obstacle to the implementation of ecological theory to environmental management (Wuijts, Driessen, & Van Rijswick, 2018). In other words, a lot of data are typically required for modelling (Verburg *et al.*, 2016). We currently do not have enough data to examine most phenomena affecting the resilience of lake ecosystems, let alone entire waterscapes, although data sets that are suitable for resilience research are increasingly becoming available for incorporation in adaptive management of waterscapes. Theoretical models alone may not be enough in making predictions of changes in lake ecosystems in waterscapes in the Anthropocene. Thus, results from these models should also be recurrently validated with empirical field data (e.g. Arhonditsis *et al.*, 2019). Ultimately, research across disciplinary fields (e.g. climatological, limnological, ecological, and societal) is needed to address the challenges that humanity faces in the Anthropocene (Alahuhta *et al.*, 2020; Heino *et al.*, 2020; Angeler *et al.*, 2020*a*), and in which lakes play an important role in providing ecosystem services.Such an approach, considering simultaneously the different forms of ecosystem services that lakes provide individually or jointly at the waterscape level, will be vital for managing the reliance of humans on biodiversity and natural ecosystems (Müller, Groot, & Willemen, 2010; Giakoumis & Voulvoulis, 2018) (Fig. 4).

VI. CONCLUSIONS

(1) Different types of lakes show different spatial organization, biological communities and ecosystem services that are spatially and temporally variable. This spatio-temporal dynamism dictates that management of lake biodiversity and ecosystem services cannot overlook feedback mechanisms.
(2) Lakes should be considered in the regional context of meta-systems, taking into account a lake's position in the landscape. Lakes high in the landscape may be relatively isolated, receiving less organisms and matter from other lakes, while still being closely associated with the surrounding terrestrial ecosystem. This isolation means, however, that biological recovery after anthropogenic disturbances may be delayed for a relatively long time because these headwater lakes are not well connected to the regional pool of dispersing organisms. By contrast, lakes low in the landscape are well connected to other lakes and the drainage system, thereby receiving a constant flux of dispersing organisms to counter temporary extinctions of species. Such high connectivity also contributes to the higher potential capacity to recover from anthropogenic impacts. However, low-lying lakes are also the ones most

affected by anthropogenic stressors, possibly resulting in long recovery times.

(3) Our main proposition is that understanding the biodiversity and ecosystem services lakes provide should be based on the waterscape approach because no lake is completely disconnected from surrounding terrestrial landscapes, other lakes or riverine systems. However, depending on the lake type, the relative roles of local and regional processes as well as anthropogenic stressors vary in determining biodiversity and ecosystem services, which should be taken into account in the adaptive management of lake ecosystems as parts of broader waterscapes in an increasingly human-dominated world.

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