Habitat complexity in shallow lakes and ponds: importance, threats, and potential for restoration

Mariana Meerhoff · María de los Ángeles González-Sagrario

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Abstract In this review we describe patterns and mechanisms by which habitat complexity is crucial for the functioning of shallow lakes and ponds, and for the abundance and diversity of biological communities in these ecosystems. Habitat complexity is affected by processes acting at different spatial scales, from the landscape to the ecosystem level (i.e., morphometric attributes) that generate different complexities, determining the potential for organisms to succeed and processes to occur, such as energy and nutrient transfer, and fluxes of greenhouse gases, among others. At the local scale, the three major habitats, pelagic, littoral, and benthic, are characterised by different degrees of structural complexity and a particular set of organisms and processes. Direct and indirect effects of changes in within-lake habitat complexity can either hinder or promote regime shifts in these systems. We also review several anthropogenic pressures (eutrophication, urbanisation, introduction of exotic species, and climate change) that decrease lake resilience through changes in habitat complexity and strategies for habitat complexity restoration. Overall, we emphasize the need to preserve and/or restore habitat complexity as key challenges to account for ecosystem integrity, maintenance of local/regional biodiversity, and for the provision of crucial ecosystem services (e.g., biodiversity, self-purification, and carbon sequestration).

Keywords Aquatic biodiversity · Alternative states · Habitat degradation · Eutrophication · Climate change

Introduction

Shallow lakes and ponds provide a myriad of ecosystem services (Millennium Ecosystem Assessment, 2005), many of which depend, directly or indirectly, on habitat complexity. Physical and chemical processes, as well as ecosystem properties such as nutrient cycling and food web structure, are also strongly affected by habitat complexity. As in most, if not all ecosystems, the abundance and diversity of different
Shallow lake biological communities typically increase with habitat complexity. The conceptual framework behind this pattern is that structural complexity potentially increases the availability of resources (food, shelter, substrate) and of habitats/microhabitats, creating new niches and supporting a higher number of taxa than similar systems with lower structural complexity. Niche partitioning allows species co-existence within a given area due to reduced interspecific competition (Pianka, 2000). Habitat complexity may also dampen predator-prey oscillations. Thus, structural complexity influences interspecific relationships, often reducing and stabilising biotic interactions and facilitating food web compartmentalization. The latter, in turn, increases community persistence and the co-existence of a larger number of species (Stouffer & Bascompte, 2011), impacting ecosystem integrity and ecological functions and processes like carbon sequestration and fluxes, nutrient cycling and translocation, among others.

Traditionally, limnological research focused on the biological communities and ecological processes happening in the spatially homogeneous water column of large, deep, nutrient-poor lakes (Wetzel, 2001). However, most lakes in the world are small and shallow (Wetzel, 1990; Downing et al., 2006). A shift of focus from the pelagic to incorporate other habitats such as the littoral and benthic zones has given empirical support to several ecological theories (e.g., Scheffer et al., 1993) and has highlighted the importance of habitat complexity for the overall functioning of these ecosystems (e.g., Vadeboncoeur et al., 2002; Vander Zanden & Vadeboncoeur, 2020). Several aspects connected to complexity are clearly identifiable in aquatic ecosystems (Tokeshi & Arakaki, 2012). This explains that intensive research in the last 30 years has contributed to understanding the connection between habitat complexity and the structure and functioning of shallow lake and pond communities.

Habitat complexity has been defined in various ways but, following Tokeshi & Arakaki (2012), here it will be interpreted as all different characteristics of structure, therefore including the spatial scale, size, density, spatial arrangement and diversity (heterogeneity) of structural elements in an ecosystem. Habitat complexity in lakes and ponds is affected by processes occurring at different spatial scales leading to a concomitant variation in the nature of the structural elements that generate complexity (Tokeshi & Arakaki, 2012).

In this review, we aim at synthesising the importance of habitat complexity for the functioning of shallow lakes and ponds. Shallow lake and pond integrity rely on biodiversity, which is affected by spatial complexity and connectivity, and largely sustained by within system habitat complexity, in particular by the presence, diversity, and density of aquatic plants. A large part of this review deals with aquatic plants, since macrophytes are the most important structural element creating habitat complexity in these ecosystems. We then focus on the connection between habitat complexity and biodiversity and several ecosystem services, as well as on the major current anthropogenic direct and indirect threats to complexity, and its restoration potential. Finally, we propose some lines for future research that emerged from the review.

**Shallow lake habitats and habitat complexity**

The structure of biological communities is defined by interactive processes (speciation, drift, selection and dispersal) operating at different spatial scales, from regional processes that regulate the movement of organisms and materials (e.g., nutrients, seeds, water) and of information (genetic variation) (Vellend, 2010), to biotic and abiotic local factors, including system morphometry, patterns of disturbance, and habitat complexity. At the local scale, i.e., inside a lake, three major zones or habitats are typically considered: the ‘pelagic’, the ‘benthic’, and the ‘littoral’ zones, each characterised by particular communities (Fig. 1). Among other characteristics, each habitat typically has different degrees of structural complexity. Particularly in shallow lakes and ponds, information, matter, and energy are widely exchanged between these habitats (Schindler & Scheuerell, 2002), in direction and degree often determined by the level of complexity within each of them.

The pelagic or water column is the least complex zone in terms of physical structure (Fig. 1). This habitat is mostly inhabited by plankton, with quite restricted movement capacity. The success of zooplankton grazing on phytoplankton, and of fish predation on zooplankton depend, among other
factors, on the probability of encounter and mutual recognition of consumers and prey. Under turbid water conditions some prey may minimise predation. However, under clear water conditions, the poor complexity in the pelagic habitat prevents the use of physical refuges by prey that have no other option than moving to avoid being eaten. Consequently, the likelihood of over-exploitation of prey resources by predators and grazers can potentially be high in this habitat (Scheffer & De Boer, 1995).

The benthos or lake bottom can vary quite largely in its degree of complexity. Lake depth, water colour, and the amount of suspended matter determine whether light reaching the bottom is enough to allow photosynthesis by benthic vegetation and, with it, an increase in physical complexity generated by these biological elements. Thus, turbid lakes and ponds often lack primary production of importance in the benthic zone, and most of its complexity is a result of the variability in sediment particle size and accumulated debris from other lake habitats or from the surrounding terrestrial environment. Sediment physical characteristics, besides lake trophic state and the outcome of biotic interactions, determine the densities and taxonomic richness of macroinvertebrates to a large extent (Free et al., 2009). Benthic complexity, given by sediment structure, the development of periphyton and submerged plants, or by structure-generating animals such as sessile mussels, can either facilitate or hinder sediment resuspension by wind or by benthic-dwelling organisms and fish. Even sandy sediments are only intermittently disturbed by water movements if they are covered by large abundances of microalgae (such as diatoms) (Moss, 1998).

The littoral zone contributes disproportionately to the overall biodiversity and ecosystem processes in lakes, mostly in shallow (e.g., Carpenter & Lodge, 1986; Scheffer et al., 1993; Jeppesen et al., 1998) but also in deep lakes (Hampton et al., 2011). The littoral habitat is characterised by different assemblages of organisms and different levels of complexity. Drawn by M. Meerhoff and Tinna Christensen. From Kosten & Meerhoff, 2014.
zone, defined as the lake area shallow enough as to potentially allow the growth of submerged plants, typically represents the highest habitat complexity in most lakes and ponds (Fig. 1). This complexity is mostly given by aquatic macrophytes of different life forms and by debris, and, often to a lesser extent, by abiotic structures such as rocks and stones. In large shallow lakes, sheltered bays and archipelagos offer a favourable environment for the development of different macrophyte species that may generate different habitat complexities, such as reeds and water lilies or free-floating plants, besides the typically more resistant submerged plants (Andersson, 2001). Lakes with a larger shoreline development would expectedly host higher species richness than simple-shaped systems. This would be the consequence of several processes, such as a stronger interaction with the surrounding terrestrial ecosystem, which act as a source of structure such as debris, besides nutrients, organic matter, and organisms. In turn, on wind-exposed shores, particularly in large lakes, scarce or negligible aquatic plants can grow (with consequent loss of associated biota) due to constant sediment resuspension or erosion caused by wave action (Chambers, 1987; Crisci et al., 2017). In addition, longer fetches lead to stronger wave action that may promote the formation of coarse, rocky littoral habitats, offering new spawning, nursery, or feeding habitats for many species that may not be present in otherwise smaller lakes (Jackson et al., 2001), promoting the maintenance of fish diversity and fisheries (Sass et al., 2006; Kauffmann et al., 2014). Long shorelines have been related to an important growth of aquatic and amphibian plants in the land–water transition (Anderson, 2001). This would be particularly expected in small lakes, since the perimeter: surface ratio is comparatively higher than in large lakes. Riparian vegetation, be it fully terrestrial or amphibian, generates different types and number of structural elements (e.g., roots, branches, debris of different sizes) and can modify physical aspects of the shore, such as bank erosion, water depth and shoreline development.

Along natural lake shorelines, emergent aquatic plants are the most common life-form, often constituting the wetlands associated with shallow lakes and ponds. In highly turbid lakes, or very large lakes, emergent plants may drive key lake processes such as the redistribution of sediment particles, thus affecting water clarity, sedimentation, and resuspension rates with associated effects on the release of the internal phosphorus loading (Horppila & Nurminen, 2002, 2005). Structural complexity can explain more of the spatial distribution of juvenile fishes in the littoral area of temperate lakes (e.g., roach, Rutilus rutilus (Linnaeus, 1758), and perch, Perca fluviatilis (Linnaeus, 1758)) than several other factors, including the biomass of potential food items (Lewin et al., 2004). A comparison of the use of different habitat complexities in the littoral zone (i.e., woody debris, reeds, and areas of different substratum size) by fish in a shallow temperate lake suggested a strong diel component, with a predominant occurrence of fish in complex habitats during the day and a partial migration of zooplanktivorous fish towards the less complex open habitats at night (Lewin et al., 2004). In ponds and in shallow lakes with gentle slopes and with sufficient light reaching the bottom, the littoral zone can extend further out from the shore into the lake with development of higher aquatic plants over large sections or the entire basin.

Habitat complexity in the alternative equilibria hypothesis and other ecological theories

The paramount importance of habitat complexity was captured in the alternative stable states or alternative equilibria hypothesis for shallow lakes (Scheffer et al., 1993). In a nutshell, this hypothesis stated that shallow lakes, over the same wide range of nutrient concentrations, may present contrasting regimes, dominated by either phytoplankton, with turbid water, or by submerged plants, with clear water. Biological and physical–chemical feedback mechanisms related to the presence or absence of submerged macrophytes cause a hysteresis effect maintaining, respectively, the clear water (with typically moderate to high complexity) or the turbid water (with low complexity) regime (e.g., Balls et al., 1989; Scheffer et al., 1993). The original idea later expanded as to include other potentially alternative regimes, such as the dominance of free-floating plants in the high end of nutrient concentrations (Scheffer et al., 2003). Although competition for resources between submerged plants and phytoplankton, and their contrasting reinforcing effects on water clarity lies at the core of the alternative equilibria hypothesis, several feedback
mechanisms are directly linked to the physical structure or complexity created by each dominant primary producer.

The structural complexity promoted by each dominant regime, i.e., submerged plants, free-floating plants, or phytoplankton, varies enormously in terms of identity, density, diversity, size, and spatial arrangement of structural elements. In particular, the spatial structure typically created by submerged plants can decrease the likelihood of catastrophic shifts between alternative states (or regimes) when nutrient loading increases (van Nes & Scheffer, 2005). Predator–prey interactions and trophic cascades are crucial for the maintenance of each regime (Genkai-Kato, 2007). Habitat complexity, generated by submerged plants, can stabilise trophic interactions and modify expected outcomes of trophic cascades by acting as an anti-predation refuge for several keystone species or groups. The high structural complexity given by submerged plants, or phytoplankton, varies enormously in terms of identity, density, diversity, size, and spatial arrangement of structural elements. In particular, the spatial structure typically created by submerged plants can decrease the likelihood of catastrophic shifts between alternative states (or regimes) when nutrient loading increases (van Nes & Scheffer, 2005). Predator–prey interactions and trophic cascades are crucial for the maintenance of each regime (Genkai-Kato, 2007).

Habitat complexity, generated by submerged plants, can stabilise trophic interactions and modify expected outcomes of trophic cascades by acting as an anti-predation refuge for several keystone species or groups. The high structural complexity given by submerged plants typically leads to a decrease in the foraging ability of predators, being piscivorous fishes (Persson & Eklöv, 1995), zooplanktivorous fishes (Schriver et al., 1995) or macroinvertebrates (Warfe & Barmuta, 2004), and to an increase in the total abundance and mean size of their respective prey. Predation-driven changes in prey community structure (biomass, density, and body-size distribution) are therefore mediated by habitat structure (Crowder & Cooper, 1982).

In temperate shallow lakes, submerged plants thus often facilitate the survival of large-bodied cladoceran zooplankton that can graze on phytoplankton (Timms & Moss, 1984) by offering a daytime refuge against visual predatory fish (Lauridsen & Buenk, 1996; Lauridsen & Lodge, 1996). The refuge effect for zooplankton often depends on complexity attributes, such as the plant architecture (e.g., Nurminen & Horppila, 2002; Meerhoff et al., 2006, 2007a), plant bed size or density (Lauridsen et al., 1996; Burks et al., 2001), and percent of the lake volume inhabited by the submerged plants (Schriver et al., 1995) (reviewed by Burks et al., 2002). Habitat complexity thus decreases the likelihood of over-exploitation of prey (Scheffer & De Boer, 1995), and increases the resilience of littoral communities to fish predation (Kornijów et al., 2016), leading to the overall promotion of biodiversity associated with the clear water, submerged-plant dominated regime in shallow lakes and ponds (Thomaz & Bini, 1998; Agostinho et al., 2003; Declerck et al., 2005; Scheffer et al., 2006; Teixeira-de Mello et al., 2009; Thomaz & Cunha, 2010).

The positive effects of submerged plants on water clarity described above seem less evident in warm regions (e.g., Bachmann et al., 2002; Jeppesen et al., 2007; Meerhoff et al., 2007a; Kosten et al., 2011). Even with abundant submerged macrophytes, a higher phytoplankton biomass at a given nutrient concentration occurred in shallow lakes in the subtropical state of Florida (USA) than in Danish temperate lakes, according to comparative studies using a large database (Jeppesen et al., 2007, 2020). In particular, the refuge capacity of submerged plants for zooplankton depends on local trophic dynamics and on climate-related community structure, with plant refuges being far less effective in warm and Mediterranean climates (Iglesias et al., 2007; Meerhoff et al., 2007a; González-Sagrario & Balserio, 2010; Tavşanoğlu et al., 2012) due to the typical association of small fishes (Teixeira de Mello et al., 2009) and macroinvertebrate predators (González-Sagrario et al., 2009; González-Sagrario & Balserio, 2010) to aquatic plants, reducing their refuge capacity.

Under high nutrient concentrations and mild or high temperatures, free-floating plants may also constitute an alternative regime to submerged plants (Scheffer et al., 2003), and also to phytoplankton dominance (Rojackers et al., 2004; de Tezanos Pinto & O’Farrell, 2014). Free-floating plants cover a large range in size, from very small taxa, such as the genera Azolla and Lemna spp, medium-sized taxa, such as Salvinia spp (water fern), and large-sized taxa, such as Pistia stratiotes L. (water lettuce) and Pontederia crassipes Mart. (water hyacinth, formerly Eichhornia crassipes (Mart.) Solms), the latter two being more common in warm areas (Sculthorpe, 1967). In contrast to submerged plants, that grow inside the water column and are mostly anchored to the sediments, most free-floating plants grow on the water surface and are freely moved by currents, waves, and winds. The habitat complexity generated by this kind of plants is indeed lower than that of submerged plants, but depends on the area covered and on the plant size. Large free-floating plants have a dense and potentially long root network, and their shoots and leaves can shade the water column when the area covered is large enough, thus limiting the growth of both submerged plants and phytoplankton (de Tezanos Pinto et al., 2007). Massive covers of free-floating plants thus decrease habitat...
complexity by reducing the biomass of submerged plants (mostly due to competition for light). Their impacts on aquatic biodiversity are quite contrasting to those of submerged plants, largely due to the often anaerobic or anoxic conditions created under dense mats of free-floating plants. Massive covers of free-floating plants are usually followed by a simplification of food webs (Moi et al., 2021) and a general impoverishment of biodiversity, including fish and macroinvertebrates (Meerhoff et al., 2003), zooplankton (Fontanarrosa et al., 2010), phytoplankton (O’Farrell et al., 2009), submerged plants (Janes et al., 1996), waterfowl, often including fish kills. Besides, the role of large free-floating plants as a potential anti-predation refuge for zooplankton seems weaker than that of submerged plants, according to comparative studies (Meerhoff et al., 2003, 2006, 2007a, b). The also floating but rooted plant, P. azurea Sw. (formerly Eichhornia azurea (Kunth)), has, in contrast, been shown in experimental studies to act as refuge for macroinvertebrates against fish predation in tropical areas (Padial et al., 2009).

Relevance of plant architecture for the generation of habitat complexity

As stated above, aquatic plants are the most important generators of habitat complexity in shallow lakes and ponds. Emergent, floating-leaved, submerged, and free-floating plants represent different life strategies and promote different habitat complexities due to variations in plant architecture, typical location within a lake, and their occupation of the water column. The average size and interstitial spaces (filling spaces) along vertical and horizontal axes, i.e., the space-size heterogeneity, is one of the most relevant drivers of taxonomical richness in aquatic environments (St. Pierre & Kovalenko, 2014). Different macrophyte life forms differ in space-size heterogeneity, which can lead to contrasting complexities and explain their different effects on biodiversity and ecosystem processes. Comparative studies on the effects of emergent and floating-leaved plants (Nurminen & Horppila, 2002; Horppila & Nurminen, 2005) and of submerged and free-floating plants (Janes et al., 1996; Meerhoff et al., 2003, 2006, 2007a, b; Netten et al., 2010) have highlighted the importance of plant architecture for biodiversity and several processes at the community level as was discussed above. Studies that have manipulated habitat complexity by keeping surface area constant have found, for instance, that macroinvertebrates respond to habitat structure independently of surface area (Warfe et al., 2008). Similarly, in a study where artificial macrophytes with three levels of complexity (from low to high) but with constant mass and surface area were introduced in experimental setups in a lake, microfaunal (mainly rotifers) abundance and richness were generally greater on the most complex substrata (Lucena-Moya & Duggan, 2011). Different architectures of aquatic plants, leading to different complexities (measured through fractal geometry), significantly affected taxon richness and total densities of tropical invertebrates, although other variables such as plant identity and area were also relevant (Tomaz et al., 2008). Moreover, a field experiment conducted in a series of temperate and subtropical shallow lakes manipulating the spatial arrangement of the same amount and type of plastic structure mimicking aquatic plants of different life forms (i.e., free-floating and submerged) found dramatic differences in the habitat use, richness, biomass and density of most aquatic organisms (Meerhoff et al., 2007a, b; Teixeira-de Mello et al., 2009; Brucet et al., 2010; Clemente et al., 2019). Such field experiments also revealed that some of the effects generated by habitat complexity differed in different climates, likely due to climate-related differences in the assemblage of fishes (Meerhoff et al., 2007a; Teixeira-de Mello et al., 2009) (Fig. 2).

Taniguchi et al. (2003) suggested that the diversity or heterogeneity of habitable space, more than the quantity of habitable space or food resources created by complexity, was the factor leading to higher taxonomic richness. In a comparative study, these authors found that the abundance of macroinvertebrates on natural plants did not differ between simple and complex forms, whereas on artificial plants more invertebrates occurred on complex than on simple forms (Taniguchi et al., 2003). The heterogeneity or diversity of filling space at different scales promotes species co-existence by dividing the surface area into a large number of structural surfaces and microhabitats (Tokeshi & Arakaki, 2012), thus generating different niches for competitor, prey, and predator organisms. Space-size heterogeneity (i.e., variable size spaces) permits the co-existence of organisms with a wide range of body sizes, potentially increasing the number.
The effects of plant architecture vary with regional climate and associated structure of classic trophic webs. In this field experiment, the same amount of artificial material mimicked submerged and free-floating plants and was placed in a series of ten similar shallow lakes under contrasting climates (temperate and subtropical). The modulating effects of aquatic plants on littoral (shown) lake communities is affected by climate, likely because of differences in local trophic web structure and in the spatial behavior of fish (depicted in the sketch below). Note the different scales used for each climate region. Modified from Meerhoff (2006)
of pathways for resource utilization and stabilizing interspecific interactions (Thomaz & Cunha, 2010; Kovalenko et al., 2012). The spatial segregation of different cohorts due to habitat complexity reduces the strength of competition and intraguild predation (examples for fish species in Thomaz & Cunha, 2010). Equally important, space-size heterogeneity reduces the encounter rates between prey and predators, thus reducing forage efficiency and stabilizing trophic food webs. The reduction of intra- and interspecific interactions between functional subgroups (e.g., large versus small omnivores) allows the compartmentalization of community structure, leading to lower connectedness and a stabilization of the food web (Stouffer & Bascompte, 2011; Kovalenko et al., 2012). A mathematical model suggested that predator–prey interactions are unstable at low and high levels of habitat complexity, conditions where populations are prone to extinction or declining (Jana & Bairagi, 2014). Field studies have demonstrated that the increase of biodiversity with increasing space-size heterogeneity is the highest at intermediate complexity levels (St. Pierre & Kovalenko, 2014); for example, highly complex habitats set limitations for fish movement and efficient foraging, thus reducing fish growth (Thomaz & Cunha, 2010 and references therein).

### Habitat complexity and ecosystem processes

Ecosystem processes can be directly or indirectly affected by habitat complexity. Submerged rooted plants can reduce sediment resuspension and therefore abiotic turbidity (Fig. 3) (Madsen et al., 2001) and concomitantly nutrient release may decrease (Horppila & Nurminen, 2003). On the other hand, plant respiration and accumulation and decomposition of settled organic matter can promote changes in the redox conditions towards anoxia and decreased exchange of oxygen with the water column; thus, potentially increasing phosphorus release (Stephen et al., 1997) from the sediments within plant stands (Fig. 3). In contrast, under low complexity conditions, sediment resuspension promotes the release of nutrients and other accumulated substances to the water column regardless of oxygen concentration, increasing the availability of resources and particularly of reactive phosphorus for pelagic organisms, such as phytoplankton, bacterioplankton, and free-floating plants if present. The release of phosphorus from the sediments (called internal load) often takes place in summer in temperate shallow lakes (Søndergaard et al., 2003) and potentially can occur all year round in warm lakes and ponds where anaerobic and anoxic conditions are more frequent.

Some greenhouse gases (GHG) can be generated in the sediments under anoxic conditions and be released by diffusion or also by ebullition in the case of methane, or being transformed or released by the activity of benthic fauna (Colina et al., 2021). Thus, the structural complexity of this particular habitat is crucial not only for the benthic biota but also for the cycling of nutrients, GHG fluxes, and the overall linkage with other habitats. Rooted submerged plants may, however, also oxygenate the sediment, decreasing methane (CH$_4$) production and promoting its consumption, leading to an overall decrease in CH$_4$ emissions (Davidson et al., 2015, 2018). Experimental studies have shown that under free-floating plant mats, in contrast, CH$_4$ production can be boosted by high organic matter production especially under anaerobic conditions; but also, a large amount of the CH$_4$ produced may become oxidised due to the reduced gas exchange under the dense mats of plants, combined with a high activity of the rhizosphere microbiome (Kosten et al., 2016). Local conditions may thus strongly modify CH$_4$ emissions in lakes and ponds dominated by free-floating plants. In turn, emergent macrophytes can play an important role in CH$_4$ emissions and are superior with respect to submerged and floating-leaved macrophytes in promoting CH$_4$ efflux. Due to their system of interconnected internal gas lacunas, emergent plants act as chimneys transporting methane from the sediments to the atmosphere (Laanbroek, 2009). Littoral areas of shallow lakes could also emit nitrous oxide (N$_2$O) if they receive excessive levels of reactive nitrogen. Submerged macrophytes seem to contribute more to the total N$_2$O emissions than other macrophyte types (Zhu et al., 2015). In contrast, shallow lakes dominated by abundant submerged plants can release less CO$_2$ (Jeppesen et al., 2016) and CH$_4$ (Colina et al., 2021) than similar clear water lakes with scarce plants, such as during initial phases of a restoration process. The efflux of CO$_2$ is expectedly lower, or even often negative, in lakes dominated by phytoplankton (Jeppesen et al., 2016).
The empirical evidence strongly supports the idea that, more than the species identity and effects related to plant physiology and metabolism (such as the production of allelochemicals), it is the structural complexity given by the different macrophyte life-forms that affects lake functioning the most.

**Current threats to shallow lakes and ponds: changes in habitat complexity and its impacts on ecosystem services**

Freshwater ecosystems are hotspots of biodiversity (Dudgeon, 2019) as they harbour about 6% of global biodiversity and even up to 35% of total vertebrate diversity, sustaining high numbers of endemic species (Rinke et al., 2019). Freshwater ecosystems are amongst the most impacted ecosystems in the world (Dudgeon et al., 2006; Carpenter et al., 2011; Rinke et al., 2019). Besides supporting a disproportionate share of biodiversity, shallow lakes and ponds provide a wide range of critical benefits for humanity (regulating, provisioning, supporting, or cultural services), such as flood control, food and water provision, water filtration, and carbon sequestration. The provision of these different ecosystem services depends on lake integrity, which in turn is determined by the combination of species inhabiting a lake and the dominant regime (Janssen et al., 2021).

A shift from submerged macrophyte to phytoplankton dominance, regimes that support the highest and lowest biodiversity, respectively, affects the quantity and type of ecosystem services provided. A lake with high habitat complexity, i.e. dominated by submerged macrophytes, supply ca. 86% of regulating and 63% of cultural potential services, while a low habitat complexity lake, i.e., dominated by phytoplankton, deliver fewer services, mostly restricted to provisioning ones (42%) (Janssen et al., 2021).

Habitat destruction or degradation is one of the main causes of the loss of biodiversity in freshwater ecosystems (Millennium Ecosystem Assessment, 2005; Collen et al., 2014; Dudgeon, 2019; IPBES, 2019). Several global threats but also local activities at the catchment or lake level can strongly affect habitat complexity and, consequently, ecosystem functioning (Table 1). The primary direct causes of habitat complexity degradation include land conversion,
eutrophication and pollution, infrastructure development, water withdrawal, introduction of invasive exotic species, and uses such as aquaculture, energy production, and reception of sewage. Below, some of the current threats to shallow lakes and ponds are summarised, in particular focusing on their direct and indirect impacts on habitat complexity and the associated changes on the provision of ecosystem services.

| Activities | Effects on shallow lakes and ponds |
|------------|-----------------------------------|
| Deforestation of catchments due to changes in land use | Increased erosion with consequent deterioration of light regime. Increased nutrient and dissolved organic carbon (DOC) loading to lakes. Loss of sources of large woody debris that represent habitat structure in littoral and benthic habitats. |
| Wetland drainage to gain land for agriculture, rangelands, or urbanisation | Potential changes in shoreline development, slope and depth of ponds and lakes. Loss of buffer zone between terrestrial and aquatic systems (higher nutrient and DOC loading). Decreased complexity of littoral structure and loss of nursery/refuge/feeding areas for invertebrates, fishes, amphibians, mammals, and waterfowl. |
| Removal of large woody debris and rocks or stones from lakeshores for urbanisation or other uses | Decreased complexity of littoral habitat. Loss of foraging and nesting habitat, predation refuges, etc. |
| Macrophyte removal to facilitate navigation, enhance aesthetics, etc | Depending on initial cover and degree of biomass removal: Decreased complexity of littoral habitat. Loss of foraging habitat, predation refuges for zooplankton and small fishes, etc. Decreased resilience of shallow clear water lakes against other external perturbations. |
| Non sustainable agriculture | Diffuse nutrient (eutrophication) and agrochemical contamination. Loss of riparian buffer zones and simplification of lake littoral areas. Increased phytoplankton biomass and light attenuation, limiting benthic algae and submerged aquatic plants with consequent reduction in littoral and benthic habitat complexity. Promotion of turbidity-tolerant aquatic plants leading to habitat homogenisation. Consequent changes in productivity in each lake habitat. Habitat simplification and overall loss of biodiversity. Expectedly higher net GHG emissions. |
| Exotic species introduction | Effects vary depending on species and density: Some species may increase benthic or littoral habitat complexity and productivity (of a particular habitat or the whole lake), while others may lead to habitat homogenisation and decreased overall complexity. |
| Water level management for irrigation, human consumption, or after construction of reservoirs | Lowered water level fluctuations may reduce seasonal flooding that is important to nutrient regeneration and riparian/littoral vegetation. Changes in water level may either facilitate or prevent the establishment and development of submerged or free-floating aquatic plants, thereby changing habitat complexity. Lower system resilience against other pressures such as eutrophication. |

Based on Schindler & Scheuerell (2002). See the text for further description of the effects of some of these activities and the mechanisms involved.
Eutrophication and other agriculture-driven impacts

The Millennium Ecosystem Assessment (2005) emphasized that regulating services are likely the most valuable ones. The buffering and control effect of lake margin wetlands is an important regulating service (self-purification), boosted by littoral macrophytes, periphyton, and riparian vegetation (Bayley et al., 2013; Walton et al., 2020). Overgrazing by livestock, drainage of wetlands and aquatic ecosystems to gain land for crop fields and rangelands (Moomaw et al., 2018; Hoffmann et al., 2020), and intensive land use cause physical habitat destruction or simplification of the lakeshore and the riparian and floodplain vegetation (Bayley et al., 2013; Jabłońska et al. 2020; Hughes & Vadas, 2021). Riparian and wetland vegetation are lost or have strongly diminished in many locations, with a concomitant decrease and impoverishment of habitat complexity at the landscape and ecosystem levels (Bayley et al., 2013; Hughes & Vadas, 2021).

Together with habitat fragmentation, eutrophication is the most widely spread impact on shallow lakes and ponds and is largely associated to productive uses in the catchments. Not least due to the loss of wetlands and riparian areas, agriculture has strongly modified lake surroundings and changed the flow of organic matter and nutrients to water bodies. Eutrophication may occur as a gradual process. In the early phases, eutrophication usually promotes an increase in density, diversity, and size of structural elements (such as emergent, submerged, or free-floating macrophytes), which may increase complexity with positive effects on the richness and abundance of many biological communities. Due to a sustained external input of nutrients, many lakes and ponds have generated widespread and productive stands of emergent macrophytes along the margins and submerged as well as floating-leaved plants within the lake. At advanced phases of the eutrophication process, habitat complexity likely decreases or disappears with the collapse of submerged plants in the most eutrophic and hypertrophic shallow lakes due to out shading by phytoplankton and/or epiphytes which are no longer controlled by their respective grazers (Phillips et al., 1978, 2016; Jones & Sayer, 2003). The system is then characterised by a high phytoplankton biomass resulting in highly turbid waters and often blooms of potentially toxic cyanobacteria, and lower biodiversity (Moss et al., 1990). Overgrowth by reeds has also become a serious problem in many large temperate eutrophic lakes since the late 1960s (Andersson, 2001). In warm regions, large free-floating plants can also respond with a dramatic increase in biomass and rapid reproduction, potentially covering large areas and promoting the collapse of submerged plants due to out shading (de Tezanos Pinto & O’Farrell, 2014).

Thus, eutrophication produces a simplification of habitat complexity and consequently, diversity loss, homogenisation towards nutrient-tolerant species and reduction of refuge, nursing, and feeding areas. As pointed out in Kovalenko et al. (2012), the initially positive effect of increased complexity is likely to level off when eutrophication increases the density of more uniform structures even further (Tokeshi & Arakaki, 2012). For example, once established in meso-eutrophic lakes, non-native shade-tolerant *Elodea* species can quickly replace native species and form a dense and closed canopy (Zehnsdorf et al., 2015). The uniformity of small structures thus increases, but the lake become “homogenously diverse” (sensu Hutchinson, 1961). In this sense, the analysis of macrophyte fossil and contemporary data from connected lakes indicates that eutrophication has reduced macrophyte and invertebrate diversity over space and time, promoting homogenisation of the assemblages (Salgado et al., 2018).

Some ecosystem processes can also be affected by the eutrophication-driven decrease in habitat complexity (Table 1). Shallow eutrophic-hypereutrophic (i.e., phytoplankton-dominated) lakes can often behave as sinks of CO₂, especially those that are very productive (Pacheco et al., 2014; Jeppesen et al., 2016; Morales-Williams et al., 2020; Zagarese et al., 2021) and have low watershed-to-lake area and lack watershed wetland cover (Morales-Williams et al., 2020; Zagarese et al., 2021) and have low watershed-to-lake area and lack watershed wetland cover (Morales-Williams et al., 2021). Instead, efflux of CO₂ can prevail in eutrophic lakes with a high watershed-to-lake area and high nitrogen loading (Morales-Williams et al., 2021). Eutrophication is, however, an important driver of CH₄ and N₂O emissions (Davidson et al., 2015, 2018; Zhu et al., 2015; Beaulieu et al., 2019; Sun et al., 2021). Eutrophication can often promote carbon sequestration in open areas of shallow lakes, but overall, most frequently contributes to net emission of GHG. Other agriculture-related effects may also include the
removal of riparian vegetation and water consumption or drainage. As the bulk of sequestered carbon by wetlands is in the soils rather than in the plant biomass, wetland and lake drainage allows the oxidation of soil organic matter boosting the release of CO₂ into the atmosphere (Moomaw et al., 2018). Thus, draining shallow lakes, ponds, and lake margin wetlands cause the loss of several ecosystem services, especially the crucial ones related to food and water provision, and self-purification and carbon sequestration (regulating services), and contribute to net emissions of GHG.

Urbanisation

Urbanisation competes with agriculture for land, exerting extra pressures on transitional natural ecosystems such as floodplains and wetlands. Chemical pollution, habitat destruction through landfiling, drainage and water regulation, and sealing of soils with consequent changes in hydrological regimes are immediate environmental consequences of urbanisation on aquatic ecosystems. As lakes shorelines are urbanised, the land–water interface degrades (Kaufmann et al., 2014). Even under conditions of relatively modest disturbance, the effects of residential development are strongly localised near to shores, leading to large changes in habitat complexity and associated biota (Hampton et al., 2011). At the local scale, property owners often reduce tree, shrubs, and reed densities along shorelines and remove natural structures from the littoral zone of lakes, leading to a dramatic reduction of fish richness and fisheries (provisioning service) (Sass et al., 2006). Extensive and intensive shoreline human activities simplify habitat structure and increase the richness and abundance of tolerant fish and bird species, reducing the richness of sensitive taxa and of native taxa in general (Kaufmann et al., 2014).

Urban lakes are typically shallow, highly artificial, and often hypertrophic, and yet receive more attention by the public than most rural, natural lakes and ponds (Birch & McCaskie, 1999), due to their important aesthetic, recreational, and cultural value. In extreme cases, urban water bodies are polluted by industrial waste, domestic sewage and drainage systems. Such ecosystems are also extremely simplified in both their structural and biological complexities with a consequent loss of recreational and conservation value (Scasso et al., 2001). Large oscillations between enormous fish biomass and massive fish kills are often common due to anoxia under warm weather conditions (Iglesias et al., 2011). Strong interventions are normally needed to recover ecosystem functions and cultural services, and the reconstruction of habitat complexity is among the most recommended measures (Moss et al., 1996; Birch & McCaskie, 1999; Scasso et al., 2001; Oertli & Parris, 2019).

Invasive species

Many exotic species exert a large variety of impacts on native communities, some of which occur through direct changes in habitat complexity, such as complexity increase, decrease, or transformation, or through direct or indirect biological interactions such as predation, herbivory, competition, hybridisation, and the transmission of pathogens to native biota (Carpenter et al., 2011). Despite their generally positive effect on biodiversity and ecosystem function, many macrophyte species of different life forms have become invasive and are considered weeds across the world. Submerged plants such as *Egeria densa* Planch., *Elodea canadensis* Michx., *Hydrilla verticillata* (L.f.) Royle and, *Myriophyllum aquaticum* (Vell.) Verdc. have become a serious nuisance in many lakes and ponds, and so have large free-floating plants such as *Salvinia molesta* D.S. Mitch., *P. stratiotes* and *P. crassipes*, to mention just a few (Bolpagni, 2021).

Environmental heterogeneity is typically associated with high diversity of native macrophytes. As with the early phases of eutrophication, initial arrival of an exotic species may increase habitat complexity by adding density and diversity of structural elements, whereas the establishment phase of such exotic species may end up in habitat homogenisation with the development of extensive monocultures (Zehnsdorf et al., 2015). Changes in native macrophyte composition, increased architectural similarity in the plant mats, and a general decline in biodiversity at local and regional levels, are often recorded after the expansion of an exotic plant (e.g., Michelan et al., 2010). Thus, the systems may shift from a status of high habitat complexity (with environmental and space-size heterogeneity) at early phases of colonisation to one of low habitat complexity due a decrease of species richness and the dominance of similar spacesizes (i.e., filling spaces) at the establishment phase.
when the system ends up homogenised (Salgado et al., 2018). Several anthropogenic changes (e.g., eutrophication, channelisation) can favour exotic macrophytes that reduce local-scale diversity via competitive exclusion (Muthukrishnan et al., 2018; Salgado et al., 2019). On the contrary, connectivity at the watershed level and dense native plant cover may prevent biotic homogeneisation (Salgado et al., 2021). Particularly, connected lakes act as sources of macrophyte species providing resistance to the invasion and counteracting the homogenisation produced by the exotic plants (Salgado et al., 2021). For example, in a survey of 1,102 Minnesota (USA) shallow lakes, the presence of invasive macrophytes did not impact species richness, however, it was associated with greater similarity in the plant community composition (i.e., biotic homogenisation), eroding spatial and temporal ecological distinctiveness across the landscape (Muthukrishnan & Larkin, 2020); thus reducing the overall complexity level of lakes. Regarding biotic interactions, Grutters et al. (2015) found that the replacement of native plants by structurally similar non-native vegetation was unlikely to affect predator–prey interactions in an important way. These authors proposed that changes in predator–prey interactions via aquatic plant invasions may only occur when the invading plants are very different in density, growth form and rigidity compared to the native plants. Invasions by macrophytes such as P. crassipes, for instance, may strongly modify underwater structural heterogeneity.

Originally from the Caspian and Black seas, the zebra mussel (Dreissena polymorpha (Pallas, 1771)) can reproduce and grow extremely fast, potentially covering the lake bottom or any other hard surfaces in relatively short times. Zebra mussel increases structural complexity in the sediments, thereby facilitating other benthic macroinvertebrates by offering substrate and refuge from predation at initial phases of colonisation (Stewart et al., 1998). It can also lead to the collapse of native mussels due to competition for space and resources. Zebra mussels can filter huge volumes of water (sometimes the whole lake volume several times a day), increasing water transparency and thus opening a window of opportunity for submerged plants to grow (reviewed in Jeppesen et al., 2012). The effects of the invasion by this mussel are therefore contradictory; while it promotes the loss of native fauna also an overall increase in habitat complexity can be expected due to the physical changes that occur after invasion. In contrast, other invasive species such as the red swamp crayfish (Procambarus clarkii Girard 1852) can promote a shift from a clear water state to a turbid water, low biodiversity state due to the consumption and mechanical destruction of aquatic plants (Gherardi & Acquistapace, 2007) and the consequent changes in sediment characteristics and loss of feeding grounds and habitat for other species.

Many species of fish are also invasive and may cause serious problems to the colonised environment, by, again, a variety of physical and biological effects that affect habitat complexity, such as the disturbance of sediments and uprooting of plants by benthivorous species and the consumption of plants by herbivorous fishes. Rather than altering habitat complexity, the modulating effects provided by macrophytes on trophic dynamics (see above) may be lost when invasive predators are involved. As found for the piscivore peacock bass (Cichla kelberi) in tropical regions, aquatic plants may provide very limited protection to native prey, probably due to the highly aggressive nature of this fish, and therefore vegetated habitats are unlikely to buffer the decline in biodiversity caused by this species (Kovalenko et al., 2010).

Invasive species could affect multiple ecosystem functions and significantly impact or change the properties of invaded (or newly created) communities, thus opening new trophic paths (Bolpagni, 2021; and references therein). As a result, invaders could either increase or decrease ecosystem services depending on how these species affect different attributes of habitat heterogeneity and trophic interactions.

Climate change

Expectedly, climate change can affect habitat complexity through a series of direct and indirect processes. This topic is subject of intensive research, and we are only starting to identify the pieces of the puzzle (e.g., Netten et al., 2010; Kosten et al., 2011; Moss et al., 2011; Meerhoff et al., 2012; Short et al., 2016). Climate change, through warming and higher frequency of droughts/floods and storms or cyclones, may affect water level and nutrient loading and concentrations through increasing (precipitations, storms) or decreasing (dry periods) runoff from the basins. The chances for shallow lakes and ponds to
recover from stochastic disturbances (e.g., storms, hurricanes) is related to antecedent lake conditions (e.g., turbidity, trophic state, macrophyte cover) which shape lake resistance and resilience (Havens et al., 2016; Thayne et al., 2021).

Given their contrasting effects on habitat complexity, biodiversity, and ecosystem processes, it is key to understand the responses of the main aquatic primary producers (e.g., phytoplankton, benthic algae, submerged and floating plants) to changes in the climate regime and climate variability. The interaction of the factors affected by climate change can directly and indirectly control plant growth, and can have overall opposing effects (Havens et al., 2016; Ersoy et al., 2020). Climate change can affect the competition between phytoplankton and aquatic plants and lead to dramatic changes in habitat complexity. Phytoplankton and particularly cyanobacteria seem to be favoured by climate warming (e.g., Paerl & Huisman, 2008; Paerl & Paul, 2012; Kosten et al., 2012; Davidson et al., 2015). In addition, heatwaves, hurricanes, and low water levels due to increased temperature/dry periods, often lead to the collapse of aquatic plants and to high phytoplankton and cyanobacteria productivity in systems with high nutrient loading (Rigosi et al., 2014; Havens et al., 2016; Ersoy et al., 2020), maintaining the lake in a poor complexity, low biodiversity, and turbid water regime.

Under eutrophic conditions, warming may favour not only phytoplankton but also free-floating macrophytes (Netten et al., 2010). Because of increasing winter minimum air temperatures, tropical and subtropical free-floating plants will probably expand their biogeographic distribution polewards (Bolpagni, 2021). This would imply dramatic changes in habitat complexity and negative impacts on lake and pond trophic dynamics (e.g., Meerhoff et al., 2007a, b; de Tezanos Pinto & O’Farrell, 2014), besides the already described negative effects on general biodiversity and water quality (Fig. 3). In contrast, the density of submerged macrophytes may increase under low nutrient loads, moderate water levels, and rising temperatures as predicted by models and mesocosm experiments (Davidson et al., 2015; Coopers et al., 2020; Ersoy et al., 2020). According to field studies in north temperate lakes, earlier start of growing seasons due to climate warming would result in greater biomass and distribution of submerged macrophytes (Rooney & Kalff, 2000). A potential enhancement of submerged plants would increase the amount and likely the diversity of structural elements within a lake ecosystem. Emergent macrophytes, in contrast, seem more affected by hydrological alterations (Short et al., 2016).

Climate change promotes a range of potentially interacting processes (i.e., nutrient loads, water level, temperature, light climate) that will favour the dominance of a particular primary producer, with direct consequences on habitat structure and complexity. Climate warming, in particular, can also interact with the expansion of exotic species (Rahel & Olden, 2008). Identification of climate impacts on habitat heterogeneity and the formulation of a generalized and global pattern is thus complicated, not least because climate change affects different regions in different manners and intensities and interacts with other anthropogenic impacts and activities.

**Restoration of degraded lakes via enhancement of habitat complexity**

Artificial manipulation of structural complexity is one of the restoration measures often applied in degraded ecosystems (Cooke et al., 2005). Trees, rocks, and stones have been introduced to increase heterogeneity in streams and rivers, often accompanying re-mean-dering of stream channels (Hoffmann et al., 2020). Although habitat coupling between terrestrial and aquatic ecosystems is critical for maintaining diverse and productive riparian and stream and river ecosystems (Naiman et al., 2000), lake ecologists seldom incorporate riparian habitats into models of ecosystem dynamics and management (Schindler & Scheuerell, 2002). Shoreline habitats degraded by urban development and loss of riparian vegetation are, however, often reconstructed in a variety of ways, including the transplantation of emergent plants and the addition of rock riprap or retaining walls to control erosion and recreate littoral complexity (although such artificial structures can be homogeneously complex). Artificial reefs (made up of wooden branches) have been tested in Amazonian floodplain lakes, finding that although overall diversity was not enhanced, rare species occurred more frequently in the more complex habitats (Yamamoto et al., 2014). Comparative studies in lakes with manmade littoral complexity have shown that fish species richness is positively correlated with...
local habitat complexity (being higher in riprap sites). However, the structure of the fish assemblage, assessed as the proportion of intolerant or tolerant species, responds to cumulative effects of small habitat modifications (Jennings et al., 1999). In urban shallow lakes and ponds, restoration strategies also include promoting larger pond sizes, modifying pond margins with indentation, constructing different-angled slopes and with large drawdown zones, permitting hydroperiods to mimic natural changes, and eliminating non-native or invasive species while promoting the presence of aquatic plants (emergent, submerged, or floating) (Oertli & Parris, 2019).

Submerged macrophytes can return after the implementation of restoration measures that increase water clarity; however, restored shallow lakes typically have a different community composition with fewer species compared with the situation 20–100 years before eutrophication worsened, according to a review by Bakker et al. (2013). Sometimes submerged vegetation may not return naturally even when clear water conditions have been re-established (Marklund et al., 2002; Lauridsen et al., 2003). Since the early 1990’s, the reintroduction of aquatic plants is thus one of the recommended measures to speed up the recovery of eutrophic lakes once nutrient loading has been reduced (Moss, 1990; Moss et al., 1996; Jeppesen et al., 2012). For this purpose, plants are often transplanted or spread as seeds and propagules (Moss et al., 1996). Studies in temperate European shallow lakes (e.g., Lauridsen et al., 2003; Hilt et al., 2006; Chaichana et al., 2011) have shown higher survival and number of plants and longer total shoot length when they are introduced in enclosures that prevent waterfowl access. Most of the experiences of aquatic plant introduction so far are from temperate lakes, but examples from subtropical and tropical areas are increasing. For instance, in subtropical China, several studies suggest that transplantation of submerged plants, even exotic ones, as a restoration tool might be successful, as long as plants are protected against fish herbivory (Chen et al., 2009; Ye et al., 2011; Zhang et al., 2016; Bai et al., 2020; Gao et al., 2020). In other cases, macrophyte transplantation is combined with fish removal and/or introduction of mussels (Yu et al., 2016; Gao et al., 2017; Zeng et al., 2017). The establishment and protection of plants as a lake restoration method, alone and in combination with other approaches, will remain an important measure in the future, although many unsolved issues remain, such as how to assure long-term effects (Jeppesen et al., 2012). For example, the continuous control of omnivorous and herbivorous fish is recommended in warm lakes to protect submerged macrophytes (Yu et al., 2016). These or other measures are likely not useful for all lakes since there might be conflicts between biodiversity conservation and other uses (such as irrigation, navigation, aquaculture, etc.).

Sometimes, artificial macrophytes have been used when natural plants do not respond as fast as required. Although direct chemical effects (e.g., uptake of nutrients and release of allelopathic substances that potentially control phytoplankton) will not occur, the generation of physical complexity can lead to strong changes in the lake function by affecting trophic interactions, and the stability of the water column and decrease of incoming light. Artificial plants may initially help to create and stabilise a clear water state by serving as a daytime refuge for zooplankton against predation by fish, as well as substrate for plant-associated macroinvertebrates (Skov & Berg, 1999; Boll et al., 2012). A cover by artificial plants of just 3–5% of the lake area can double zooplankton densities, as found in a shallow temperate lake in Denmark (Schou et al., 2009). Artificial recreation of habitat structural complexity seems, however, not sufficient to mimic the whole array of effects associated with natural habitat complexity. Interestingly, in streams where restoration efforts have been more widely applied than in lentic systems, restoring habitat heterogeneity has seldom promoted an increase in macroinvertebrate diversity (as shown in a meta-analysis by Palmer et al., 2010), indicating that the ultimate processes behind the effects of habitat complexity on biodiversity and fauna abundance have not been completely elucidated (Kovalenko et al., 2012). The advantage of using artificial structures is that they can be introduced all year round and are much less sensitive to environmental conditions and grazing by herbivorous fishes and waterfowl, although unfortunate cases of waterfowl consuming plastic structures, likely trying to catch the associated macroinvertebrates, have occurred (M. Meerhoff pers. obs.). The potential release of chemical substances and micro and nanoplastics from the artificial plants should also be thoroughly analysed and weighted against the potential benefits.
The examination of the effectiveness of several active restoration measures has resulted in different outcomes: ecosystem and submerged macrophyte recovery, no improvement, or initial improvement and then a return to eutrophic conditions (McCrackin et al., 2017). On top of that, restored lakes and ponds in warm regions recover more slowly than those in cold areas (Jeppesen et al., 2007, 2012). Thus, under any restoration scenario, it is still key to decrease the nutrient load to aquatic ecosystems (Moss et al., 2011; McCrackin et al., 2017; Hoffmann et al., 2020).

**Future directions**

In this section, we review a series of topics that, in our view, deserve deeper studies due to their potential impact on our understanding on shallow lakes and pond functioning, and on conservation or restoration strategies, ordered by increasing spatial scale.

1. Space-size heterogeneity and food web stability. Heterogeneity in space-filling offers a variation of refuge sizes that might decouple trophic interactions and promote the compartmentalization of food webs; as pointed out by Kovalenko et al. (2012). This is still a line of research not yet sufficiently explored.

2. Relevance of different attributes of habitat complexity for sustaining biodiversity. The exact mechanism by which habitat complexity impacts taxon richness or density, and with those, impact ecosystem processes, is still not fully elucidated despite that several experimental studies have addressed the topic. For instance, space-size heterogeneity (i.e., variation in space sizes) has been highlighted as more important for macroinvertebrate taxonomic richness than overall complexity, and than other complexity attributes, plant biomass, and density of stems (St. Pierre & Kovalenko, 2014).

3. Interacting effects of habitat complexity and food web structure. Interestingly, habitat complexity interacts with lake characteristics such as water transparency (Snickars et al., 2004; Pekcan-Hekim et al., 2010) and trophic web characteristics. Rennie & Jackson (2005) demonstrated that small-scale variation in littoral microhabitat complexity shapes patterns of macroinvertebrate distribution but also that such effects were systematically different in the presence or absence of fish (i.e., greater complexity promoted higher density of invertebrates only in the presence of fish), suggesting that habitat complexity effects are at least partly mediated through top-down mechanisms. Climate-related differences in trophic web structure should also be considered here.

4. Habitat complexity and fluxes of greenhouse gases (GHG). In this growing field of investigation, studies have yielded contradictory results about the role of different lake zones with contrasting habitat complexity on GHG fluxes (e.g., Zhu et al., 2015; Kosten et al., 2016; Janssen et al., 2021). Habitat complexity may interact with nutrient loads and with trophic structure of lakes and ponds, among other factors, thus influencing net GHG influx or efflux (Zhu et al., 2015; Morales-Williams et al., 2021). Thus, it is necessary to understand the mechanisms that may transform different lake zones (littoral, benthic, or pelagic) or whole ecosystems (with contrasting habitat complexity) on “hotspots” of GHG emissions and its connection to whole lake budgets.

5. Connection between habitat complexity and spatial complexity at the landscape level. Despite historically being treated as relatively discrete microcosms (Forbes, 1887), shallow lakes and ponds are open ecosystems that are inseparable from their catchments (Moss, 1998). The importance of spatial complexity at the catchment and landscape level for regional but also for local richness has been recently highlighted (Fahrig, 2013), not least through interactive effects with in-lake habitat complexity. In ponds, individual pond size and isolation (habitat patchiness), together with the presence of emergent vegetation (within-lake complexity), can, for instance, significantly influence waterfowl diversity, as found in a series of Mediterranean ponds (Paracuellos & Tellería, 2004). Connectedness in heterogeneous landscapes may lead to high local biodiversity and resilience via a spatial insurance effect (Loreau et al., 2003). However, higher richness at the regional level may be expected when the lakes and ponds in a waterscape show different degrees of connectivity, due to stochastic events,
ecological interactions, and different in-lake complexity (Scheffer et al., 2006).

Conclusions

Organizational elements that promote habitat complexity differ across spatial scales from the landscape to within-lake microhabitats; nevertheless, all organizational elements and certain characteristics (e.g., lake connectivity, size and shape, shoreline development, within-lake complexity, etc.) contribute to determining ecosystem processes, functions, and services. Despite the importance of the effects produced by the physical structure of aquatic plants, there are no standardised methods to measure plant complexity, limiting comparisons among different plant species and among ecosystems (reviewed in Kovalenko et al., 2012). Besides, determining the effects strictly associated with habitat complexity can be difficult as different potentially explanatory variables are often highly associated, as is the case of plant cover and lake trophic state (Declerck et al., 2005).

Several anthropogenic threats to lake and pond complexity often operate simultaneously at different spatial scales, promoting habitat destruction or alteration and/or decoupling between lakes and their riparian areas or with other aquatic systems. Some of such threats against habitat integrity occur at the landscape level (e.g., disruption of natural hydrological cycles through channelisation and dam construction, changing or preventing connectivity among lake and pond systems), while others affect the lake and within-lake microhabitat levels. In addition, lake and within-lake microhabitats are severely affected by the destruction of riparian vegetation and lake/pond shore margins, point or diffuse nutrient pollution, drainage or water overexploitation, introduction of exotic species and/or fluctuations in water levels induced by climate change. Eutrophication, largely due to nutrient inputs from agricultural areas, and despite not being a linear process, most often ends up with a major loss in complexity with negative implications for biodiversity, nutrient cycles, and emissions of greenhouse gases. Climate change impacts on habitat complexity largely depends on antecedent lake conditions which, on the other hand, may contribute to lake resilience and resistance to climatic disturbances such as storms, hurricanes, drought and flood periods. The loss or degradation of riparian and littoral vegetation of shallow lakes and ponds translates into an alteration of ecosystem functions, such as heavily reduced capacity to provide food, refuge and nursing areas for aquatic and amphibious species, recycle nutrients and purify water, sequester carbon, flood and hazard mitigation, and soil formation.

The recognition of these impacts has promoted the implementation of mitigation measures to improve habitat quality, targeting at different components and spatial scales (e.g., nutrient transport and drainage control, re-establishment of riparian and buffer zones, restoration of shallow lakes, reconstruction of ghost ponds). Particularly, large re-establishment of wetland buffer zones is an effective action to reduce N and P pollution in agricultural catchments. Its implementation seems mostly related to policy priorities rather than to financial impossibilities (Jabłońska et al., 2020) and it is an action currently applied in different parts of the world (e.g., Hoffmann et al., 2020; Walton et al., 2020). At the lake scale, the current evidence highlights that different active measures applied, such as macrophyte transplantation, fish removal, and exotic mussel/macrophyte introductions have different outcomes.

Reviews considering lake recovery from eutrophication, particularly those evaluating the re-establishment of submerged macrophytes, have mostly focused on temperate systems (e.g., Søndergaard et al., 2005; McCrackin et al., 2017; although see Jeppesen et al., 2012 for other examples). So far, it seems that in subtropical lakes greater efforts are necessary to maintain or speed up the recovery of littoral habitats, by performing continuous fish removal and combining this with major nutrient reductions (Yu et al., 2016). More examples from Mediterranean, tropical, and subtropical areas are needed to understand the effectiveness of different restoration measures across a broad range of climates and conditions. Until more information is synthesised, reduction of nutrient loading and preservation of the existing natural habitat complexity at different spatial scales seems to be one of the key measures to maintain the resilience of lake and pond ecosystems against global and local anthropogenic impacts. Habitat complexity, from the landscape (i.e., occurrence of water bodies with different habitat complexities) to the within-system levels, needs to be prioritised by environmental managers.
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