

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

2 Mariana Meerhoff^{1,2}, María de los Ángeles González-Sagrario³

3 1 Departamento de Ecología y Gestión Ambiental, Centro Universitario de Regional del Este- Universidad de la
4 República, Maldonado, Uruguay. <https://orcid.org/0000-0001-6482-1332>

5 2 Department of Bioscience, Aarhus University, Silkeborg, Denmark.

6 3 Instituto de Investigaciones Marinas y Costeras (IIMYC), Facultad de Ciencias Exactas y Naturales, Universidad
7 Nacional de Mar del Plata, CONICET, Mar del Plata, Argentina. <https://orcid.org/0000-0002-6882-8547>

8 E-mail: mm@bios.au.dk

9 **Abstract**

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

23 **Keywords:**

24 aquatic biodiversity, alternative states, habitat degradation, eutrophication, climate change.

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62 Introduction

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

75 Traditionally, limnological research focused on the biological communities and ecological processes
76 happening in the spatially homogeneous water column of large, deep, nutrient poor lakes (Wetzel, 2001). However,
77 most lakes in the world are small and shallow (Wetzel, 1990; Downing et al., 2006). Millions of water bodies smaller
78 than 1 km² occur on the planet, and small lakes and ponds (between 0.001 and 0.1 km²) represent most of the world's
79 lacustrine area (Downing et al., 2006). A shift of focus from the pelagic to incorporate other habitats such as the littoral
80 and benthic zones has given empirical support to several ecological theories (e.g., Scheffer et al., 1993) and has
81 highlighted the importance of habitat complexity for the overall functioning of these ecosystems (e.g., Vadeboncoeur et
82 al., 2001; Vander Zanden & Vadeboncoeur, 2020). Several aspects connected to complexity are clearly identifiable in
83 aquatic ecosystems (Tokeshi & Arakaki, 2012). This explains that intensive research in the last 30 years has contributed
84 to understanding the connection between habitat complexity and the structure and functioning of shallow lake and pond
85 communities.

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

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

99 **Shallow lake habitats and habitat complexity**

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

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

116 The benthos or lake bottom can vary quite largely in its degree of complexity. Lake depth, water colour, and
117 the amount of suspended matter determine whether light reaching the bottom is enough to allow photosynthesis by
118 benthic vegetation and, with them, an increase in physical complexity generated by these biological elements. Thus,
119 turbid lakes and ponds often lack primary production of importance in the benthic zone, and most of its complexity is a

120 result of the variability in sediment particle sizes and accumulated debris from other lake habitats or from the
121 surrounding terrestrial environment. Sediment physical characteristics, besides lake trophic state and the outcome of
122 biotic interactions, largely determine the densities and taxonomic richness of macroinvertebrates to a large extent (Free
123 et al., 2009). Benthic complexity, given by sediment structure, the development of periphyton and submerged plants, or
124 by structure-generating animals such as sessile mussels, can either facilitate or hinder sediment resuspension by wind or
125 by benthic-dwelling organisms and fish. Even sandy sediments are only intermittently disturbed by water movements if
126 they are covered by large abundances of microalgae (such as diatoms) (Moss, 1998).

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

148 Along natural lake shorelines, emergent aquatic plants are the most common life-form, often constituting the
149 wetlands associated with shallow lakes and ponds. In highly turbid lakes, or very large lakes, emergent plants may drive

150 key lake processes such as the redistribution of sediment particles, thus affecting water clarity, sedimentation, and
151 resuspension rates with associated effects on the release of the internal phosphorus loading (Horppila & Nurminen,
152 2002; 2005). Structural complexity can explain more of the spatial distribution of juvenile fishes in the littoral area of
153 temperate lakes (e.g., roach, *Rutilus rutilus* (Linnaeus, 1758), and perch, *Perca fluviatilis* (Linnaeus, 1758)) than several
154 other factors, including the biomass of potential food items (Lewin et al., 2004). A comparison of the use of different
155 habitat complexities in the littoral zone (i.e., woody debris, reeds, and areas of different substratum size) by fish in a
156 shallow temperate lake suggested a strong diel component, with a predominant occurrence of fish in complex habitats
157 during the day and a partial migration of zooplanktivorous fish towards the less complex open habitats at night (Lewin
158 et al., 2004). In ponds and in shallow lakes with gentle slopes and with sufficient light reaching the bottom, the littoral
159 zone can extend further out from the shore into the lake with development of higher aquatic plants over large sections or
160 the entire basin.

161

162 **Habitat complexity in the alternative equilibria hypothesis and other ecological theories**

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

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

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

186 In temperate shallow lakes, submerged plants thus often facilitate the survival of large-bodied cladoceran
187 zooplankton that can graze on phytoplankton (Timms & Moss, 1984) by offering a daytime refuge against visual
188 predatory fish (Lauridsen & Lodge, 1996; Lauridsen & Buenk, 1996). The refuge effect for zooplankton often depends
189 on complexity attributes, such as the plant architecture (e.g., Nurminen & Horppila, 2002; Meerhoff et al., 2006,
190 2007a), plant bed size or density (Lauridsen et al., 1996; Burks et al., 2001), and percent of the lake volume inhabited
191 by the submerged plants (Schriver et al., 1995) (reviewed by Burks et al., 2002). Habitat complexity thus decreases the
192 likelihood of over-exploitation of prey (Scheffer & De Boer, 1995), and increases the resilience of littoral communities
193 to fish predation (Kornijów et al., 2016), leading to the overall promotion of biodiversity associated with the clear
194 water, submerged- plant dominated regime in shallow lakes and ponds (Thomaz & Bini, 1998; Agostinho et al., 2003;
195 Declerck et al., 2005; Scheffer et al., 2006; Teixeira-de Mello et al., 2009; Thomaz & Cunha, 2010).

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

206 Under high nutrient concentrations and mild or high temperatures, free-floating plants may also constitute an
207 alternative regime to submerged plants (Scheffer et al., 2003), and also to phytoplankton dominance (Roijackers et al.,
208 2004; de Tezanos Pinto & O'Farrell, 2014). Free-floating plants cover a large range in size, from very small taxa, such
209 as the genera *Azolla* and *Lemnas pp*, medium-sized taxa, such as *Salvinias pp* (water fern), and large-sized taxa, such as

210 *Pistia stratiotes* L. (water lettuce) and *Pontederia crassipes* Mart. (water hyacinth, formerly *Eichhornia crassipes*
211 (Mart.) Solms), the latter two being more common in warm areas (Sculthorpe, 1967). In contrast to submerged plants,
212 that grow inside the water column and are mostly anchored to the sediments, free-floating plants grow on the water
213 surface and are freely moved by currents, waves, and winds. The habitat complexity generated by this kind of plants is
214 indeed lower than that of submerged plants, but depends on the area covered and on the plant size. Large free-floating
215 plants have a dense and potentially long root network, and their shoots and leaves can shade the water column when the
216 area covered is large enough, thus limiting the growth of both submerged plants and phytoplankton (de Tezanos Pinto et
217 al., 2007). Massive covers of free-floating plants thus decrease habitat complexity by reducing the biomass of
218 submerged plants (mostly due to competition for light). Their impacts on aquatic biodiversity are quite contrasting to
219 those of submerged plants, largely due to the often anaerobic or anoxic conditions created under dense mats of free-
220 floating plants. Massive covers of free-floating plants are usually followed by a simplification of food webs (Moi et al.,
221 2021) and a general impoverishment of biodiversity, including fish and macroinvertebrates (Meerhoff et al., 2003),
222 zooplankton (Fontanarrosa et al., 2010), phytoplankton (O'Farrell et al., 2009), submerged plants (Janes et al., 1996),
223 waterfowl, and often fish kills. Besides, the role of large free-floating plants as a potential anti predation refuge for
224 zooplankton seems weaker than that of submerged plants, according to comparative studies (Meerhoff et al., 2003;
225 2006; 2007a, b). The also floating but rooted plant, *P. azurea* Sw. (formerly *Eichhornia azurea* (Kunth)), has, in
226 contrast, been shown in experimental studies to act as refuge for macroinvertebrates against fish predation in tropical
227 areas (Padial et al., 2009).

228 **Relevance of plant architecture for the generation of habitat complexity**

229 As stated above, aquatic plants are the most important generators of habitat complexity in shallow lakes and
230 ponds. Emergent, floating-leaved, submerged, and free-floating plants represent different life strategies and promote
231 different habitat complexities due to variations in plant architecture, typical location within a lake, and their occupation
232 of the water column. The average size and interstitial spaces (filling spaces) along vertical and horizontal axes, i.e., the
233 space-size heterogeneity, is one of the most relevant drivers of taxonomical richness in aquatic environments (St. Pierre
234 & Kovalenko, 2014). Different macrophyte life forms differ in space-size heterogeneity, which can lead to contrasting
235 complexities and explain their different effects on biodiversity and ecosystem processes. Comparative studies on the
236 effects of emergent and floating-leaved plants (Nurminen & Horppila, 2002; Horppila & Nurminen, 2005) and of
237 submerged and free-floating plants (Janes et al., 1996; Meerhoff et al., 2003; 2006; 2007 a, b; Netten et al., 2010) have
238 highlighted the importance of plant architecture for biodiversity and several processes at the community level as was
239 discussed above. Studies that have manipulated habitat complexity by keeping surface area constant have found, for

240 instance, that macroinvertebrates respond to habitat structure independently of surface area (Warfe et al., 2008).
241 Similarly, in a study where artificial macrophytes with three levels of complexity (from low to high) but with constant
242 mass and surface area were introduced in experimental set-ups in a lake, microfaunal (mainly rotifers) abundance and
243 richness were generally greater on the most complex substrata (Lucena-Moya & Duggan, 2011). Different architectures
244 of aquatic plants, leading to different complexities (measured through fractal geometry), significantly affected taxon
245 richness and total densities of tropical invertebrates, although other variables such as plant identity and area were also
246 relevant (Thomaz et al., 2008). Moreover, a field experiment conducted in a series of temperate and subtropical shallow
247 lakes manipulating the spatial arrangement of the same amount and type of plastic structure mimicking aquatic plants of
248 different life forms (i.e., free-floating and submerged) found dramatic differences in the habitat use, richness, biomass
249 and density of most aquatic organisms (Meerhoff et al., 2007 a, b; Teixeira-de Mello et al., 2009; Bruçet et al., 2010;
250 Clemente et al., 2019). Such field experiments also revealed that some of the effects generated by habitat complexity
251 differed in different climates, likely due to climate-related differences in the assemblage of fishes (Meerhoff et al., 2007
252 a; Teixeira-de Mello et al., 2009) (Fig. 2).

253 Taniguchi et al. (2003) suggested that the diversity or heterogeneity of habitable space, more than the quantity
254 of habitable space or food resources created by complexity, was the factor leading to higher taxonomic richness. In a
255 comparative study, these authors found that the abundance of macroinvertebrates on natural plants did not differ
256 between simple and complex forms, whereas on artificial plants more invertebrates occurred on complex than on simple
257 forms (Taniguchi et al., 2003). The heterogeneity or diversity of filling space at different scales promotes species co-
258 existence by dividing the surface area into a large number of structural surfaces and microhabitats (Tokeshi & Arakaki,
259 2012), thus generating different niches for competitor, prey, and predator organisms. Space-size heterogeneity (i.e.,
260 variable size spaces) permits the co-existence of organisms with a wide range of body sizes, potentially increasing the
261 number of pathways for resource utilization and stabilizing interspecific interactions (Kovalenko et al., 2012; Thomaz
262 & Cunha, 2010). The spatial segregation of different cohorts due to habitat complexity reduces the strength of
263 competition and intraguild predation (examples for fish species in Thomaz & Cunha, 2010). Equally important, space-
264 size heterogeneity reduces the encounter rates between prey and predators, thus reducing forage efficiency and
265 stabilizing trophic food webs. The reduction of intra- and interspecific interactions between functional subgroups (e.g.,
266 large versus small omnivores) allows the compartmentalization of community structure, leading to lower connectedness
267 and a stabilization of the food web (Stouffer & Bascompte, 2011; Kovalenko et al., 2012). A mathematical model
268 suggested that predator-prey interactions are unstable at low and high levels of habitat complexity, conditions where
269 populations are prone to extinction or declining (Jana & Bairagi, 2014). Field studies have demonstrated that the

270 increase of biodiversity with increasing space-size heterogeneity is the highest at intermediate complexity levels (St.
271 Pierre & Kovalenko, 2014); for example, highly complex habitats set limitations for fish movement and efficient
272 foraging, thus reducing fish growth (Thomaz & Cunha, 2010 and references therein).

273 **Habitat complexity and ecosystem processes**

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

285 Some greenhouse gases (GHG) can be generated in the sediments under anoxic conditions and be released by
286 diffusion or also by ebullition in the case of methane, or being transformed or released by the activity of benthic fauna
287 (Colina et al., 2021). Thus, the structural complexity of this particular habitat is crucial not only for the benthic biota but
288 also for the cycling of nutrients, GHG fluxes, and the overall linkage with other habitats. Rooted submerged plants may,
289 however, also oxygenate the sediment, decreasing methane (CH₄) production and promoting its consumption, leading to
290 an overall decrease in CH₄ emissions (Davidson et al., 2018; Davidson et al., 2015). Experimental studies have shown
291 that under free-floating plant mats, in contrast, CH₄ production can be boosted by high organic matter production
292 especially under anaerobic conditions; but also, a large amount of the CH₄ produced may become oxidized due to the
293 reduced gas exchange under the dense mats of plants, combined with a high activity of the rhizosphere microbiome
294 (Kosten et al., 2016). Local conditions may thus strongly modify CH₄ emissions in lakes and ponds dominated by free-
295 floating plants. In turn, emergent macrophytes can play an important role in CH₄ emissions and are superior with
296 respect to submerged and floating-leaved macrophytes in promoting CH₄ efflux. Due to their system of interconnected
297 internal gas lacunas, emergent plants act as chimneys transporting methane from the sediments to the atmosphere
298 (Laanbroek, 2010). Littoral areas of shallow lakes could also emit nitrous oxide (N₂O) if they receive excessive levels

299 of reactive nitrogen. Submerged macrophytes seem to contribute more to the total N₂O emissions than other macrophyte
300 types (Zhu et al., 2015). In contrast, shallow lakes dominated by abundant submerged plants can release less CO₂ than
301 similar clear water lakes with scarce plants, such as during initial phases of a restoration process. The efflux of CO₂ is
302 expectedly lower, or even often negative, in lakes dominated by phytoplankton (Jeppesen et al., 2016).

303 The empirical evidence strongly supports the idea that, more than the species identity and effects related to
304 plant physiology and metabolism (such as the production of allelochemicals), it is the structural complexity given by the
305 different macrophyte life- forms that affects lake functioning the most.

306

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

308 Freshwater ecosystems are hotspots of biodiversity (Dudgeon, 2019) as they harbour about 6% of global
309 biodiversity and even up to 35% of total vertebrate diversity, sustaining high numbers of endemic species (Rinke et al.,
310 2019). Freshwater ecosystems are amongst the most impacted ecosystems in the world (Dudgeon et al., 2005; Carpenter
311 et al., 2011; Rinke et al., 2019). Besides supporting a disproportionate share of biodiversity, shallow lakes and ponds
312 provide a wide range of critical benefits for humanity (regulating, provisioning, supporting, or cultural services), such
313 as flood control, food and water provision, water filtration, and carbon sequestration. The provision of these different
314 ecosystem services depends on lake integrity, which in turn is determined by the combination of species inhabiting a
315 lake and the dominant regime (Janssen et al., 2021).

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

321 Habitat destruction or degradation is one of the main causes of the loss of biodiversity in freshwater
322 ecosystems (Collen et al., 2014; Dudgeon, 2019; Millennium Ecosystem Assessment, 2005; IPBES, 2019). Several
323 global threats but also local activities at the catchment or lake level can strongly affect habitat complexity and,
324 consequently, ecosystem functioning (Table 1). The primary direct causes of habitat complexity degradation include
325 land conversion, eutrophication and pollution, infrastructure development, water withdrawal, introduction of invasive
326 exotic species, and uses such as aquaculture, energy production, and reception of sewage. Below, some of the current

327 threats to shallow lakes and ponds are summarised, in particular focusing on their direct and indirect impacts on habitat
328 complexity and the associated changes on the provision of ecosystem services.

329 *Eutrophication and other agriculture-driven impacts*

330 The Millennium Ecosystem Assessment (2005) emphasized that regulating services are likely the most
331 valuable ones. The buffering and control effect of lake margin wetlands is an important regulating service (self-
332 purification), boosted by littoral macrophytes, periphyton, and riparian vegetation (Bayley et al., 2013; Walton et al.,
333 2020). Overgrazing by livestock, drainage of wetlands and aquatic ecosystems to gain land for crop fields and
334 rangelands (Moomaw et al., 2018; Hoffmann et al., 2020), and intensive land use cause physical habitat destruction or
335 simplification of the lakeshore and the riparian and floodplain vegetation (Bayley et al., 2013; Jabłońska et al. 2020;
336 Hughes & Vadas, 2021). Riparian and wetland vegetation are lost or have strongly diminished in many locations, with a
337 concomitant decrease and impoverishment of habitat complexity at the landscape and ecosystem levels (Bayley et al.,
338 2013; Hughes & Vadas, 2021).

339 Together with habitat fragmentation, eutrophication is the most widely spread impact on shallow lakes and
340 ponds and is largely associated to productive uses in the catchments. Not least due to the loss of wetlands and riparian
341 areas, agriculture has strongly modified lake surroundings and changed the flow of organic matter and nutrients to water
342 bodies. Eutrophication may occur as a gradual process. In the early phases, eutrophication usually promotes an increase
343 in density, diversity, and size of structural elements (such as emergent, submerged, or free-floating macrophytes), which
344 may increase complexity with positive effects on the richness and abundance of many biological communities. Due to a
345 sustained external input of nutrients, many lakes and ponds have generated widespread and productive stands of
346 emergent macrophytes along the margins and submerged as well as floating-leaved plants within the lake. At advanced
347 phases of the eutrophication process, habitat complexity likely decreases or disappears with the collapse of submerged
348 plants in the most eutrophic and hypertrophic shallow lakes due to out shading by phytoplankton and/or epiphytes
349 which are no longer controlled by their respective grazers (Phillips et al., 1978; Jones & Sayer, 2003; Phillips et al.,
350 2016). The system is then characterised by a high phytoplankton biomass resulting in highly turbid waters and often
351 blooms of potentially toxic cyanobacteria, and lower biodiversity (Moss et al., 1990). Overgrowth by reeds has become
352 a serious problem in many large temperate eutrophic lakes since the late 1960s (Andersson, 2001). In warm regions,
353 large free-floating plants can also respond with a dramatic increase in biomass and rapid reproduction, potentially
354 covering large areas and promoting the collapse of submerged plants due to out shading (de Tezanos Pinto & O'Farrell,
355 2014).

356 Thus, eutrophication produces a simplification of habitat complexity and consequently, diversity loss,
357 homogenization towards nutrient-tolerant species and reduction of refuge, nursing, and feeding areas. As pointed out in
358 Kovalenko et al. (2012), the initially positive effect of increased complexity is likely to level off when eutrophication
359 increases the density of more uniform structures even further (Tokeshi & Arakaki, 2011). For example, once established
360 in meso-eutrophic lakes, non-native shade-tolerant *Elodea* species can quickly replace native species and form a dense
361 and close canopy (Zehnsdorf et al., 2015). The uniformity of small structures thus increases, but the lake become
362 “homogenously diverse”(sensu Hutchinson, 1961). In this sense, the analysis of macrophyte fossil and contemporary
363 data from connected lakes indicates that eutrophication has reduced macrophyte and invertebrate diversity over space
364 and time, promoting homogenization of the assemblages (Salgado et al., 2018).

365 Some ecosystem processes can also be affected by the eutrophication-driven decrease in habitat complexity
366 (Table 1). Shallow eutrophic-hypereutrophic (i.e., phytoplankton-dominated) lakes can often behave as sinks of CO₂,
367 especially those that are very productive (Pacheco et al., 2014; Jeppesen et al., 2016; Morales-Williams et al., 2020;
368 Zagarese et al., 2021) and have low watershed-to-lake area and lack watershed wetland cover (Morales-Williams et al.,
369 2020). Instead, efflux of CO₂ can prevail in eutrophic lakes with a high watershed-to-lake area and high nitrogen
370 loading (Morales-Williams et al., 2020). Eutrophication is, however, an important driver of CH₄ and N₂O emissions
371 (Zhu et al., 2015; Beaulieu et al., 2021; Sun et al., 2021). Eutrophication can often promote carbon sequestration in
372 open areas of shallow lakes, but overall, most frequently contributes to net emission of GHG. Other agriculture-related
373 effects may also include the removal of riparian vegetation and water consumption or drainage. As the bulk of
374 sequestered carbon by wetlands is in the soils rather than in the plant biomass, wetland and lake drainage allows the
375 oxidation of soil organic matter boosting the release of CO₂ into the atmosphere (Moomaw et al., 2018). Thus, draining
376 shallow lakes, ponds, and lake margin wetlands cause the loss of several ecosystem services, especially the crucial ones
377 related to food and water provision, and self-purification and carbon sequestration (regulating services), and contribute
378 to global emission of GHG.

379 *Urbanisation*

380 Urbanisation competes with agriculture for land, exerting extra pressures on transitional natural ecosystems
381 such as floodplains and wetlands. Chemical pollution, habitat destruction through landfilling, drainage and water
382 regulation, and sealing of soils with consequent changes in hydrological cycles are immediate environmental
383 consequences of urbanisation on aquatic ecosystems. As lakes shorelines are urbanised, the land–water interface
384 degrades (Kaufmann et al., 2014). Even under conditions of relatively modest disturbance, the effects of residential

385 development are strongly localised near to shores, leading to large changes in habitat complexity and associated biota
386 (Hampton et al., 2011). At the local scale, property owners often reduce tree, shrubs, and reed densities along shorelines
387 and remove natural structures from the littoral zone of lakes, leading to a dramatic reduction of fish richness and
388 fisheries (provisioning service) (Sass et al., 2006). Extensive and intensive shoreline human activities simplify habitat
389 structure and increase the richness and abundance of tolerant fish and bird species, reducing the richness of sensitive
390 taxa and of native taxa in general (Kaufmann et al., 2014).

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

400 *Invasive species*

401 Many exotic species exert a large variety of impacts on native communities, some of which occur through
402 direct changes in habitat complexity, such as complexity increase, decrease, or transformation, or through direct or
403 indirect biological interactions such as predation, herbivory, competition, hybridisation, and the transmission of
404 pathogens to native biota (Carpenter et al., 2011). Despite their generally positive effect on biodiversity and ecosystem
405 function, many macrophyte species of different life forms have become invasive and are considered weeds across the
406 world. Submerged plants such as *Egeria densa* Planch., *Elodea canadensis* Michx., *Hydrilla verticillata* (L.f.) Royle and
407 *Myriophyllum aquaticum* (Vell.) Verdc. have become a serious nuisance in many lakes and ponds, and so have large
408 free-floating plants such as *Salvinia molesta* D.S. Mitch., *P. stratiotes* and *P. crassipes*, to mention just a few (Bolpagni,
409 2021).

410 Environmental heterogeneity is typically associated with high diversity of native macrophytes. As with the
411 early phases of eutrophication, initial arrival of an exotic species may increase habitat complexity by adding density and
412 diversity of structural elements, whereas the establishment phase of such exotic species may end up in habitat
413 homogenization with the development of extensive monocultures (Zehnsdorf et al., 2015). Changes in native

414 macrophyte composition, increased architectural similarity in the plant mats, and a general decline in biodiversity at
415 local and regional levels, are often recorded after the expansion of an exotic plant (e.g., Michelan et al., 2010). Thus, the
416 systems may shift from a status of high habitat complexity (with environmental and space-size heterogeneity) at early
417 phases of colonization to one of low habitat complexity due a decrease of species richness and the dominance of
418 similar space-sizes (i.e., filling spaces) at the establishment phase when the system ends up homogenized (Salgado et
419 al., 2018). Several anthropogenic changes (e.g., eutrophication, channelization) can favour exotic macrophytes that
420 reduce local-scale diversity via competitive exclusion (Muthukrishnan et al., 2018; Salgado et al., 2019); on the
421 contrary, connectivity at the watershed level and dense native plant cover may prevent biotic homogenization (Salgado
422 et al., 2021). Particularly, connected lakes act as sources of macrophyte species providing resistance to the invader
423 species and counteracting the homogenization produced by the exotic plants (Salgado et al., 2021). For example, in a
424 survey of 1,102 Minnesota (USA) shallow lakes, the presence of invasive macrophytes did not impact species richness,
425 however, it was associated with greater similarity in the plant community composition (i.e., biotic homogenization),
426 eroding spatial and temporal ecological distinctiveness across the landscape (Muthukrishnan & Larkin, 2020); thus
427 reducing the overall complexity level of lakes. Regarding biotic interactions, Grutters et al. (2015) found that the
428 replacement of native by structurally similar non-native vegetation was unlikely to affect predator-prey interactions in
429 an important way. These authors proposed that changes in predator-prey interactions via aquatic plant invasions may
430 only occur when the invading plants are very different in density, growth form and rigidity compared to native plants.
431 Invasions by macrophytes such as *P. crassipes* may strongly modify underwater structural heterogeneity.

432 Originally from the Caspian and Black seas, the zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) can
433 reproduce and grow extremely fast, potentially covering the lake bottom or any other hard surfaces in relatively short
434 times. Zebra mussel increases structural complexity in the sediments, thereby facilitating other benthic
435 macroinvertebrates by offering substrate and refuge from predation at initial phases of colonisation (Stewart et al.,
436 1998). It can also lead to the collapse of native mussels due to competition for space and resources. Zebra mussels can
437 filter huge volumes of water (sometimes the whole lake volume several times a day), increasing water transparency and
438 thus opening a window of opportunity for submerged plants to grow (reviewed in Jeppesen et al., 2012). The effects of
439 the invasion by this mussel are therefore contradictory; while it promotes the loss of native fauna also an overall
440 increase in habitat complexity can be expected due to the physical changes that occur after invasion. In contrast, other
441 invasive species such as the red swamp crayfish (*Procambarus clarkii* Girard 1852) can promote a shift from a clear
442 water state to a turbid water, low biodiversity state due to the consumption and mechanical destruction of aquatic plants

443 (Gherardi & Acquistapace, 2007) and the consequent changes in sediment characteristics and loss of feeding grounds
444 and habitat for other species.

445 Many species of fish are also invasive and may cause serious problems to the colonised environment, by,
446 again, a variety of physical and biological effects that affect habitat complexity, such as the disturbance of sediments
447 and uprooting of plants by benthivorous species and the consumption of plants by herbivorous fishes. Rather than
448 altering habitat complexity, the modulating effects provided by macrophytes on trophic dynamics (see above)
449 may be lost when invasive predators are involved. As found for the piscivore peacock bass (*Cichla kelberi* Kullander &
450 Ferreira, 2006) in tropical regions, aquatic plants provide very limited protection to native prey probably due to the
451 highly aggressive nature of this fish, and therefore vegetated habitats are unlikely to buffer the decline in biodiversity
452 caused by this species (Kovalenko et al., 2010).

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

457 *Climate change*

458 Expectedly, climate change can affect habitat complexity through a series of direct and indirect processes. This
459 topic is subject of intensive research, and we are only starting to identify the pieces of the puzzle (e.g., Netten et al.,
460 2010; Kosten et al., 2011; Moss et al., 2011; Meerhoff et al., 2012, Short et al., 2016). Climate change, through
461 warming and higher frequency of droughts/floods and storms or cyclones, affects water level and nutrient loading and
462 concentrations through increasing (precipitations, storms) or decreasing (dry periods) runoff from the basins. The
463 chances for shallow lakes and ponds to recover from stochastic disturbances (e.g., storms, hurricanes) is related with
464 antecedent lake conditions (e.g., turbidity, trophic state, macrophyte cover) which shape lake resistance and resilience
465 (Havens et al., 2016; Thayne et al., 2021).

466 Given their contrasting effects on habitat complexity, biodiversity, and ecosystem processes, it is key to
467 understand the responses of the main aquatic primary producers (e.g., phytoplankton, benthic algae, submerged and
468 floating plants) to changes in the climate regime and climate variability. The interaction of the factors affected by
469 climate change can directly and indirectly control plant growth, and can have overall opposing effects (Havens et al.,
470 2016; Ersoy et al., 2020). Climate change can affect the competition between phytoplankton and aquatic plants and lead
471 to dramatic changes in habitat complexity. Phytoplankton and particularly cyanobacteria seem to be favoured by

472 climate warming (e.g., Paerl & Huisman, 2008; Paerl & Paul, 2012; Kosten et al., 2012; Davidson et al., 2015). In
473 addition, heatwaves, hurricanes, and low lake water levels due to increased temperature/dry periods, often lead to the
474 collapse of aquatic plants and to high phytoplankton and cyanobacteria productivity in systems with high nutrient
475 loading (Rigosi et al., 2014; Havens et al., 2016; Ersoy et al., 2020), maintaining the lake in a poor complexity, low
476 biodiversity, and turbid water regime.

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

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

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

495 Artificial manipulation of structural complexity is one of the restoration measures often applied in degraded
496 ecosystems (Cooke et al., 2005). Trees, rocks, and stones have been introduced to increase heterogeneity in streams and
497 rivers, often accompanying re-meandering of stream channels (Hoffmann et al., 2020). Although habitat coupling
498 between terrestrial and aquatic ecosystems is critical for maintaining diverse and productive riparian and stream and
499 river ecosystems (Naiman et al., 2000), lake ecologists seldom incorporate riparian habitats into models of ecosystem
500 dynamics and management (Schindler & Scheuerell, 2002). Shoreline habitats degraded by urban development and loss

501 of riparian vegetation are, however, often reconstructed in a variety of ways, including the transplantation of emergent
502 plants and the addition of rock riprap or retaining walls to control erosion and recreate littoral complexity (although
503 such artificial structures can be homogeneously complex). Artificial reefs (made up of wooden branches) have been
504 tested in Amazonian floodplain lakes, finding that although overall diversity was not enhanced, rare species occurred
505 more frequently in the more complex habitats (Yamamoto et al., 2014). Comparative studies in lakes with manmade
506 littoral complexity have shown that fish species richness is positively correlated with local habitat complexity (being
507 higher in riprap sites). However, the structure of the fish assemblage, assessed as the proportion of intolerant or tolerant
508 species, responds to cumulative effects of small habitat modifications (Jennings et al., 1999). In urban shallow lakes and
509 ponds, restoration strategies also include promoting larger pond sizes, modifying pond margins with indentation,
510 constructing different-angled slopes and with large drawdown zones, permitting hydroperiods to mimic natural changes,
511 and eliminating non-native or invasive species while promoting the presence of aquatic plants (emergent, submersed, or
512 floating) (Oertli & Parris, 2019).

513 Submerged macrophytes can return after the implementation of restoration measures that increase water
514 clarity; however, restored shallow lakes typically have a different community composition with fewer species compared
515 with the situation 20-100 years before eutrophication worsened, according to a review by Bakker et al. (2013).
516 Sometimes submerged vegetation may not return naturally even when clear water conditions have been re-established
517 (Marklund et al., 2002; Lauridsen et al., 2003). Since the early 1990's, the reintroduction of aquatic plants is thus one of
518 the recommended measures to speed up the recovery of eutrophic lakes once nutrient loading has been reduced (Moss,
519 1990; Moss et al., 1996; Jeppesen et al., 2012). For this purpose, plants are often transplanted or spread as seeds and
520 propagules (Moss et al., 1996). Studies in temperate European shallow lakes (e.g., Lauridsen et al., 2003; Hilt et al.,
521 2006; Chaichana et al., 2011) have shown higher survival and number of plants and longer total shoot length when they
522 are introduced in enclosures that prevent waterfowl access. Most of the experiences of aquatic plant introduction so far
523 are from temperate lakes, but examples from subtropical and tropical areas are increasing. For instance, in subtropical
524 China, several studies suggest that transplantation of submerged plants, even exotic ones, as a restoration tool might be
525 successful, as long as plants are protected against fish herbivory (Chen et al., 2009; Ye et al., 2011; Zhang et al., 2016;
526 Bai et al., 2020; Gao et al., 2020). In other cases, macrophyte transplantation is combined with fish removal and /or
527 introduction of mussels (Yu et al., 2016; Gao et al., 2017; Zeng et al., 2017). The establishment and protection of plants
528 as a lake restoration method, alone and in combination with other approaches, will remain an important measure in the
529 future, although many unsolved issues remain, such as how to assure long term effects (Jeppesen et al., 2012). For
530 example, the continuous control of omnivorous and herbivorous fish is recommended in warm lakes to protect

531 submerged macrophytes (Yu et al., 2016). These or other measures are likely not useful for all lakes since there might
532 be conflicts between biodiversity conservation and other uses (such as irrigation, navigation, aquaculture, etc.).

533 Sometimes, artificial macrophytes have been used when natural plants do not respond as fast as required.
534 Although direct chemical effects (e.g., uptake of nutrients and excretion of allelopathic substances that potentially
535 control phytoplankton) will not occur, the generation of physical complexity can lead to strong changes in the lake
536 function by affecting trophic interactions, and the stability of the water column and decrease of incoming light.
537 Artificial plants may initially help to create and stabilise a clear water state by serving as a daytime refuge for
538 zooplankton against predation by fish, as well as substrate for plant-associated macroinvertebrates (Skov & Berg, 1999;
539 Boll et al., 2012). A cover by artificial plants of just 3-5% of the lake area can double zooplankton densities, as found in
540 a shallow temperate lake in Denmark (Schou et al., 2009). Artificial recreation of habitat structural complexity seems,
541 however, not sufficient to mimic the whole array of effects associated with natural habitat complexity. Interestingly, in
542 streams where restoration efforts have been more widely applied than in lentic systems, restoring habitat heterogeneity
543 has seldom promoted an increase in macroinvertebrate diversity (as shown in a meta-analysis by Palmer et al., 2010),
544 indicating that the ultimate processes behind the effects of habitat complexity on biodiversity and fauna abundance have
545 not been completely elucidated (Kovalenko et al., 2012). The advantage of using artificial structures is that they can be
546 introduced all year round and are much less sensitive to environmental conditions and grazing by herbivorous fishes and
547 waterfowl, although unfortunate cases of waterfowl consuming plastic structures, likely trying to catch the associated
548 macroinvertebrates, have occurred (M. Meerhoff pers. obs.). The potential release of chemical substances and micro
549 and nanoplastics from the artificial plants should also be thoroughly analysed and weighted against the potential
550 benefits.

551 The examination of the effectiveness of several active restoration measures has resulted in different outcomes:
552 ecosystem and submerged macrophyte recovery, no improvement, or initial improvement and then a return to eutrophic
553 conditions (McCrackim et al., 2017). On top of that, restored lakes and ponds in warm regions recover more slowly than
554 those in cold areas (Jeppesen et al., 2007; 2012). Thus, under any restoration scenario, it is still key to decrease the
555 nutrient load to aquatic ecosystems (Moss et al., 2011; McCrackim et al., 2017; Hoffmann et al., 2020).

556 **Future directions**

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

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

562 2. Relevance of different attributes of habitat complexity to sustain biodiversity.The exact mechanism by which
563 habitat complexity impacts taxon richness or density, and with those, impact ecosystem processes, is still not fully
564 elucidated despite that several experimental studies have addressed the topic. For instance, space-size heterogeneity
565 (i.e., variation in space sizes) has been highlighted as more important for macroinvertebrate taxonomic richness than
566 overall complexity, and than other complexity attributes, plant biomass, and density of stems (St. Pierre & Kovalenko,
567 2014).

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

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

582 5. Connection between habitat complexity and spatial complexity at the landscape level. Despite historically
583 being treated as relatively discrete microcosms (Forbes, 1887), shallow lakes and ponds are open ecosystems that are
584 inseparable from their catchments (Moss, 1998). The importance of spatial complexity at the catchment and landscape
585 level for regional but also for local richness has been recently highlighted (Fahrig, 2013), not least through interactive
586 effects with in-lake habitat complexity. In ponds, individual pond size and isolation (habitat patchiness), together

587 with the presence of emergent vegetation (within-lake complexity), can, for instance, significantly influence waterfowl
588 diversity, as found in a series of Mediterranean ponds (Paracuellos & Tellería, 2004). Connectedness in heterogeneous
589 landscapes may lead to high local biodiversity and resilience via a spatial insurance effect (Loreau et al., 2003).
590 However, higher richness at the regional level may be expected when the lakes and ponds in a waterscape show
591 different degrees of connectivity, due to stochastic events, ecological interactions, and different in-lake complexity
592 (Scheffer et al., 2006).

593

594 **Conclusions**

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

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

616 capacity to provide food, refuge and nursing areas for aquatic and amphibious species, recycle nutrients and purify
617 water, sequester carbon, flood and hazards mitigation, and soil formation.

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

626 Reviews considering lake recovery from eutrophication, particularly those evaluating the re-establishment of
627 submerged macrophytes, have mostly focused on temperate systems (e.g., Søndergaard et al., 2005; McCrackim et al.,
628 2017; although see Jeppesen et al., 2012). So far, it seems that in subtropical lakes greater efforts are necessary to
629 maintain or speed up the recovery of littoral habitats, by performing continuous fish removal and combining this with
630 major nutrient reduction (Yu et al., 2016). More examples from Mediterranean, tropical, and subtropical areas are
631 needed to understand the effectiveness of different restoration measures across a broad range of climates and conditions.
632 Until more information is synthesized, reduction of nutrient loads and preservation of the existing natural habitat
633 complexity at different spatial scales seems to be one of the key measures to maintain the resilience of lake and pond
634 ecosystems against global and local anthropogenic impacts. Habitat complexity, from the landscape to the within-
635 system levels, needs to be prioritized by environmental managers and policymakers, as it impacts directly on
636 biodiversity and several ecosystem services supplied by lakes and ponds.

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1054 **Table 1.** Anthropogenic activities that can directly or indirectly affect habitat complexity in shallow lakes and ponds,
 1055 and some of the expected effects on lake processes and overall functioning. Based on Schindler & Scheuerell (2002).
 1056 See the text for further description of the effects of some of these activities and the mechanisms involved.

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 source of large woody debris that represents 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 (nutrients, DOC loading). Decreased complexity of littoral structure and loss of nursery/refuge/feeding areas for invertebrates, fishes, 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.

	<p>Loss of riparian buffer zones and simplification of lake littoral areas.</p> <p>Increased phytoplankton biomass and light attenuation, limiting benthic algae and submerged aquatic plants with consequent reduction in littoral and benthic habitat complexity.</p> <p>Promotion of turbidity-tolerant aquatic plants leading to habitat homogenisation.</p> <p>Consequent changes in productivity in each lake habitat.</p> <p>Habitat simplification and overall loss of biodiversity. Expectedly higher net GHG emissions.</p>
<p>Exotic species introduction</p>	<p>Effects vary depending on species:</p> <p>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 homogenization and decreased complexity.</p>
<p>Water level management for irrigation, human consumption or after construction of reservoirs</p>	<p>Lowered water level fluctuations may reduce seasonal flooding that is important to nutrient regeneration and riparian/littoral vegetation.</p> <p>Changes in water level may either facilitate or prevent the establishment and development of submerged or free-floating aquatic plants, thereby changing habitat complexity.</p> <p>Lower system resilience against other pressures such as eutrophication.</p>

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1058 **Figure legends**

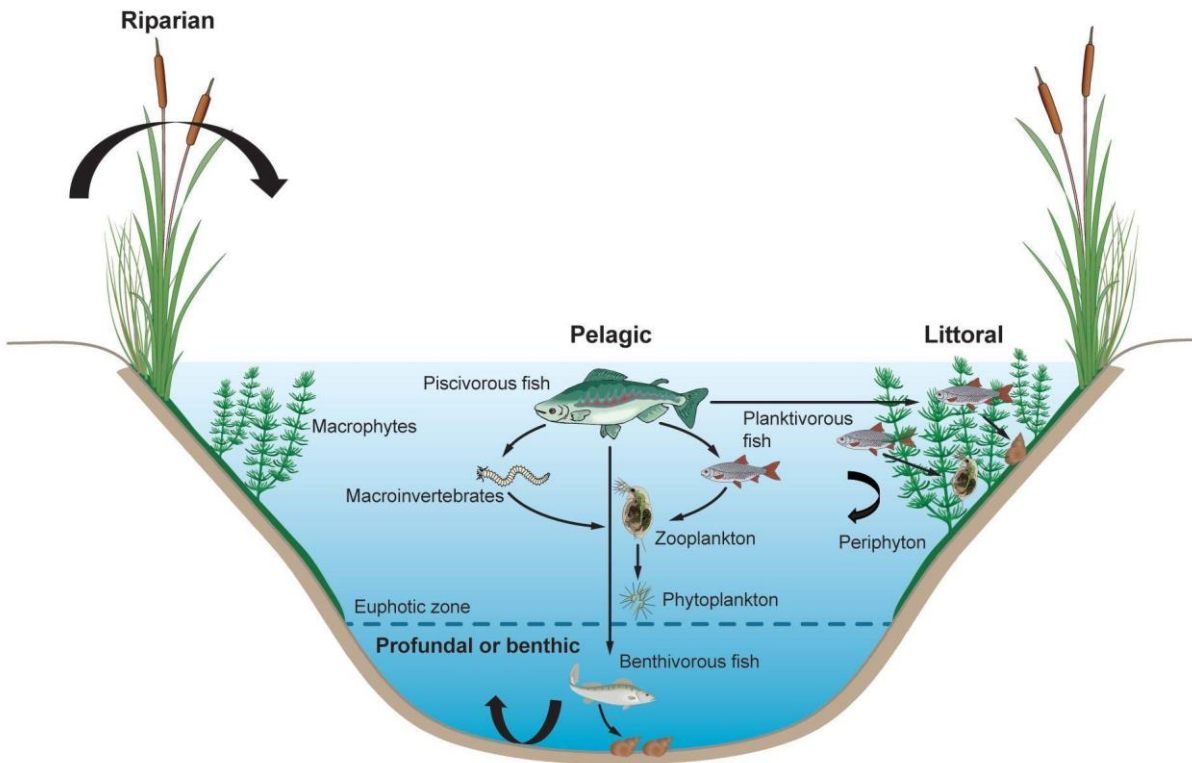
1059 **Fig. 1** Habitat complexity in lakes at the ecosystem level. Three major within-lake habitats are recognized: the pelagic,
1060 the benthic and the littoral zone, all interacting with the adjacent terrestrial ecosystem through the riparian zone. Each
1061 lake habitat is characterised by different assemblages of organisms and different levels of complexity. Drawn by
1062 M.Meerhoff and Tinna Christensen. From Kosten & Meerhoff, 2014

1063 **Fig. 2** The effects of plant architecture vary with regional climate and associated structure of classic trophic webs. In
1064 this field experiment, the same amount of artificial material mimicked submerged and free-floating plants and was
1065 placed in a series of ten similar shallow lakes under contrasting climates (temperate and subtropical). The modulating
1066 effects of aquatic plants on littoral (shown) lake communities is affected by climate, likely because of differences in
1067 local trophic web structure and in the spatial behavior of fish (depicted in the sketch below). Note the different scales
1068 used for each climate region. Modified from Meerhoff (2006)

1069 **Fig. 3** Effects of aquatic plants on physical, chemical and biological processes in shallow lakes and ponds, and
1070 ecosystem services. The processes that are directly related to the habitat complexity created by the plants are
1071 highlighted. All processes are relevant for submerged plants, and many are shared with some other plant life-forms,
1072 please see the text for elaboration. Modified with permission from Moss et al. (1996)

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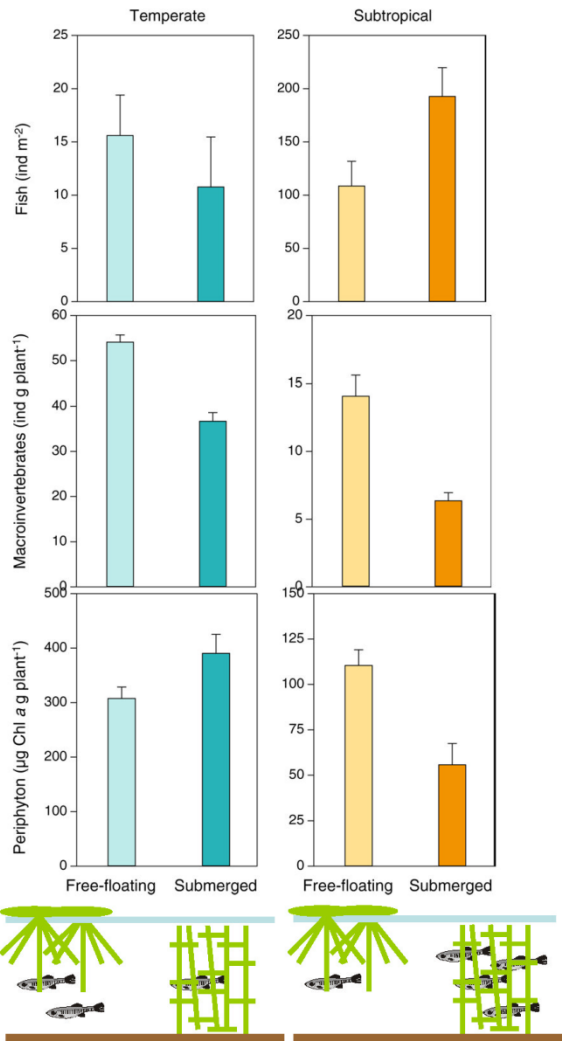
1076 **Fig. 1**

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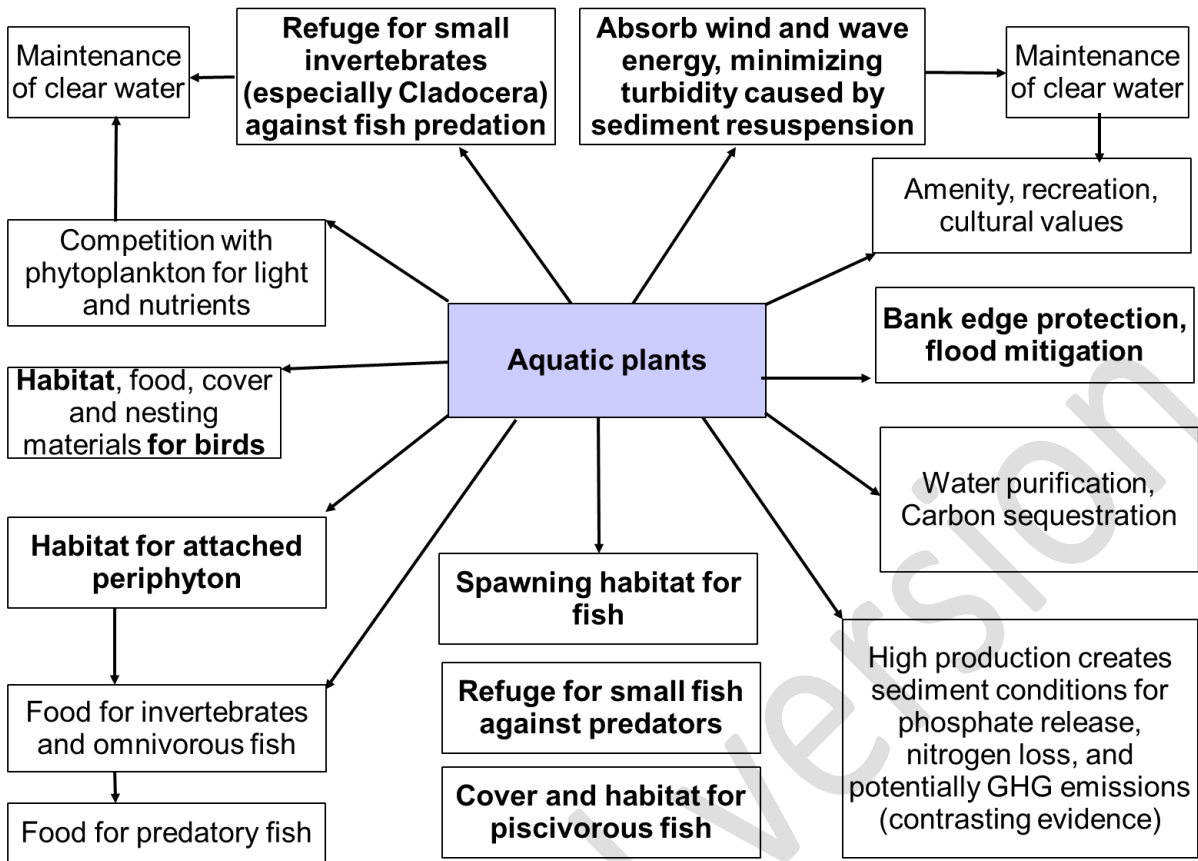


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Fig. 2

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1084 **Fig. 3**