

## Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems

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1     **Assessing the role of large herbivores in the structuring and**  
2     **functioning of freshwater and marine angiosperm ecosystems**

3

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16

17

## 18 **Abstract**

19           While large herbivores can have strong impacts on terrestrial ecosystems, much  
20 less is known of their role in aquatic systems. We reviewed the literature to determine:  
21 (1) which large herbivores (>10 kg) have a (semi-)aquatic lifestyle and are important  
22 consumers of submerged vascular plants, (2) their impact on submerged plant  
23 abundance and species composition and (3) their ecosystem functions.

24           We grouped herbivores according to diet, habitat selection and movement  
25 ecology: (1) Fully aquatic species, either resident or migratory (manatees, dugongs,  
26 turtles), (2) Semi-aquatic species that live both in water and on land, either resident or  
27 migratory (swans), (3) Resident semi-aquatic species that live in water and forage  
28 mainly on land (hippopotamuses, beavers, capybara), (4) Resident terrestrial species  
29 with relatively large home ranges that frequent aquatic habitats (cervids, water buffalo,  
30 lowland tapir).

31           Fully aquatic species and swans have the strongest impact on submerged plant  
32 abundance and species composition. They may maintain grazing lawns. Because they  
33 sometimes target belowground parts, their activity can result in local collapse of plant  
34 beds. Semi-aquatic species and turtles serve as important aquatic-terrestrial linkages, by  
35 transporting nutrients across ecosystem boundaries. Hippopotamuses and beavers are  
36 important geomorphological engineers, capable of altering the land and hydrology at  
37 landscape scales. Migratory species and terrestrial species with large home ranges are  
38 potentially important dispersal vectors of plant propagules and nutrients. Clearly, large  
39 aquatic herbivores have strong impacts on associated species and can be critical  
40 ecosystem engineers of aquatic systems, with the ability to modify direct and indirect  
41 functional pathways in ecosystems. While global populations of large aquatic

42 herbivores are declining, some show remarkable local recoveries with dramatic  
43 consequences for the systems they inhabit. A better understanding of these functional  
44 roles will help set priorities for the effective management of large aquatic herbivores  
45 along with the plant habitats they rely on.

46

## 47 **Introduction**

48           By virtue of their size, large herbivores are critical agents of change and  
49 maintenance of the ecosystems they inhabit (Owen-Smith 1988). However, while their  
50 functional roles in terrestrial ecosystems are well established, it is unclear if, and how,  
51 aquatic ecosystems are modified by the activity of large herbivores. Marine and  
52 freshwater systems differ in important ways from terrestrial systems and may respond  
53 very differently to herbivory impact. In addition, large aquatic herbivores are not a  
54 species-rich group, and their numbers are on the decline (Marsh and Lefebvre 1994,  
55 McCauley et al. 2015). However, these species share many common traits with their  
56 terrestrial counterparts, and from what is known of the impacts of terrestrial species on  
57 their ecosystems, it raises the question of whether large aquatic herbivores may be at  
58 least as capable of modifying aquatic ecosystems in potentially significant ways.

59

## 60 **The role of large herbivores across ecosystems**

61           The effect of large terrestrial herbivores on the structure and functioning of the  
62 ecosystems they inhabit is linked to the particular requirements of being large. Their  
63 size, feeding choices, metabolic requirements, social behaviour, movement patterns and  
64 other life history traits work together to make many large herbivores important  
65 ecosystem engineers (Jones et al. 1994), with the ability to change grazing plant  
66 communities (Olf and Ritchie 1998, Knapp et al. 1999, Bakker et al. 2006) habitat  
67 structure (Asner et al. 2009), nutrient flows (McNaughton et al. 1997, Augustine and  
68 Frank 2001) and trophic dynamics through direct and indirect pathways (Pringle et al.  
69 2007). Apart from the direct consequences of their high consumption rates, several traits  
70 associated with allometric scaling of herbivore body size result in disproportionately

71 large impacts on the habitats they inhabit. Large herbivores tend to have more  
72 generalised diets, have slower ingestion and defecation rates, and are predominantly  
73 herding species that typically occupy larger home ranges than smaller herbivores (Peters  
74 1983, Owen-Smith 1988, Belovsky 1997, Cumming and Cumming 2003). This results  
75 in a series of very specific effects on plant communities, habitat structure and critical  
76 ecosystems processes. The direct effects on plants include reductions in canopy  
77 structure and height (Asner et al. 2009), increases in trampling effects (Cumming and  
78 Cumming 2003, Schrama et al. 2013) and increases in seed dispersal rates (Clausen et  
79 al. 2002) among others. These, in turn, have a host of indirect effects on ecosystems.  
80 These include modifications to plant species competition, to the benefit of grazing-  
81 adapted species (McNaughton 1984, Knapp et al. 1999), flow-on effects to structure-  
82 dependent species (Pringle et al. 2007, Huntzinger et al. 2008), changes in the  
83 productivity of the system which directly and/or indirectly affects carbon and nutrient  
84 cycles (Knapp et al. 1999, Olofsson et al. 2004, Bakker et al. 2009), an increase in the  
85 heterogeneity of landscapes, increases in nutrient transport between ecosystems or  
86 decreases in fire regimes (Asner et al. 2009), among others. Taken together, these  
87 effects make large terrestrial herbivores key modifiers and maintainers of ecosystem  
88 dynamics and habitat complexity (Jones et al. 1994, Wright et al. 2002, Pringle 2008,  
89 Waldram et al. 2008). Moreover, their decline since the Late Pleistocene due to hunting  
90 and other human-related causes has been linked to major shifts in the structure and  
91 functioning of the systems they were once abundant in (Johnson 2009, Corlett 2013,  
92 Cromsigt and te Beest 2014, Gill 2014). Equally, local increases in their number, either  
93 as a result of conservation initiatives or the faster decline of their predators (Estes et al.  
94 2011), has also resulted in serious consequences for the ecosystems they depend on;  
95 population overshoots of large herbivores or concentrations within restricted areas

96 (National Parks and reserves for instance) can result in major ecosystem alterations (e.g.  
97 Cumming et al. 1997).

98 Aquatic herbivores have, in contrast, received much less attention and little is  
99 known of the consequences of the functional roles they perform in freshwater and  
100 marine environments. The list of extant species is relatively small, a mere fraction of the  
101 large aquatic herbivores that were once present in aquatic ecosystems. Prehistorically, a  
102 rich assemblage of large aquatic herbivores coexisted, including sirenians and  
103 Hippopotamidae, of which both fully aquatic and semi-aquatic species have been  
104 documented (Domning 2001, Boisserie et al. 2011). Furthermore, Oligocene-to-recent  
105 proboscideans are thought to be derived from amphibious ancestors, which consumed  
106 freshwater vegetation (Liu et al. 2008). Several large-tusked dugongines were also  
107 present in ancient seas, some of which may have acted as keystone species, disrupting  
108 climax seagrass communities, thereby increasing their productivity and diversity, with  
109 presumed positive effects on sirenian diversity (Domning 2001). Unlike most seagrass  
110 systems today, which, in the absence of large herbivores, are mostly detritus based, until  
111 around 2±3 Ma, most primary productivity in seagrass beds was presumably consumed  
112 by herbivores (Domning 2001).

113 Today, even these few contemporary species of large aquatic herbivores are  
114 mostly in decline, particularly the fully aquatic ones. Although the defaunation of  
115 aquatic animals began more recently than in terrestrial systems (McCauley et al. 2015),  
116 the effect of this reduction on aquatic large herbivores has been dramatic in the last  
117 century (Marsh and Lefebvre 1994, McCauley et al. 2015). Effective management has  
118 been successful in reversing these trends for some aquatic species such as the moose,  
119 Eurasian elk, beavers, green turtles and swans (Nolet and Rosell 1998, Halley and  
120 Rosell 2002, Chaloupka et al. 2008, Gayet et al. 2014). However, populations of many

121 large aquatic herbivores like dugongs, manatees or hippopotamuses have been declining  
122 to critical levels in the last centuries (Jackson 2001, D'Souza et al. 2013, Pennisi 2014),  
123 and they may no longer be sufficiently abundant to effectively perform their functional  
124 role in the ecosystems they inhabit (McCauley et al. 2015).

125         Together with their low numbers, the aquatic environment they inhabit makes it  
126 inherently more difficult to track, monitor and gauge any potential influence these  
127 species may have on these systems; studies that have examined their ecosystem impacts  
128 have been necessarily opportunistic, making use of locally high concentrations  
129 (Hauxwell et al. 2004b, Heithaus et al. 2014). On the face of it, there is little to suggest  
130 that large aquatic herbivores are qualitatively different from their terrestrial  
131 counterparts. Most fully aquatic herbivores such as sirenids have sizes, feeding choices,  
132 metabolic requirements, social behaviours and movement patterns comparable to large  
133 terrestrial herbivores (Owen-Smith 1988). Additionally, a significant number of large  
134 terrestrial herbivores also feed on aquatic systems, including moose, swans or turtles  
135 among others. Given these similarities in traits, it is likely that their influence on aquatic  
136 habitats may be at least as large as terrestrial systems. From what is known of aquatic  
137 macrophyte-dominated communities like kelp beds, seagrass meadows and macroalgal  
138 communities, they may be highly modified by herbivory, and large herbivores are likely  
139 to play a potentially non-trivial role in contributing to these processes (Burkepile and  
140 Hay 2006, Valentine and Duffy 2006). In fact, several aquatic macrophytes show a  
141 series of adaptations to herbivory including compensatory growth, protected rhizomes  
142 or clonal growth that are typical of highly grazed systems (Valentine and Heck 1999,  
143 Nolet 2004, Valentine and Duffy 2006, Vergés et al. 2008).

144

145 **Ecosystem characteristics that can influence aquatic plant-large herbivore**  
146 **interactions**

147         Despite the evident similarities between terrestrial and aquatic systems, it must  
148 be remembered that aquatic systems may respond very differently to large herbivores  
149 compared to terrestrial ecosystems, as a function of inherent differences in plant  
150 reproductive strategies and generation times, plant size and structure or differences in  
151 ecosystem scale and connectivity; each of these can have major implications for the way  
152 aquatic herbivores use and influence these systems.

153         For a start, the bulk of aquatic primary production is mostly unavailable for large  
154 herbivores to consume, dominated as it is by phytoplankton, which large herbivores are  
155 generally incapable of harvesting. This restricts them to feed close to shores where they  
156 can access benthic primary production, principally dominated by macroalgae and  
157 aquatic angiosperms. In terrestrial systems, the structural tissue produced by woody  
158 species is, for the most part, unsuitable as a primary food source to large herbivores,  
159 even though large browsers and mixed feeders do consume twigs and bark (Bakker et  
160 al. 2015). In contrast, aquatic macrophytes in general have fewer structural defences  
161 than their terrestrial counterparts, yielding them more edible, although macroalgae can  
162 strongly compensate with chemical defences (Hay and Fenical 1988).

163         The reproductive strategies and population dynamics of aquatic plants may also  
164 strongly mediate the ability of these systems to cope with large herbivore foraging.  
165 Generation times may differ greatly between aquatic primary producers, in particular  
166 the smaller algae having rapid turnover rates, making them differentially susceptible to  
167 sustained herbivory, an important consideration particularly when evaluating the  
168 prevalence and strength of trophic cascades in aquatic systems. While submerged

169 angiosperms may be annual, clonal species of vascular plants (like *Posidonia oceanica*),  
170 can have generation times that span millennia (Arnaud-Haond et al. 2012), making them  
171 respond in similar ways to herbivory as terrestrial grasslands, also dominated by clonal  
172 primary producers (Burkepile 2013).

173         A final vital contrast between terrestrial and aquatic systems is that the latter are  
174 considered to be generally better connected (e.g. Tanner 2006), governed by higher flow  
175 rates of nutrients and other materials, holoplanktonic organisms and reproductive  
176 propagules (Carr et al. 2003). In particular, marine environments present few barriers to  
177 movements, enabling large herbivores to travel vast distances (often spanning entire  
178 oceans) without impediment. However, while connectivity may be high, the habitats  
179 themselves may be highly discontinuous (Goodsell 2009). Marine macrophytes  
180 (seagrasses and algae) are clearly limited by light and substrate availability, resulting in  
181 marine macrophyte habitats being very patchy in their distribution (Hemminga and  
182 Duarte 1999). For herbivores using these systems, the distance between feeding areas  
183 could be separated by hundreds or thousands of kilometres, particularly in the open sea.  
184 Freshwater macrophyte dominated habitats are also characterised by similar  
185 discontinuities. Here though, it is the water bodies themselves that can be highly  
186 disconnected. Thus, for both marine and freshwater systems, large herbivores whose  
187 forage requirements may not be satisfied at a single location, may necessarily have to  
188 undertake much larger-scale movements than their terrestrial counterparts (McCauley et  
189 al. 2015). This may make them much less predictable in space and time. The impacts of  
190 their herbivory, although locally high, may be distributed over a much wider area than  
191 terrestrial species, diluting their overall importance to ecosystem functioning. Clearly,  
192 there is no agreement on how foraging and behavioural traits interact with the

193 peculiarities of the aquatic environment to determine the functional importance of large  
194 aquatic herbivores on their habitats and ecosystems.

195

## 196 **Objectives**

197         We conducted a comprehensive review of extant herbivores in aquatic systems  
198 to document the potential impacts of large aquatic herbivores on the structure and  
199 functioning of aquatic ecosystems. We restrict our review to aquatic angiosperm-  
200 dominated systems, since these constitute the primary habitats in which extant large  
201 herbivores feed. In particular, our objectives were to determine which large herbivorous  
202 species can be classed as consumers of submerged angiosperms. In addition, we  
203 documented the direct impacts their foraging and use could have on the habitats and  
204 ecosystems they inhabit. Further, we asked if these species have the ability to modify  
205 ecosystem structure and function and under what conditions this is likely to take place.  
206 Finally, if large aquatic herbivores are capable of ecosystem modification, we ask what  
207 implications this has for the way we manage their populations and the ecosystems they  
208 depend on.

209

## 210 **List of large aquatic herbivores**

211 *Large aquatic herbivores: which species consume aquatic angiosperms?*

212         There is no universal definition of large aquatic herbivores. In this review, we  
213 included herbivores with a body mass of 10 kg and greater, which represent meso- to  
214 megaherbivores according to Owen-Smith (2013). We include animals consuming  
215 submerged angiosperms in both marine and freshwater environments. In marine systems

216 this includes dugongs, manatees and turtles. In freshwater systems it is less clear which  
217 animals can be considered large aquatic herbivores, and we included aquatic and semi-  
218 aquatic animals, as all of them consume aquatic plants. In fact, only freshwater  
219 manatees are fully aquatic and depend completely on submerged and floating  
220 macrophytes as a food source. The group of semi-aquatic animals consists of animals  
221 that are frequently found in aquatic systems. We acknowledge that this category is  
222 somewhat arbitrary. We identified three distinct vertebrate classes that could be  
223 considered large aquatic or semi-aquatic herbivores: mammals, birds and reptiles (Table  
224 1). We did not find examples of herbivore fish greater than 10 kg that graze on  
225 submerged vascular macrophytes; therefore fish were left out of this review. The body  
226 mass of the selected aquatic herbivores ranges from about 10 kg (swans) to 3200 kg  
227 (hippopotamus). Interestingly, the list includes the largest species from a variety of  
228 guilds/families of animals. Whereas a swan of 10 kg will likely have less per capita  
229 impact on submerged plants than a manatee of 300 kg, within the guild of water birds,  
230 swans have disproportionate impacts, which is directly related to their body size (Wood  
231 et al. 2012a).

232

### 233 *Diets*

234 The diets of all the large aquatic herbivores included in this review are presented  
235 in Table 1. None feed exclusively on submerged angiosperms. In fact, although most of  
236 the species in Table 1 are primarily plant consumers, they generally also feed on algae,  
237 invertebrates (e.g. cnidarians) and other animal material (O'Hare et al. 2007, Cardona et  
238 al. 2009, Reisser et al. 2013). The marine dugong appears to be the most specialist  
239 feeder, with a diet of mostly seagrass (Heinsohn et al. 1977). It feeds indiscriminately

240 on aboveground and belowground parts, just as beavers and swans. While migrating,  
241 swans apparently depend largely on tubers as their principal food source (Nolet and  
242 Drent 1998, Nolet et al. 2002, LaMontagne et al. 2003). Recently, green turtles have  
243 also been observed to dig up and eat belowground tissues of seagrasses, which has been  
244 interpreted as a sign of local turtle overpopulation and food limitation (Christianen et al.  
245 2014). The belowground parts of vascular plants are rich in carbohydrates and starch,  
246 which provides energy-rich food to aquatic herbivores (Nolet and Klaassen 2005).

247         Several species feed both on marine and freshwater angiosperms, including the  
248 West-Indian and West African manatee as well as the swan species (Table 1). All  
249 manatees are fully aquatic and feed mostly on submerged and floating macrophytes,  
250 occasionally feeding on emergent species. Most herbivores that consume submerged  
251 macrophytes in freshwater systems also consume terrestrial plants, with aquatic  
252 angiosperms often being a very small component of their diet. Even semi-aquatic  
253 herbivorous species such as the hippopotamus, the capybara and the beaver, which are  
254 adapted to spend much of their time half submerged, having their eyes and nostrils on  
255 the upper part of their head, feed mostly on land and only occasionally consume  
256 submerged macrophytes (Creed 2004). It should however, be noted that the diets of  
257 these species have not been very intensively investigated; it is therefore possible that  
258 aquatic macrophytes may be a larger portion of their diet than is presumed.

259         The other mammals that sporadically consume freshwater vascular plants are  
260 perhaps more rightly terrestrial animals that frequent swamps and marshy areas,  
261 including moose, Eurasian elk and several other deer species (Table 1). A recent review  
262 shows that their incidence of feeding on submerged angiosperms may be seriously  
263 underestimated as all better studied cervid species occasionally consume submerged  
264 vascular plants and macro-algae (Ceacero et al. 2014). This suggests that less studied

265 species may also opportunistically consume aquatic angiosperms when these are  
266 available. In fact, some terrestrial herbivores (e.g. moose) may specifically seek out  
267 aquatic angiosperms to obtain valuable nutrients, such as sodium, the concentrations of  
268 which are higher in aquatic vascular plants than terrestrial plants (Belovsky and Jordan  
269 1978). In addition, other minerals or proteins could drive herbivores to use aquatic  
270 angiosperms as a supplementary source to a primarily terrestrial diet, particularly in  
271 periods of high physiological demand (Ceacero et al. 2014).

272

## 273 **Impact on aquatic vascular plant abundance and species composition**

### 274 *Herbivory rates compared to primary production*

275 Current rates of herbivory in terrestrial habitats are relatively low. In a recent  
276 review, Turcotte et al. (2014) showed that, when averaged across all major lineages of  
277 vascular plants, herbivores consume 5.3% of the leaf tissue produced annually. Previous  
278 estimates of the mean annual rate of leaf herbivory across terrestrial plants ranged  
279 between 10 and 20% (Cyr and Pace 1993, Frank et al. 1998, Cebrian and Lartigue 2004,  
280 Maron and Crone 2006). By any estimate, these values are clearly lower than rates  
281 reported in aquatic systems, where herbivores have been shown to consume between  
282 30-80% of primary production on average (Lodge 1991, Cyr and Pace 1993, Burkepile  
283 2013, Gruner and Mooney 2013). At the highest extremes, large aquatic herbivores can  
284 consume well above 100% of annual primary production (Table 2); it is not uncommon  
285 for turtles and swans to consume ca. 100% of primary production in a given season  
286 (Rivers and Short 2007, Hidding et al. 2009, Kelkar et al. 2013a, Christianen et al.  
287 2014). A lot of the variation in herbivory rates observed among studies is likely due to  
288 variation in herbivore densities (e.g. Wood et al. 2012a).

289

290 *Effects on canopy height and above and below ground biomass*

291           Large aquatic herbivores significantly affect plant abundance and vegetation  
292 structure (Table 2). Reduction of the aboveground standing crop varies considerably,  
293 but can be very high at some locations (see above) resulting in an almost complete  
294 removal of submerged vegetation beds. By removing aboveground plant material,  
295 aquatic herbivores alter the vegetation structure (e.g. Christianen et al. 2014) or increase  
296 the patchiness on a small spatial scale (Dos Santos et al. 2012, Christianen et al. 2013).  
297 Thus, by grazing on the upper plant parts, aquatic herbivores reduce shoot length and  
298 the mean height of the vegetation (Tatu et al. 2007). More importantly, some large  
299 aquatic herbivores appear to specifically target belowground storage. In fact, this may  
300 be a key difference between terrestrial and aquatic herbivores: while terrestrial species  
301 seldom consume belowground parts, large aquatic herbivores can, on average, reduce  
302 belowground biomass by 60% (comparing grazed versus ungrazed areas; see Table 2)  
303 (Preen 1995). While mute swans do consume roots and rhizomes, this is often a minor  
304 portion of their diet that mostly consists of aboveground plant material (Bailey et al.  
305 2008). Other species, in contrast, specifically target belowground plant parts while  
306 feeding. Dugongs, manatees, hippopotamuses, cervids, beavers and whooper and  
307 trumpeter swans, have all been identified as consumers of plant below ground biomass  
308 (Preen 1995, Nacken and Reise 2000, LaMontagne et al. 2003, Källander 2005, Dos  
309 Santos et al. 2012, Law et al. 2014). Indeed, dense populations of green turtles  
310 overgrazing above ground biomass have been reported (in Indonesian seagrass  
311 meadows) to exploit the below ground compartment by digging up the rhizomes  
312 (Christianen et al. 2014, Heithaus et al. 2014). Similarly, black swans (*Cygnus atratus*),  
313 Bewick swans and whooper swans (the former two at the limit of what we class as large

314 herbivores (>10 kg) in this review), forage on leaves, rhizomes and roots on macrophyte  
315 meadows, producing a pitted waterscape (Hidding et al. 2010a, Dos Santos et al. 2012).  
316 Dugongs (and also manatees) are specialist belowground feeders, and the feeding trails  
317 they produce have a 50-87% lower shoot density, and 51-75% reduction in  
318 belowground biomass (see Table 2).

319

### 320 *Changes in species composition*

321 All of the large aquatic herbivores examined (for which sufficient data was  
322 available) have impacts on plant species composition, usually transforming meadows  
323 dominated by slow growing, large plants into meadows dominated by fast-growing  
324 smaller species that cope better with herbivore-induced disturbances in the above- and  
325 below-ground compartments (Preen 1995, Burkholder et al. 2013, Kelkar et al. 2013b).  
326 They can alter species composition and diversity of macrophyte beds by preferentially  
327 grazing on certain species or by unselective bulk grazing, which will mostly affect the  
328 dominant or most sensitive species, thus changing the relative abundance among species  
329 assemblages. This can promote species diversity when herbivores graze on the  
330 dominant plant species, thereby releasing subordinates from competition or creating  
331 generation niches for subordinates (Olf and Ritchie 1998). Equally though, they reduce  
332 diversity by selectively removing the subordinate species. These alternative impacts can  
333 be illustrated by the grazing of mute swans, which like to feed on *Potamogeton*  
334 *pectinatus*. They preferentially consumed *P. pectinatus* amongst vegetation dominated  
335 by charophytes, thus enhancing charophyte dominance (Hidding et al. 2010a), whereas  
336 in vegetation dominated by *P. pectinatus*, they strongly reduced its biomass, which  
337 favoured the subordinate species *Potamogeton pusillus* that would otherwise be

338 outcompeted (Hidding et al. 2010b). Interestingly, herbivores can also reduce the  
339 biomass of a species, while simultaneously increasing its relative share in species  
340 composition. In a brackish lagoon, grazing impacts by waterfowl on *Zostera noltii* was  
341 dual, mainly favouring its relative abundance by reducing competing macroalgae, but  
342 conversely reducing its biomass through direct impact (Gayet et al. 2012). Similar  
343 examples can be found in marine systems. Green turtles in the Lakshadweep  
344 archipelago precipitate species shifts in meadows from the long-lived, slow-growing  
345 seagrass *Thalassia heimprichii*, on which they preferentially feed, to the faster growing  
346 small seagrass *Cymodocea rotundata*; with sustained grazing, turtles can cause  
347 meadows to shift to monospecific *C. rotundata* stands (Kelkar et al. 2013b). This is  
348 similar to some reports of dugongs that appear to be responsible for maintaining  
349 seagrass meadows with short-lived *Halophila spp.* and *Halodule spp.* species (Preen  
350 1995). In contrast, in freshwater systems, belowground foraging on *P. pectinatus* tubers  
351 in autumn or spring by whooper swans and Bewick swans, generally enhances species  
352 diversity, as it reduces the dominance of *P. pectinatus* in the following growing season  
353 and creates regeneration niches through sediment disturbance, to which particularly  
354 annual species, such as *Najas marina* and *Zannichellia palustris*, respond favourably  
355 (Hidding et al. 2010a, b). Even when no net effect on aboveground plant standing crop  
356 is measured, early season tuber foraging by trumpeter or whooper swans may result in a  
357 shift of species composition, with increased abundance of subordinate species in the  
358 aboveground vegetation (LaMontagne et al. 2003, Hidding et al. 2010b). Moose grazing  
359 can also reduce aquatic plant species richness, but the underlying mechanism remains  
360 unknown (Qvarnemark and Sheldon 2004).

361

362 **Direct and indirect effects of large aquatic herbivores on ecosystem**  
363 **functioning**

364           Given the review above, it is unsurprising that large herbivores may have the  
365 ability to influence aquatic ecosystem functioning. By consuming submerged vegetation  
366 they have strong direct and indirect effects on their habitat, often cascading to other  
367 organisms. Due to their size, large aquatic herbivores can transform entire landscapes,  
368 and promote spatial heterogeneity in plant beds, wetlands and river valleys, with very  
369 strong consequences for other organisms (Table 3). We discuss five main ecosystem  
370 functions that large aquatic herbivores may contribute to: structuring habitat, modifying  
371 productivity, modifying geomorphology, altering nutrient cycling and transport of  
372 organisms.

373

374 *Habitat modification for other organisms*

375           Not unlike terrestrial grasslands, in the presence of large herbivores, many  
376 aquatic vascular plant systems are transformed to low canopy habitats, with low above  
377 ground biomass and high turnover of plant tissues, often referred to as grazing lawns  
378 (McNaughton 1984, Frank et al. 1998, Table 3). Green turtles, dugongs and swans can  
379 produce strong habitat modifications by reducing shoot densities, above and  
380 belowground biomass, changing species composition and reducing canopies of the  
381 submerged plant ecosystems they feed on (Lock 1972, Nolet 2004, Skilleter et al. 2007,  
382 Sandsten and Klaassen 2008, Arthur et al. 2013, Table 3). Hippopotamuses create  
383 grazing lawns on land, thereby enhancing larger scale spatial heterogeneity of  
384 vegetation (Lock 1972), which attracts a rich herbivore assemblage (Eltringham 1974,  
385 Verweij et al. 2006, Waldram et al. 2008, Kanga et al. 2013). However, facilitative

386 effects will depend strongly on large herbivore density. Hippopotamuses may facilitate  
387 other herbivores by creating grazing lawns, but at very high densities, they reduce the  
388 standing crop of vegetation to a level that makes it difficult for other herbivores to find  
389 enough food, causing them to compete with each other (Eltringham 1974). The  
390 circumstances under which facilitative effects can be found may further depend on the  
391 type of ecosystem and the availability of resources for plant (re)growth.

392 Altogether, the removal of plant material, changes in species composition or  
393 changes to the structural complexity provided by the vegetation due to grazing by large  
394 aquatic herbivores has indirect implications for other organisms that use this spatially  
395 heterogeneous habitat for foraging, breeding, and as a refuge from predation (Coen et  
396 al. 1981, Marklund et al. 2002, Skilleter et al. 2007). Skilleter et al. (2007) found that up  
397 to 85% fewer animals were present in dugong feeding trails, and that the overall  
398 composition of benthic infaunal assemblages in the grazed areas was different from that  
399 in ungrazed areas. Similarly, Arthur et al. (2013) found that total biomass density of  
400 seagrass-associated fish recruits was about 12 times lower in seagrass meadows grazed  
401 by green turtles. At its extreme, high populations of large herbivores such as green  
402 turtles, dugongs or manatees concentrate in space, resulting in habitats that can be  
403 completely overgrazed (Preen 1995, Hauxwell et al. 2004a, Skilleter et al. 2007,  
404 Christianen et al. 2012, Table 3).

405

#### 406 *Production modification*

407 In aquatic systems, herbivores are more often reported to suppress primary  
408 productivity rather than facilitate growth, prompting a 49-68% decrease in producer  
409 abundance on average (Gruner et al. 2008, Hillebrand et al. 2009, Poore et al. 2012,

410 Table 3). However, large grazers have also been reported to increase primary  
411 production by up to 40% compared to ungrazed areas by removing heavily-epiphytized  
412 seagrass blades, which presumably reduces light limitation and facilitates the production  
413 of new, fast growing shoots (Moran and Bjorndal 2005, Valentine et al. 2014, Table 3).  
414 Similarly, autumn foraging by Bewick's swans (which are just below 10 kg) enhanced  
415 the production of tubers of *Potamogeton pectinatus*, at intermediate grazing pressure,  
416 through an overcompensation response of the remaining tubers (Nolet 2004).

417

#### 418 *Geomorphological modification*

419         Perhaps one of the strongest effects large aquatic herbivores can exert on  
420 systems is the modification of sediment characteristics (e.g. granulometry) while  
421 foraging, that mobilizes fine particles and increases water turbidity (Skilleter et al. 2007,  
422 Christianen et al. 2014, Green and Elmberg 2014, Table 3). Sediment mobilization by  
423 herbivores may influence primary producers by increasing rates of plant burial or by  
424 reducing transparency (Christianen et al. 2014). It may also influence other organisms  
425 living in these habitats either through direct mortality as a result of burial or reduced  
426 visibility (Skilleter et al. 2007), incidental consumption (as seen in terrestrial systems,  
427 Gomez and Gonzalez-Megias 2002), or indirectly because of the close association  
428 between soft sediment fauna and sedimentary parameters (Skilleter et al. 2007 Table 3).  
429 Large herbivores may also cause a reduction in sediment stability, not just through the  
430 loss of submerged plants, but due to the loss of features such as animal tubes  
431 (Luckenbach 1986). This is not the only effect. Trampling by large herbivores damages  
432 plants directly, resulting in bare soil, but also compacts the soil, and on land, prevents  
433 rapid infiltration of rain water, resulting in wetter habitats (Lock 1972, Schrama et al.

434 2013). Furthermore, in freshwater habitats, large herbivores have two principal effects  
435 on the geomorphology of their habitat: they alter the areas where they reside and, due to  
436 their foraging movements between water to land, impact the entire riparian zone  
437 (Naiman and Rogers 1997). Hippopotamuses create pathways through wetland  
438 vegetation during their nightly foraging bouts on land as they consistently use the same  
439 trails (McCarthy et al. 1998, Mosepele et al. 2009). These maintained trails can  
440 potentially become water or rivers channels, pools alongside rivers, or even lakes (Lock  
441 1972, Naiman and Rogers 1997, McCarthy et al. 1998, Mosepele et al. 2009), that serve  
442 as a habitat for fish, invasive red-swamp crayfish and larger animals such as crocodiles  
443 (Naiman and Rogers 1997, Mosepele et al. 2009, Grey and Jackson 2012, Table 3).

444 Analogous patterns of strong engineering effects of large aquatic herbivores can  
445 be found in northern latitudes. Beavers strongly modify channel geomorphology and  
446 hydraulic conditions through their dam building activities (Naiman et al. 1986, Wright  
447 et al. 2002, Rosell et al. 2005, Hood and Larson 2015). The creation of ponds and  
448 stream diversions has profound long-term consequences for the entire drainage network  
449 (Naiman et al. 1986), by reducing water flow and increasing sedimentation rates  
450 (Naiman and Rogers 1997, McCarthy et al. 1998, Rosell et al. 2005). As a result,  
451 beavers can act as a whole-community facilitator for a wide variety of aquatic animals,  
452 making the habitat structurally more diverse and productive (Jones et al. 1994, Wright  
453 et al. 2002, Rosell et al. 2005, Nummi and Holopainen 2014). Moose and elk also create  
454 a dense network of foraging trails in the riparian zone when moving between water and  
455 land (Naiman and Rogers 1997).

456

457 *Nutrient cycle modification*

458           Large herbivores can modify nutrient cycling in two main ways: alteration of  
459 nutrient cycling and transport of nutrients in or out of the system. Direct consumption  
460 by large herbivores can accelerate the detrital cycle by accelerating decomposition, but  
461 also modifies the nutrient cycle in plants themselves. Sustained grazing has been shown  
462 to modify the nutrient content of plants, particularly through enhanced nitrogen content,  
463 in both aquatic (Hunter 1980, Moran and Bjorndal 2006, Aragones et al. 2006) and  
464 terrestrial habitats (McNaughton 1979, Knapp et al. 1999, Bakker et al. 2009). In this  
465 way, by gardening plants, large aquatic herbivores may increase forage quality for  
466 themselves and other herbivores in the system (Moran and Bjorndal 2006, Aragones et  
467 al. 2006). Herbivores may indirectly fertilize benthic primary producers; the shortened  
468 grazed canopy facilitates the flux of nutrients from the water column to producers,  
469 thereby decreasing nutrient limitation (Carpenter and Williams 2007). However, the  
470 most common mechanism by which large aquatic herbivores increase plant nutrient  
471 levels is by stimulating the plant's compensatory growth (Moran and Bjorndal 2006,  
472 Vergés et al. 2008, Christianen et al. 2012).

473           Nutrient flows in aquatic systems can be radically different from terrestrial  
474 habitats, where fertilization through urine and dung are recycled largely within the same  
475 broad area (McNaughton et al. 1997, Subaluski et al. 2015). In contrast, in freshwater  
476 and marine systems, water motion and currents on the one hand, and the larger home  
477 ranges of herbivores on the other, make it unlikely that herbivores could fertilize the  
478 same benthic primary producers they have consumed directly via their excretions  
479 (Burkepile 2013). Many marine animals have on average significantly larger adult home  
480 ranges (McCauley et al. 2015) and disperse greater distances as juveniles than their  
481 terrestrial counterparts (Kinlan and Gaines 2003). In addition, larger animals usually  
482 display larger home ranges (McCauley et al. 2015). This makes large aquatic fauna

483 potentially important mobile links, capable of being long-distance vectors of nutrients  
484 between habitats and ecosystems (Lundberg and Moberg 2003, Heck et al. 2008, Green  
485 and Elmberg 2014). Most large aquatic herbivores may have the potential to transfer  
486 nutrients within and between the habitats within their home range, and those that use  
487 both terrestrial and aquatic habitats, may even be cross-ecosystem links. This has been  
488 shown for the moose (Belovsky and Jordan 1978, Bump et al. 2009), green turtles  
489 (Vander Zanden et al. 2012), beavers (Rosell et al. 2005), hippopotamuses (Subaluski et  
490 al. 2015) and swans (Hahn et al. 2008, Wood et al. 2013); by eating in one system and  
491 defecating and excreting in another, these species may serve as powerful links and be  
492 considered ecosystem engineers. Thanks to this capacity of exporting nutrients out of  
493 the system, large aquatic herbivores may also function as alleviators of anthropogenic  
494 nutrient inputs to seagrass or macrophyte meadows. This has been confirmed for  
495 seagrass meadows grazed by green turtles (Christianen et al. 2012). Grazing increases  
496 seagrass production, thereby increasing the food availability for green turtles and the  
497 amount of seagrass biomass and nutrients exported by the turtles out of the system.  
498 According to Christianen et al. (2012), this export by large aquatic herbivores is  
499 probably the most important controlling factor for seagrass under grazing and high  
500 nutrient loads. When nutrients increase, grazing can potentially improve conditions for  
501 seagrass.

502

### 503 *Transport of organisms*

504         Apart from transporting nutrients, large herbivorous fauna can transport  
505 propagules of aquatic plants and animals when moving between wetlands or aquatic  
506 plant beds. This dispersal ability has been mainly examined in waterbirds (Green and

507 Elmberg 2014), but may be extended to other large aquatic herbivores. Seeds of aquatic  
508 plants and resting stages of numerous invertebrate species are transported both by endo-  
509 and exozoochorous means (Clausen et al. 2002, van Leeuwen et al. 2012). Internal  
510 transport is the most common form of dispersal (Brochet et al. 2010). The maximum  
511 distance of endozoochorous dispersal depends strongly on the body size of the vector:  
512 larger waterbirds fly faster and have longer gut retention times, which allows for a  
513 longer travel distance before the last propagule is excreted (Clausen et al. 2002, van  
514 Leeuwen et al. 2012). Furthermore, the viability of seeds after gut passage is higher in  
515 larger birds (van Leeuwen et al. 2012), even though seeds excreted after shorter  
516 retention times are generally more viable (Charalambidou et al. 2003). Whereas large  
517 waterbirds consume relatively fewer seeds and more green plant material than smaller  
518 birds (Wood et al. 2012a), they inadvertently consume large amounts of macro-  
519 invertebrates and seeds while feeding on green plant material (O'Hare et al. 2007).  
520 Altogether, this makes larger species, such as swans, suitable vectors for long distance  
521 travel of propagules. While most propagules will be lost as they may be digested or  
522 excreted in unsuitable habitats, rare, successful long distance dispersal events can be of  
523 high significance for instance in promoting species range expansions or in maintaining  
524 gene flow between distant populations (Figuerola et al. 2005, Brochet et al. 2009,  
525 Sanchez et al. 2012). Whereas for other groups of large aquatic herbivores little  
526 information on dispersal is available, similar processes may occur in marine  
527 environments, where large herbivores transport seeds of seagrasses (Sumoski and Orth  
528 2012, McMahon et al. 2014) whereas in freshwater habitats mammalian herbivores can  
529 also carry seeds (Jaroszewicz et al. 2013). Their potential as dispersal vectors of  
530 submerged plants will depend strongly on the digestion physiology and movement  
531 ecology of the species.

532

## 533 **Outlook and conclusions**

534 *Large aquatic herbivores as ecosystem engineers: from species to functional groups*

535 Our review highlights that much research on large aquatic herbivores has  
536 focused on species forage or habitat requirements, without much consideration of the  
537 influence of this foraging on the aquatic habitats themselves. Even for the beaver, a  
538 classic textbook example of an ecosystem engineer capable of modifying entire  
539 landscapes (Jones et al. 1994, Marshall et al. 2013, Hood and Larson 2015), there is  
540 limited knowledge of its impact on submerged freshwater vegetation (Parker et al.  
541 2007). However, from an early discounting of any potential impact herbivory may have  
542 as a dominant ecosystem pathway (Lodge 1991, Lodge et al. 1998), more recent  
543 evaluations have shown that large aquatic herbivores could, under some circumstances,  
544 become key agents of aquatic ecosystem functioning (Christianen et al. 2014, Green and  
545 Elmberg 2014, Pennisi 2014, Heithaus et al. 2014).

546 While large aquatic herbivores all consume submerged angiosperms and have an  
547 aquatic lifestyle, there are enough differences between species to make it impossible to  
548 generalise on the impact of a generic large aquatic herbivore. Instead, it is helpful to  
549 classify large aquatic herbivores on the basis of shared traits according to their diet,  
550 habitat selection and movement ecology. Based on these criteria we divided the large  
551 aquatic herbivores listed in Table 1 into four categories (Fig. 1):

552 (a) *Fully aquatic species that may be both resident or migratory (manatees,*  
553 *dugongs, turtles)*

554 Their diets consist mostly of submerged vascular plants and they live most of the  
555 time fully submerged.

556 (b) *Semi-aquatic species adapted to life on the water, but frequent both water*  
557 *and land, and can be both resident and migratory (swans)*

558 They consume a lot of submerged vascular plants and can sustain themselves for  
559 prolonged periods on submerged vascular plants but can also survive on  
560 terrestrial vegetation.

561 (c) *Semi-aquatic species that live in the water and forage mainly on land*  
562 *according to a central-place foraging pattern; they are residents*  
563 *(hippopotamuses, beavers, capybara)*

564 They are adapted to spend extended periods almost submerged, leaving only  
565 their ears, eyes and nose above the water surface. They retreat to the water when  
566 scared. While they do consume submerged angiosperms, this appears to  
567 generally be a minor part of their diet, although most species are data deficient  
568 when it comes to foraging on submerged vascular plants.

569 (d) *Terrestrial species that frequent aquatic habitats; resident species with*  
570 *relatively large home ranges (cervids, water buffalo, lowland tapir)*

571 They are adapted to frequent wetlands: interdigital membranes, extended hooves  
572 or relatively long limbs, their nose may function as a snorkel as in case of the  
573 tapir. They consume submerged vascular plants; this is a minor but seemingly  
574 important part of their diet, although also most of these species are data deficient  
575 when it comes to quantification of foraging on submerged angiosperms.

576           The ecosystem functions of large aquatic herbivores differ between these four  
577 groups (Fig. 2). The strongest impacts on submerged plant production, both positive and  
578 negative, are found for the fully submerged herbivore species that live most closely  
579 associated with submerged angiosperms (Fig. 1a). Both the fully submerged grazers and  
580 the swans (Fig. 1b) can reduce plant standing crop considerably, which is also due to  
581 their habit of foraging on belowground plant parts. The removal or reduction of plant  
582 beds has flow-on effects on other fauna, mostly reducing their abundance. The central-  
583 place foragers (Fig. 1c) that forage mostly on land, typically create gradients of grazing  
584 pressure, most intense in or close to the water and less intense further away on land  
585 (Lock 1972, Fryxell 1999, Kanga et al. 2013). As a result they create strong spatial  
586 heterogeneity in vegetation structure (see Fig. 1c), which has positive effects on other  
587 flora and fauna. It should be noted that no data are available for capybara's.  
588 Unsurprisingly, both beavers and hippopotamuses (category c) also have the strongest  
589 geomorphological and hydrological engineering effects.

590           The transport of nutrients and dispersal of submerged angiosperm propagules is  
591 closely linked to the travelling distance of the animals as well as their targeted  
592 movement between habitats or habitat patches (Bauer and Hoye 2014, Green and  
593 Elmberg 2014). Semi-aquatic species have strong roles linking aquatic and terrestrial  
594 habitats and import nutrients mainly into the water (category b and c) or on land  
595 (category d). Long distance migrants (category a and b) can be of particular importance  
596 in propagule dispersal between unconnected habitat patches; large terrestrial herbivores  
597 moving between aquatic habitats in their large home ranges (category d) likely also  
598 perform this function, but data on their role as dispersal agents of submerged vascular  
599 plants are lacking.

600

601 *Trophic downgrading and ecosystem collapse*

602           Whereas large aquatic herbivores have a number of important ecosystem effects,  
603 their actual impact depends strongly on their density (Wood et al. 2012a, Kelkar et al.  
604 2013b). Where the largest herbivores (> 1000 kg), such as elephants and rhinoceroses,  
605 are considered to be predation free due to their size (Owen-Smith 1988), at least as  
606 adults, most aquatic large herbivores are too small (< 500 kg, see Table 1) to be  
607 completely predation free under natural conditions. Large roving predators may have  
608 direct impact on the survival of large aquatic herbivores, but even more so through their  
609 indirect effect of inducing a landscape of fear where foraging movements of herbivores  
610 are restricted to less risky habitats (Burkholder et al. 2013). Of the large aquatic  
611 herbivores only the hippopotamus is a true megaherbivore (>1000 kg), which may be  
612 considered predation free under natural conditions. However, other species of large  
613 aquatic herbivores like dugongs or green turtles are seldom predated in today's waters  
614 due to the lack of predators. Indeed, megafauna is generally declining, and this decline  
615 is not random. The largest species typically experience the strongest decline (Dirzo et  
616 al. 2014, Ripple et al. 2015), but also, predators decline faster than herbivores (Estes et  
617 al. 2011, McCauley et al. 2015). This has led to the phenomenon of trophic  
618 downgrading, where the relative abundance of herbivores increases, due to the faster  
619 decline of predators and a subsequent release from predation (Estes et al. 2011). A  
620 similar effect is observed when herbivores are protected from hunting or other forms of  
621 human disturbance and there are no natural predators to compensate for the release of  
622 hunting pressure. In these cases, herbivores can become locally very numerous, and  
623 exert very strong grazing pressure on the submerged vegetation, such as in marine  
624 reserves, where locally large populations of green turtles can seriously threaten  
625 ecosystem stability by removing seagrass beds, which could lead to ecosystem collapse

626 (Christianen et al. 2014, Heithaus et al. 2014). This is because, unlike most terrestrial  
627 megaherbivores, many aquatic species (both marine and fresh water) consume not  
628 merely the above-ground biomass but sometimes target the below-ground storage of the  
629 primary producers that structure aquatic plant communities. It is well established that  
630 these belowground reserves are critical to ensure the buffer capacity of these ecosystem,  
631 and by targeting these reserves large aquatic herbivores may contribute to considerable  
632 ecosystem instability in the systems they inhabit. Similarly, very high densities of  
633 hippopotamus result in hypertrophic pools and rivers (Subaluski et al. 2015),  
634 particularly at periods of low water levels, which can result in algal blooms, anoxia and  
635 fish kills (Pennisi 2014). In some instances, ecosystems modified by large aquatic  
636 herbivores go through a pattern of rotational collapse and recovery, spurred by large-  
637 scale movements of herbivore populations (Arthur et al. 2013, Heithaus et al. 2014). In  
638 other cases, systems may even collapse beyond recovery thresholds. A confinement of  
639 large aquatic herbivores to reserves, without the possibility to follow their natural  
640 migration patterns, and a lack of natural predation in combination are the root cause of  
641 recorded detrimental effects of large herbivore grazing and the collapse of entire plant  
642 beds. Other species have recovered successfully from population declines, such as the  
643 mute swan, which has expanded its range through introductions in new habitats,  
644 particularly the USA. Here, the mute swan is an exotic species and rapidly increasing in  
645 population size, with concomitant effects on submerged plant beds (Conover and Kania  
646 1994, Tatu et al. 2007, Gayet et al. 2014).

647

648 *Conserving large aquatic herbivores and the ecosystems they rely on*

649           Taken together, this evaluation raises important questions for the management of  
650 large marine and freshwater herbivores. Many of these species are globally threatened  
651 and conserving their populations is a critical concern. As a first, for large herbivores,  
652 their size itself becomes a clear threat as has already been observed in terrestrial large  
653 herbivores (Dirzo et al. 2014). Large animals are more difficult to conserve because  
654 they have higher food requirements, larger home ranges, longer life spans and lower  
655 reproductive success among other size-specific traits that limit their reproduction and  
656 impede conservation efforts (Owen-Smith 1988). Large aquatic herbivores have to deal  
657 with additional issues. They have, on average, larger home ranges (Peters 1983,  
658 McCauley et al. 2015) that makes conservation a significant challenge as species move  
659 freely between different conservation jurisdictions (Bauer and Hoye 2014). Unlike their  
660 terrestrial counterparts, large aquatic herbivores cannot be protected with fences within  
661 restricted areas where protection can be maximized; most marine protected areas are not  
662 large enough to protect these species (McCauley et al. 2015). This results in locally  
663 difficult-to-resolve artefacts, such as the dilemma how freshwater plant beds can be  
664 restored in the presence of manatees, which immediately consume newly planted shoots  
665 – whereas they also rely on healthy meadows for survival (Hauxwell et al. 2004b).

666

## 667 *Conclusions*

668           It is clear that large herbivores that feed on aquatic systems can be critical  
669 ecosystem engineers, with the ability to modify both direct and indirect functional  
670 pathways in the ecosystems they inhabit. It is evident that extant aquatic herbivores may  
671 play roles very similar or even greater than their terrestrial counterparts and, in  
672 conditions of decline or over-abundance, may precipitate large, ecosystem-wide effects,

673 including entire collapse (Strong 1992, Shurin et al. 2006). Management of large  
674 aquatic herbivores requires a careful understanding of the roles they play in aquatic  
675 vascular plant communities. Currently we know very little about the ecosystem impacts  
676 of some of the most charismatic animals in the world, such as manatees, dugongs, sea  
677 turtles, hippopotamuses and swan species, and next to nothing about some less  
678 charismatic animals, such as capybara, water buffalo, lowland tapir and swamp and  
679 marsh deer. Tourism alone could be an ecosystem service that economically justifies the  
680 preservation of charismatic large aquatic animals (Sala et al. 2013, Roman et al. 2014).  
681 However, beyond conserving these species as flagships, we need further studies to  
682 examine how best to manage the populations of large aquatic herbivores at appropriate  
683 scales, keeping in mind the capacity of extant aquatic plant communities to sustain these  
684 populations. Furthermore, a much better understanding of their roles in aquatic  
685 ecosystems is warranted. This will help understand the ecology of aquatic vascular  
686 plants and their habitats that have evolved in the presence of a diversity of large aquatic  
687 and semi-aquatic herbivores, and will lead to a better appreciation of the importance to  
688 strive for the conservation of complete ecosystems.

689

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1146 **Table 1.** List of large aquatic and semi-aquatic herbivores (>10 kg) that consume submerged angiosperms, with indication of their body mass, home range,  
 1147 diet and conservation status, according to IUCN. EN- endangered, VU-vulnerable, LC- least concern. Several other large herbivore species occasionally  
 1148 consume submerged angiosperms, including other cervids, mainly based on availability and comprising only a minor fraction of their diets, as far as data are  
 1149 available. **Sources:** Data on habitat, diet and range for mammals from MacDonald (2001), for waterbirds from Kear (2005), for turtles the Encyclopaedia of  
 1150 Life (EOL www.eol.org); data supplemented with references indicated in the Table. Data on conservation status, population size and population trend from  
 1151 IUCN: The IUCN Red List of Threatened Species. Version 2014.3. www.iucnredlist.org. Downloaded on 26 January 2015.

English name	Latin name	Habitat	Geographic range	Home range (km <sup>2</sup> ) and migration	Diet selection	Body mass (kg)	Conservation status; population size; -trend (IUCN)
Green sea turtle	<i>Chelonia mydas</i> (L.)	Marine; fully aquatic	Circumglobal, tropical-subtropical	4-39 (Seminoff et al. 2002); migratory	Herbivorous: mostly seagrass, algae, but also cnidarians, mangroves (Cardona et al. 2009, Reisser et al. 2013)	68–190	EN; unknown number; declining
Loggerhead sea turtle	<i>Caretta caretta</i> (L.)	Marine; fully aquatic	Circumglobal, tropical-subtropical	300-1900 (Marcovaldi et al. 2010); migratory	Omnivorous: Seagrass, algae, cnidarians and other invertebrates	80-200	EN; population size and trend unknown
Amazonian manatee	<i>Trichechus inunguis</i> (Natterer)	Freshwater; floodplain lakes, rivers and	Amazon river drainage basin	Unknown; resident	Herbivorous: Emergent, floating or submerged mostly freshwater	120-270	VU; population size and trend unknown

		channels; fully aquatic			vegetation		
West-Indian manatee (subspecies: Florida and Caribbean)	<i>Trichechus manatus</i> (L.)	Marine to freshwater; shallow coastal waters, estuaries and rivers; fully aquatic	Atlantic coast from Florida and Caribbean to central Brazil	202-5156 (Castelblanco-Martínez et al. 2013); migratory	Herbivorous: Seagrass, algae, cnidarians, freshwater macrophytes, mangroves	200-600	VU; <10.000 animals, declining
West African manatee	<i>Trichechus senegalensis</i> (Link)	Marine to freshwater; similar to West-Indian manatee; fully aquatic	West-Africa (Senegal to Angola)	Unknown; resident	Herbivorous (mostly); seagrass and other marine and freshwater plants	450	VU: population size and trend unknown
Dugong	<i>Dugong dugon</i> (Müller)	Marine; coastal shallows; fully aquatic	South-West Pacific Ocean and Indian Ocean	4.1-43.4 (Iongh et al. 1998, Sheppard et al. 2010); resident	Herbivorous: mostly seagrass (above and belowground biomass)	290-360	VU; population size and trend unknown
Mute swan	<i>Cygnus olor</i> (Gmelin)	Lakes, rivers, freshwater and brackish marshes; semi-aquatic	Eurasia	Mostly resident, can be migratory (<200 km) EOL	Submerged and emergent aquatic vegetation, grasses and cereals, below-ground parts of aquatic plants infrequently (Bailey et al. 2008)	7-16	LC; 600.000-610.000 animals; increasing

Trumpeter swan	<i>Cygnus buccinator</i> (Richardson)	Freshwater and brackish wetlands; semi-aquatic	North America	Migratory (>200 km) EOL	Aquatic vegetation, cereals and root crops	9.5-13.5	LC; population size unknown; increasing
Whooper swan	<i>Cygnus cygnus</i> (L.)	Wetlands; semi-aquatic	Eurasia	Migratory (>200 km, even 945 km) (Gardarsson 1991)	Omnivorous; mostly aquatic vegetation, cereal crops, mussels	7.4-14	LC; >180.000 animals; trend unknown
Capybara	<i>Hydrochoerus hydrochaeris</i> (L.)	Freshwater; flooded savanna or grassland next to water holes, also along poles and rivers in tropical forest; semi-aquatic	South-America	0.1-0.3; resident	Herbivorous, mostly (aquatic) grasses (Do Valle Borges and Gonçalves Colares 2007, Corriale et al. 2011, Desbiez et al. 2011), coprophagy (Borges et al. 1996)	50	LC, regulated hunting and harvesting; population size and trend unknown
Hippopotamus	<i>Hippopotamus amphibius</i> (L.)	Freshwater; short grasslands (at night), rivers, wallows and lakes (by day); semi-aquatic	Sub-Saharan Africa	Hippos seldom travel more than 2–3 km from water to feed (Lock 1972, O'Connor and Campbell 1986); resident	Herbivorous (mostly); terrestrial grasses (de Iongh et al. 2011) and dicots (Codron et al. 2007, Cerling et al. 2008, Michez et al. 2013), supplementary aquatic vegetation (Grey and Harper 2002)	1600-3200	VU; 125.000-150.000 animals; declining
Pygmy hippopotamus	<i>Hexaprotodon liberiensis</i>	Lowland forests and swamps;	West Africa	0.4-1.5 (Roth et al. 2004); resident	Herbivorous; fallen fruits, ferns, dicots and grasses	180-275	EN; <2000-3000 animals;

	(Morton)	semi-aquatic					declining
North American beaver	<i>Castor canadensis</i> (Kuhl)	Riparian wetlands; semi-aquatic	North America	0.04-0.25 (Bloomquist et al. 2012); resident	Herbivorous; wood, grasses, roots (Parker et al. 2007, Severud et al. 2013a, b)	13-32	LC; population size unknown; stable
Eurasian beaver	<i>Castor fiber</i> (L.)	Riparian wetlands; semi-aquatic	North West and Central Eurasia	-; resident	Herbivorous; woody plants, herbs, grasses, roots (Krojerová-Prokešová et al. 2010, Law et al. 2014)	13-35	LC; > 639.000 animals; increasing
Lowland tapir	<i>Tapirus terrestris</i> (L.)	Freshwater; lowland rain forest and lower montane forest; largely terrestrial	South America	Big; resident	Herbivorous; leaves, fruits, seeds, stems, aquatic plants (Allin et al. 2011, Chalukian et al. 2013, Prado et al. 2013)	150-250	VU; population size unknown, decreasing
Wild water buffalo	<i>Bubalus arnee</i> (Kerr)	Freshwater; near and in large rivers in grass jungles and marshes, riparian forests; largely terrestrial	India and (South East) Asia	3.6 EOL; resident	Herbivorous; predominately a grazer on grasses; also eats herbs; aquatic plants, leaves, agricultural crops	800-1200	EN; <4000 or <200 or no purebreds existent; decreasing
Moose	<i>Alces americanus</i>	Freshwater; boreal and mixed	North-America	27.6-42.9 (Murray et al. 2012); resident	Herbivorous; both terrestrial and aquatic	360-800	LC; population size unknown;

	(Clinton)	deciduous forests; largely terrestrial			vegetation		stable
Eurasian elk	<i>Alces alces</i> (L.)	Freshwater; boreal and mixed deciduous forests; largely terrestrial	Northern Europe and Russia	15.6-52.2 (Olsson et al. 2010); resident	Herbivorous; both terrestrial and aquatic vegetation (Ohlson and Staaland 2011)	270- 770	LC; ~1.5 million animals; increasing
Marsh deer	<i>Blastocerus dichotomus</i> (Illiger)	Freshwater; marshes, floodplains, savannas; largely terrestrial	Central Brazil to North Argentina	Unknown; resident	Herbivorous; aquatic plants (Tomas and Salis 2000, Allin et al. 2011)	89- 125	VU; population size; decline
Swamp deer (Barasingha)	<i>Cervus duvaucelii</i> (G. Cuvier)	Freshwater; swamps, grassy plains; largely terrestrial	North and Central India, South Nepal	14.1-20  Can walk 2-3 km straight line daily (Nandy et al. 2012); resident	Herbivorous; mostly grasses, some woody species (Wegge et al. 2006) and aquatic plants	172- 181	VU; 3500-5100 animals; declining

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1154 **Table 2.** Impact of large aquatic herbivores on submerged angiosperm abundance and species composition. “-“ No data available. Data refer to natural  
 1155 vegetation, apart from the first study, where *Trichechus manatus* consumed introduced *Vallisneria* plants.

Herbivore	Location	Herbivory rate	Effects on					References
			Plant height	Shoot density and cover	Above-ground biomass	Below-ground biomass	Species composition	
<i>Trichechus manatus</i>	Central and North America	80% of introduced <i>Vallisneria americana</i> consumed	-	-		-	-	(Hauxwell et al. 2004b)
<i>Dugong dugon</i>	Indian, Pacific oceans	15% of primary production consumed (range 4-40 %)	-	50-87% lower shoot density	60-86 % removal	51-75 % decrease	Changes in species composition	(Heinsohn et al. 1977, Preen 1995, Masini et al. 2001, Skilleter et al. 2007)
<i>Chelonia mydas</i>	Indian, Pacific, Atlantic oceans	40-200% of primary production consumed	40-70% reduction	45-67% decrease in shoot density	40% removal	65 % reduction	Changes in species composition	(Moran and Bjorndal 2005, Christianen et al. 2012, 2014, Arthur et al. 2013, Burkholder et al. 2013, Kelkar et al. 2013a, b, Heithaus et al. 2014)
<i>Cygnus olor</i>	North	30-60% of	40%	0-79%	0-95% reduction	0-34%	Changes in	(Conover and Kania 1994,

	America, Europe	primary production consumed	reduction	reduction in cover 76% reduction in shoot density		reduction	species composition 0- ~20% reduction in diversity	Allin and Husband 2003, O'Hare et al. 2007, Tatu et al. 2007, Hidding et al. 2009, 2010a, b, Gayet et al. 2011, 2012, Wood et al. 2012b, Stafford et al. 2012)
<i>Cygnus buccinator</i>	North America	-	-	-	No effect of spring tuber grazing on aboveground biomass in summer	24% reduction	Changes in species composition	(LaMontagne et al. 2003)
<i>Castor canadensis</i> and <i>C. fiber</i>	North America, UK	-	-	-	45-60% reduction*	-	Changes in species composition* 70% increase in species richness*	(Ray et al. 2001, Parker et al. 2007, Law et al. 2014)
<i>Alces americanus</i>	North America	-	-	-	45% reduction	-	Lower species richness (72%) and diversity (95%) in grazed plots	(Qvarnemark and Sheldon 2004)

1156 \* mixed emergent and submerged species.

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1158 **Table 3.** Ecosystem functions of large aquatic herbivores.

<b>Ecosystem Function</b>	<b>Specific Function</b>	<b>Description</b>	<b>Species (plus references)</b>
<i>Habitat modification</i>	Altering the structure of plant beds	Decreased structure (biomass, density, or canopy height of plants), grazing lawn formation	Hippopotamus, dugong, green turtle, mute swan, moose  (Lock 1972, Eltringham 1974, Preen 1995, Qvarnemark and Sheldon 2004, Källander 2005, Verweij et al. 2006, O’Hare et al. 2007, Skilleter et al. 2007, Tatu et al. 2007, Hidding et al. 2009, Arthur et al. 2013)
	Increasing access to food source	Digging up belowground plant parts or removing tough green plant structures which benefits smaller herbivores (feeding facilitation)	Hippopotamus, whooper swans  (Källander 2005, Gyimesi et al. 2012, Kanga et al. 2013)
	Increasing heterogeneity in the landscape	Increasing structural diversity of the habitat that benefits other species (habitat facilitation)	Beaver, hippopotamus, swan  (Eltringham 1974, Wright et al. 2002, Källander 2005, Verweij et al. 2006, Waldram et al. 2008, Gyimesi et al. 2012, Kanga et al. 2013, Nummi and Holopainen 2014)
	Impairing habitat for other species	Decreasing habitat structural complexity that harms other species (habitat destruction)	Dugong, green turtles, swans  (Marklund et al. 2002, Skilleter et al. 2007, Arthur et al. 2013)
	Habitat collapse	Trophic cascades and potential ecosystem collapse	Dugong, green turtles  (Skilleter et al. 2007, Christianen et al. 2014)

<i>Production modification</i>	Increasing primary production	Increasing primary production of submerged plants	Green turtle, dugong, whooper swan  (Preen 1995, Nolet 2004, Moran and Bjorndal 2005, Aragones et al. 2006, Kuiper-Linley et al. 2007, Valentine et al. 2014)
	Decreasing primary production	Suppressing primary production	Green turtle, dugong, black swan  (Gruner et al. 2008, Hillebrand et al. 2009, Poore et al. 2012, Dos Santos et al. 2012, Kelkar et al. 2013a)
<i>Nutrient cycle modification</i>	Nutrient cycling enhancement	Increasing nutrient recycling by consumption, increasing compensatory growth in plants, increasing or decreasing nutrient content in plants	Green turtle, dugong  (Moran and Bjorndal 2006, Aragones et al. 2006)
	Nutrient export to other habitats	Transport of nutrients by commuting animals between patches or habitats or from aquatic to terrestrial habitats or vice versa	Green turtle, waterfowl, swan, hippopotamus, moose, beaver  (Wolanski and Gereta 1999, Rosell et al. 2005, Hahn et al. 2008, Bump et al. 2009, Mosepele et al. 2009, Chaichana et al. 2010, Vander Zanden et al. 2012, Wood et al. 2013, Pennisi 2014, Subaluski et al. 2015)
	Nutrient alleviation	Reduction of nutrient stress in the system under high nutrient loads	Green turtle  (Christianen et al. 2012)
<i>Transport</i>	Transport of other	Dispersal of aquatic plants and animals	Swans, moose

<i>modification</i>	organisms	through endo- and exozoochory	(Clausen et al. 2002, van Leeuwen et al. 2012, Jaroszewicz et al. 2013, Green and Elmberg 2014)
<i>Geomorphological modification</i>	Geomorphological engineering	Dam creation	Beaver  (Naiman et al. 1986, Wright et al. 2002, Rosell et al. 2005)
		Increasing burial, holes, wallows and trails, increasing erosion and trampling impacts, maintaining ponds during draw periods	Hippopotamus, green turtle, moose, elk, beaver, dugongs, water buffalo  (Luckenbach 1986, Naiman and Rogers 1997, McCarthy et al. 1998, MacDonald 2001, Deocampo 2002, Skilleter et al. 2007, Mosepele et al. 2009, Grey and Jackson 2012, Heithaus et al. 2014, Hood and Larson 2015)
	Hydrological engineering	Altering water levels and flow of water through the landscape by construction work	Beaver, hippopotamus  (McCarthy et al. 1998, Mosepele et al. 2009, Marshall et al. 2013, Hood and Larson 2015)
	Mixing of water layers	Improving oxygen availability through moving water	Hippopotamus  (Wolanski and Gereta 1999, Pennisi 2014)
		Re-suspending sediment and increasing of water turbidity	Dugong, green turtle, waterfowl  (Skilleter et al. 2007, Christianen et al. 2014, Green and Elmberg 2014)

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1162 **Figure captions**

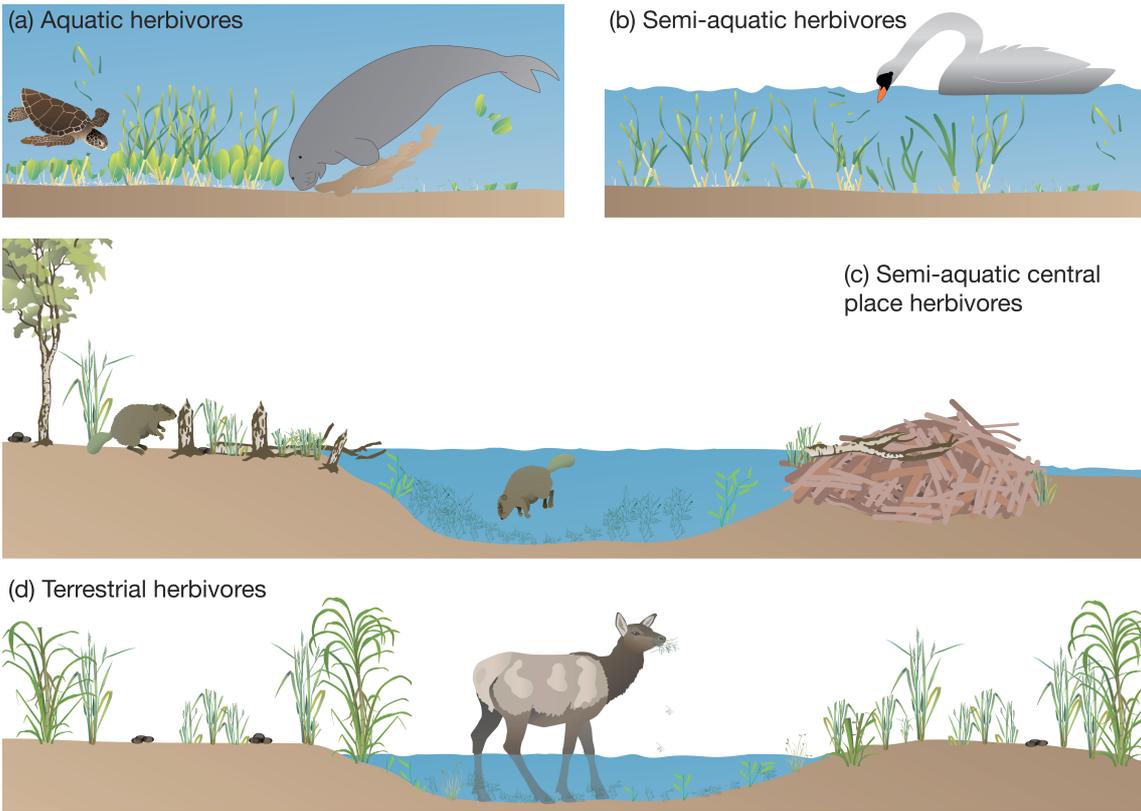
1163 **Fig. 1.** Large aquatic herbivore categories: (a) Fully aquatic herbivores (dugongs, turtles  
1164 and manatees) that live and forage under water. They may be resident or migrant. They  
1165 strongly impact plant beds, especially if resident. They may transport nutrients and plant  
1166 material within their large home range. (b) Semi-aquatic species (swans) adapted to life  
1167 on water, but that frequent both water and terrestrial habitats. They usually display  
1168 migration behaviour. (c) Semi-aquatic central place foragers (hippopotamus, beaver,  
1169 capybara). They are residents and have strong impacts on plants within their core areas.  
1170 (d) Terrestrial species that frequent aquatic habitats (cervids, water buffalos, lowland  
1171 tapir) in search of food supplements/complements (e.g. sodium).

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1173 **Fig. 2.** Ecosystem processes modified by large aquatic herbivores. The figure provides a  
1174 key to the range of impacts and functions that are mediated by the four aquatic  
1175 herbivore functional groups (see Fig. 1). The colour codes associated with each  
1176 functional group refer to the processes listed in the key on the left. See Table 3 for  
1177 species-specific details of functional roles and impacts.

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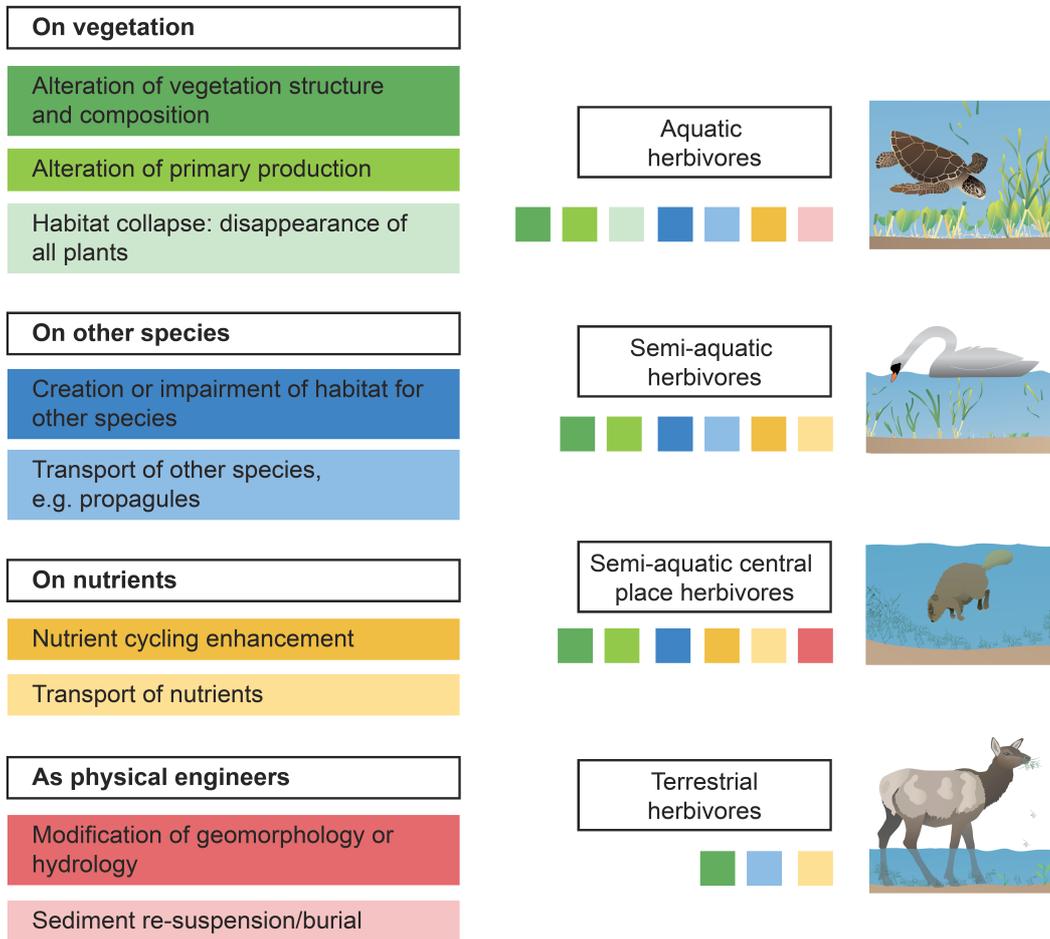
1179 Figure 1



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### Ecosystem impacts and functions



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