

1 **Herbivores enforce sharp boundaries between terrestrial and aquatic ecosystems**

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23 **Author contributions:** ESB, JMS and WR conceived the study, ESB, GFV, JMS and NH
24 performed the research, GFV and JMS analyzed data, ESB and JMS wrote the paper.

25

26 **Running head:** Grazing and environment shape sharp ecotones

27 **Abstract**

28 The transitions between ecosystems (ecotones) are often biodiversity hotspots, but we know little
29 about the forces that shape them. Today, often sharp boundaries with low diversity are found
30 between terrestrial and aquatic ecosystems. This has been attributed to environmental factors
31 that hamper succession. However, ecosystem properties are often controlled by both bottom-up
32 and top-down forces, but their relative importance in shaping riparian boundaries is not known.

33 We hypothesize that 1) herbivores may enforce sharp transitions between terrestrial and
34 aquatic ecosystems by inhibiting emergent vegetation expansion and reducing the width of the
35 transition zone and 2) the vegetation expansion, diversity and species turnover are related to
36 abiotic factors in the absence of herbivores, but not in their presence. We tested these
37 hypotheses in 50 paired grazed and ungrazed plots spread over ten wetlands, during two years.
38 Excluding grazers increased vegetation expansion, cover, biomass and species richness. In
39 ungrazed plots, vegetation cover was negatively related to water depth whereas plant species
40 richness was negatively related to the vegetation N:P ratio. The presence of (mainly aquatic)
41 herbivores overruled the effect of water depth on vegetation cover increase but did not interact
42 with vegetation N:P ratio. Increased local extinction in the presence of herbivores explained the
43 negative effect of herbivores on species richness, as local colonization rates were unaffected by
44 grazing.

45 We conclude that (aquatic) herbivores can strongly inhibit expansion of the riparian
46 vegetation and reduce vegetation diversity over a range of environmental conditions.
47 Consequently, herbivores enforce sharp boundaries between terrestrial and aquatic ecosystems.

48

49 **Keywords**

50 Biodiversity, Ecotone, Herbivory, Nutrient availability, Riparian vegetation, Species turnover,
51 Succession, Spatial patterns, Transition zones, Vegetation N:P ratio, Water depth.

52 **Introduction**

53 It is increasingly recognized that ecological transition zones or ecotones between habitat patches
54 or ecosystems should be regarded as separate entities as they can play a critical role in
55 controlling or modifying flows of organisms and material between bordering ecosystems
56 (Cadenasso and Pickett 2000; Yarrow and Marin 2007). Although a lot of progress has been
57 made in conceptualizing key concepts and terminology, less is known about the ecological
58 processes that shape ecotones and their, often high, biodiversity (Yarrow and Marin 2007).

59 The transition between freshwater and terrestrial systems (the riparian zone) is
60 characterized by a relatively high floral and faunal species richness and is therefore considered a
61 diversity hotspot in the landscape (Nilsson and Svedmark 2002). Despite their relatively small
62 size, riparian zones have disproportionately important functions for larger scale processes of both
63 biodiversity and biogeochemistry of the two bordering systems (Naiman and Decamps 1997;
64 Nilsson and Svedmark 2002). For instance, as they modulate the flux of particulate organic
65 matter into the aquatic system, their width influences the resilience of the bordering aquatic
66 system to regime shifts between alternative clear and turbid states (Sollie and others 2008). The
67 species richness of riparian zones is positively related to the width of the transition zone, as well
68 as its structural diversity of the vegetation (Sarneel and others 2011). Today, often sharp
69 boundaries with low diversity are found between terrestrial and aquatic ecosystems. This has
70 been attributed to a range of environmental and anthropogenic factors including eutrophication,
71 accumulation of toxic compounds and wave action (Lamers and others 2014), which inhibit
72 wetland plant growth. In the bordering aquatic and terrestrial systems it has been recognized that
73 both bottom-up (abiotic conditions) and top-down forces (consumer-prey relations) can strongly
74 influence plant growth, species turnover and succession (Olf and Ritchie 1998; Wassen and
75 others 2005; Bakker and others 2006). A recent meta-analysis showed that in terrestrial
76 ecosystems species richness generally increases with grazing and decreases with fertilization
77 level while in freshwater systems most often opposite relations are found with both grazing and
78 nutrient availability (Hillebrand and others 2007). Because of these contrasting effects in the
79 bordering systems, it is not immediately clear how, or whether, herbivores determine plant

80 diversity along a gradient from water to land and how, or whether, herbivores can shape the
81 riparian zone by modulating bottom-up control of the riparian vegetation.

82 In ponds, the riparian ecosystem is shaped by succession that, in the absence of
83 disturbances or management, causes open water to gradually fill with organic material after
84 successive colonization by submerged aquatic plants, emergent riparian vegetation, wetland
85 plants and trees (Liira and others 2010; Lamers and others 2014). This succession causes a very
86 species rich spatial vegetation zonation (Fig 1a). The phase with emergent vegetation plays a
87 crucial role for succession as it contains many ecosystem engineers that turn water into land
88 (Sarneel and others 2010; Hidding and others 2014). The emergent vegetation expansion rate
89 has been shown to increase with increasing nutrient availability and decrease with water depth
90 while vegetation diversity generally decreases with both increasing nutrient availability and water
91 depth (Wassen and others 2005; Sarneel and others 2010; Bornette and Puijalón 2011).
92 However, it has recently been shown that next to abiotic drivers, herbivores can have strong
93 negative effects on the establishment of riparian plant species (Veen and others 2013) and
94 influence community composition (Chaichana and others 2011). For early successional and
95 aquatic plant communities highly variable grazing effects have been found (Marklund and others
96 2002; Bakker and others 2013). Yet, possible interactions between top-down and bottom-up
97 effects as determinants for emergent vegetation expansion and community assembly in the
98 different zones of the riparian transition have not been addressed. In this study, we tested the
99 effect of herbivory on emergent vegetation expansion and riparian plant diversity and its relative
100 importance in relation to abiotic conditions (nutrient availability and water depth).

101 Whereas the impact of herbivory on emergent vegetation expansion may be direct
102 because they prefer and graze away the young expanding shoots and rhizomes (van den
103 Wyngaert and others 2003), the impact of herbivores on riparian plant species richness depends
104 on their effect on the balance between local colonization and extinction rates (Olf and Ritchie
105 1998; Bakker and others 2006). Herbivores can increase species richness when they enhance
106 colonization rates by transferring seeds between habitats (Figuerola and Green 2002) or by
107 creating bare soil for seedling establishment (Bakker and Olf 2003). Herbivores can also

108 increase species richness when they reduce local extinction by releasing plants from competition
109 by reducing the biomass of dominant species (Olf and Ritchie 1998). Conversely, they can
110 decrease species richness when they increase local extinction through selective feeding on
111 subordinate species (Gibson and Brown 1991). By affecting vegetation expansion, establishment
112 success and species dominance, both land-bound and aquatic herbivores have shown to be able
113 to accelerate, retard and deflect succession in different ecosystems such as arctic and temperate
114 salt marshes (Kuijper and Bakker 2005), boreal and temperate grasslands (Weltzin and others
115 1997; Speed and others 2013) and tundra's (Eskelinen and others 2012), but interactions
116 between grazing and abiotic factors as shaping forces of (riparian) transition zones remain largely
117 unknown (Speed and others 2013).

118 We tested the effect of herbivores on emergent vegetation expansion, riparian plant
119 diversity and species turnover in riparian ecosystems and addressed the potential interaction with
120 the two most important drivers of emergent vegetation expansion and riparian community
121 assembly (nutrient availability and water depth) in a field enclosure experiment in ten wetlands.
122 We hypothesize that 1) herbivores may enforce sharp transitions between terrestrial and aquatic
123 ecosystems by inhibiting emergent vegetation expansion and reducing the width of the riparian
124 transition zone and 2) the emergent vegetation expansion, diversity and species turnover of the
125 riparian ecotone are related to abiotic factors in the absence of herbivores, but not in their
126 presence, and that herbivores thus can overrule abiotic drivers of vegetation assembly and
127 succession.

128

129 **Methods**

130 **Experimental design**

131 We built enclosures in ten Dutch wetlands thereby covering a wide range of environmental
132 conditions (Table 1). We used the paired plot design frequently used in enclosure studies (Bakker
133 and others 2006; Gayet and others 2011; Eskelinen and others 2012; Veen and others 2013). In
134 each wetland we selected five banks representative of the area. The plots differed in aspect and
135 direction to the main wind direction and were mainly dominated by *Phragmites australis*, *Glyceria*

136 *maxima* and *Typha* species. We installed a paired enclosure and an open control plot accessible
137 for grazers on each of the 50 banks in March 2011 before the growing season started.

138 Each plot (3 m wide and 6 m long; See Fig. 1b) was placed at the edge of the marginal
139 wetland zone (fig 1a), perpendicular to the bank. The plots thus captured the whole transition
140 from water to land and included on average $79\% \pm 1.4$ S.E. ($n = 100$) open water to allow space
141 for expansion of emergent vegetation fringe.

142 Enclosures were made by building a fence of chicken wire (mesh size 2.5 cm) supported
143 by 6 poles. The fence protruded on average 1 m above the water and was firmly pushed into the
144 sediment, using pegs when necessary. On top we put thick orange wire in a cross pattern and
145 zigzag pattern to prevent grazing birds to enter from above. The accessible control plot was
146 marked with poles on the four corners. The paired enclosure and control plots had similar water
147 depth (Generalized Linear Mixed Model (GLMM); treatment effect: $\chi^2 = 0.001$, $P = 0.976$ see
148 'Data analyses') and initial vegetation cover (GLMM; treatment effect; emergent vegetation cover:
149 $\chi^2 = 0.39$, $P = 0.531$; floating and submerged vegetation cover: $\chi^2 = 0.77$, $P = 0.380$).

150

151 **Vegetation sampling**

152 In 2011, we sampled our control plots and enclosures regularly from April until August 2011 (0, 4,
153 8, 14 and 20 weeks respectively after establishing the plots). This revealed that peak standing
154 crop was reached in July (Appendix 1). In 2012, vegetation cover was therefore recorded before
155 the growing season started in March and at peak standing crop in July.

156 With each visit the total cover of emergent plants was estimated using cover classes that
157 increased with 10% and 3 extra classes for covers <10% (Following Braun Blanquet; Barkman
158 and others 1964). In July 2011 and 2012 we made detailed vegetation relevés of a transect which
159 ran through the middle of each plot (2 x 50 = 100 relevés; being 0.75 m wide and 6 m long; see
160 Fig. 1b). As measure of emergent vegetation expansion we measured the distance (m) between
161 the bank ward plot end and the most distant emergent shoot in the water for each plot and
162 calculated the emergent cover increase between July 2011 and 2012. In July 2011 and 2012 we
163 determined the percentage of stems that were damaged (with ripped off leaves and broken

164 stems, signs of grazing) from the ten stems of *Phragmites* and *Typha* that were most distant from
165 the bank (Fig 1b).

166 In August 2011 we harvested aboveground biomass (a circular 0.2 m² area) from three
167 locations next to each riparian transect. One sample was taken within the marginal wetland zone,
168 another one on the edge of the emergent vegetation fringe and the last one in the open water
169 (respectively ± 1, 3 and 5 m from the bank ward plot end, see Fig 1b). The biomass samples
170 were taken to the lab, rinsed to remove mud and algae, sorted to species, dried (48 hours at 60
171 °C) and weighed. In July 2012, we collected a sample of 0.2 m² of the marginal wetland zone
172 inside the exclosures and weighed the total biomass after drying (48 hours at 60 °C).

173

174 **Habitat characteristics**

175 We determined the most important habitat characteristics that determine the growth and diversity
176 of freshwater plant communities (reviewed by Bornette and Pujalon 2011), standing biomass
177 (described before) and herbivore densities.

178

179 *Nutrients*

180 The ratio between nitrogen (N) and phosphorus (P) concentrations in the aboveground plant
181 biomass has been shown to be an important predictor of wetland plant diversity (Koerselman and
182 Meuleman 1996; Gusewell and others 2003; Fujita and others 2014), even though the underlying
183 mechanisms remain to be resolved (for discussion on the interpretation of N:P-ratios see Fujita
184 and others 2014). We analyzed N and P content of the biomass samples taken from the marginal
185 wetland zone of the exclosures in 2011 and 2012 (see 'vegetation sampling'). After grinding the
186 samples, N concentration (% of dry weight) was determined by combustion, using a FLASH 2000
187 Organic Elemental Analyzer (Interscience, Breda, the Netherlands). P-content (% of dry weight)
188 was determined through acid digestion (with 2% persulphate; 30 min at 121 °C) after incinerating
189 the samples for 30 min at 500 °C. The digested samples were analyzed using a QuAAtro
190 segmented flow analyzer (Seal analytical Inc., Beun de Ronde, Abcoude).

191

192 *Water*

193 Water depth (m) was measured in the plots at every meter along a 6 m long transect in April
194 2011. Depths were averaged to obtain the initial water depth per plot. With use of daily water
195 level fluctuations measurements (measured with pressure data loggers; van Essen instruments,
196 Delft, the Netherlands) we calculated the average water depth during our study period in each
197 enclosure and control plot. From the water level data we also calculated the range of water level
198 fluctuations (the 5 – 95% range; in m). As a measure of wave exposure of the plots we
199 determined wind fetch by calculating the weighted mean of the distances of open water (m) in
200 front of the sample point in a range of -42° to +42° (in 6 ° increments) from the prevailing wind
201 direction (obtained from the Royal Netherlands Meteorological Institute; KNMI).

202 We collected 100 ml water samples in each control plot in June 2011. We fixed 5 ml with
203 glutaraldehyde within 12 hours (final concentration 0.025% by mass) and measured algae
204 concentrations ($\mu\text{g l}^{-1}$) using a Phyto-PAM (Heinz Walz GmbH, Effeltrich, Germany). We
205 determined transparency of the surface water of the control plots with a Secchi disk (m) in July
206 2011.

207

208 *Herbivores*

209 We measured the density of potential herbivores in each study area by counting the herbivorous
210 waterfowl that we encountered (which were Mallards, Greylag geese, Mute swans and Coots)
211 upon each field visit in 2011 (5 visits).

212 Four of the ten wetland areas were grazed by livestock (cows and sheep) during a part of
213 the growing season. However, livestock were discarded from the analyses as almost all
214 enclosures were placed at locations where livestock could not reach the expanding vegetation
215 fringe (Appendix 2). In two cases where they could, they destroyed the enclosures; these plots
216 were excluded from the analyses (Appendix 2).

217 Muskrat densities were calculated as number of muskrats caught per year by muskrat
218 catchers in 2011 and 2012 (data obtained from Hoogheemraadschap De Stichtse Rijnlanden).

219 Waterfowl and muskrats densities were expressed for each species in kg body mass ha⁻¹ (Proulx
220 1997; Wood and others 2012) and summed to obtain a measure of aquatic herbivore density.

221

222 **Data analyses**

223 We analyzed vegetation cover, species richness and vegetation diversity in control plots and
224 exclosures for all species and separately for emergent and floating and submerged species at
225 peak standing crop in July 2011 and 2012. Shannon species diversity indexes were calculated
226 with R 2.15.2 (R_Core_Team 2013) using the package Vegan . As a measure of vegetation
227 expansion and grazing impact we further analyzed the distance of the furthest stem in July 2012,
228 emergent cover increase between July 2011 and 2012 and the percentage of damaged stems in
229 July 2012. Two measures of species turnover were calculated: the proportion of species in the
230 transect that went locally extinct (i.e. were found in 2011 but not in 2012) and that colonized the
231 transect (i.e. were found in 2012 but not in 2011), both as percentage of the total species
232 richness found for each transect in July 2011 (following Merritt and others 2010). Homogeneity of
233 variance was tested with a Levene's test, and normal distribution of the residuals was tested with
234 a Shapiro Wilk's test in R 2.15.2. Arcsine and Ln+1 transformations were applied to improve
235 homogeneity and normality (indicated in Table 2).

236 The overall effect of exclosure treatment on the vegetation parameters, expansion and
237 species turnover was analyzed with generalized linear mixed models (GLMM) in the package
238 lme4 in R 2.15.2, using maximum likelihood estimation (analysis 1, A1). To correct for the block
239 structure of our experimental setup, we added a random factor that nested paired plots within
240 area (see also Veen and others 2013). To determine effects of our fixed factor (exclosure
241 treatment) we used a likelihood ratio test to compare models with and without the variable of
242 interest (Crawley 2007). Furthermore, to test the effect of exclosure treatment on biomass in the
243 different parts of the riparian transect, we used GLMM including the fixed factors (exclosure
244 treatment and location along the transect) and a random factor accounting for the nested
245 structure of the samples in the transect (A2). We used likelihood ratio test to compare models
246 with and without the fixed factors and their interaction.

247 We performed multiple stepwise regressions (in SPSS 19.0; IBM Corporation, Armonk,
248 New York) to select which of the environmental variables determined increase of emergent cover
249 and species turnover (A3). Based on this analysis we selected water depth and vegetation N:P
250 ratio (Appendix 3) to further analyze the hypothesized interactive effects of these environmental
251 conditions and grazing on emergent cover and riparian species richness. We performed an
252 ANCOVA analysis in R (A4), using GLMM models with a random effect for the block structure of
253 our set up (as in A1) and subsequent maximum likelihood estimation tests to compare models (as
254 in A1).

255

256 **Results**

257 *Grazing effects on vegetation dynamics*

258 Vegetation expansion (distance of the furthest stem) was higher inside the enclosure after two
259 years (Ln+1 transformed, GLMM, $\chi^2 = 25.72$, $P < 0.001$, Fig. 1a), while the number of damaged
260 stems was lower there (Ln+1 transformed, GLMM, $\chi^2 = 80.20$, $P < 0.001$, Fig. 1b). Over the two
261 years, the emergent vegetation cover increased more in the enclosures than in the control plots
262 (Ln+1 transformed, GLMM, $\chi^2 = 22.55$, $P < 0.001$, Fig. 1c). More specifically, the emergent cover
263 in the control plots did not change over the years (One-sample t-test on cover change in control
264 plots, $P = 0.41$) while the increase was significantly higher than 0 in the enclosures (One-sample
265 t-test, $P < 0.001$).

266

267 *Grazing effects on vegetation abundance and diversity*

268 Total cover, total species richness and species diversity of the vegetation transects was
269 significantly higher in enclosure than in control plots for both 2011 and 2012 (Fig. 2, Table 2). This
270 pattern was consistent (and significant for cover and species richness) within both the emergent
271 and floating and submerged species (Table 2). Species composition changed over the years and
272 on average 30% of the species observed in 2011 were replaced by other species in 2012. The
273 proportion of species that was found in 2012 but not in 2011, and thus must have colonized the
274 surveyed transect, did not differ between enclosure treatments, but the proportion of species that

275 disappeared from the surveyed transect between 2011 en 2012 was significantly higher in the
276 control plots (GLMM, $\chi^2 = 5.50$, $P = 0.019$, Fig. 2d) compared to the exclosures.

277

278 *Grazing effects across the successional gradient*

279 Exclosure effects were consistent in the biomass samples of all three spatial sub locations of the
280 surveyed transect (Fig. 3). Plant standing crop decreased over the gradient from the marginal
281 wetland to open water (Fig. 3a) but was consistently higher in samples from the exclosures
282 (GLMM; Sub location effect; $\chi^2 = 174.12$, d.f. = 2, $P < 0.001$; Exclosure treatment effect $\chi^2 =$
283 32.48, d.f. = 1, $P < 0.001$; no significant interaction). Species richness of the harvested biomass
284 samples decreased towards the open water (Fig. 3b) and the species richness seemed higher in
285 the exclosures, but this was not significant (GLMM, Sub location effect; $\chi^2 = 62.34$, d.f. = 2, $P <$
286 0.001; Exclosure treatment effect; $\chi^2 = 3.30$, d.f. = 1, $P = 0.069$; no significant interaction).

287

288 *Grazing effects across environmental gradients*

289 The vegetation N:P ratio and water depth appeared as the two most important environmental
290 variables related to emergent vegetation cover and riparian species richness (Appendix 3).
291 Decreasing N:P ratios correlated with increases in P concentrations and not with N
292 concentrations (Appendix 3). Emergent vegetation cover was consistently higher in the
293 exclosures compared to the control plots, and was not related to vegetation N:P ratio (Table 3,
294 Fig. 4a). Riparian species richness was also consistently higher in the exclosures compared to
295 the control plots and decreased with increasing N:P ratio (Table 3, Fig. 4c). Exclosure treatment
296 effects did not interact with vegetation N:P ratios for both emergent vegetation cover and species
297 richness (Table 3). Both species colonization and extinction from the transect decreased with
298 increasing vegetation N:P ratio, but did not interact with grazing (Table 3).
299 Emergent vegetation cover strongly declined with water depth in the exclosures, whereas grazing
300 overruled the effect of water depth in the control plots. This interaction was significant (Table 3,
301 Fig. 4b). As a result, emergent vegetation cover was much higher in the exclosures compared to
302 the control plots in shallow water, whereas emergent vegetation cover was similarly low in deeper

303 water (about 1.5 m deep). Riparian species richness depended on enclosure treatment and was
304 not significantly related to water depth (Table 3; Fig. 4d). The number of species that colonized
305 the transect decreased with increasing water depth, whereas no relation with water depth was
306 observed for species richness and turnover (Table 3). In 2011, the relations between enclosure
307 treatment, vegetation N:P ratio, water depth and vegetation parameters were similar and can be
308 found in Appendix 4.

309

310 **Discussion**

311 We found a strong and direct effect of herbivore enclosures on riparian vegetation composition
312 and development within the limits determined by abiotic conditions. Excluding grazers increased
313 total vegetation cover, riparian species richness, species diversity, aboveground biomass and
314 expansion of the emergent vegetation fringe, whereas the number of damaged stems and
315 proportional species loss was decreased in enclosures compared to control plots. We therefore
316 conclude that top-down regulation can enforce a sharp transition between aquatic and terrestrial
317 ecosystems and decrease vegetation diversity in situations where abiotic conditions otherwise
318 would favor plant growth. Below we discuss the importance of bottom-up and top-down effects for
319 the functioning of our riparian transition and its implications for larger spatial scales.

320

321 *Expansion and Succession*

322 Exclusion of herbivores in the riparian ecotone led to a rapid expansion of the zone with emergent
323 macrophytes with ca. 1.3 m per year. This matches quite well with the long-term succession rate
324 calculated by (Bakker and others 1994) who observed on aerial photographs that mesotrophic,
325 manmade, narrow, shallow and long ponds of ca. 40 m wide were filled with emergent and marsh
326 vegetation within ca. 20 year, i.e. implying a mean expansion rate of 1 m per year. Also the
327 expansion of 2.2 m year⁻¹ observed by Liira and others (2010) of riparian vegetation in the
328 shallow, eutrophic Lake Vörtsjärv lies within the range of values observed inside our enclosures.

329 In the open, grazed plots, we observed a stable and narrow transition zone between
330 water and land. The wide variety of hypotheses that were brought up previously to explain this

331 observation include poor water or sediment quality and toxic compounds, wave action, changed
332 hydrology and absence of ecosystem engineers which may facilitate vegetation expansion
333 (Sarneel and others 2011; Bakker and others 2013; Hidding and others 2014; Lamers and others
334 2014). However, restoration activities that aim to improve these abiotic restrictions often had
335 limited effect (Sarneel and others 2011). As we observed an immediate and large increase in the
336 expansion of emergent vegetation already one and two growing seasons after placing the
337 exclosures, we now demonstrate that the impact of aquatic grazers can pose a strong constraint
338 on expansion of the riparian zone within the limits determined by bottom-up forces.
339 Simultaneously, we may conclude that previous explanations of bottom-up forces such as poor
340 water and sediment quality are not the main explanation for the sharp transition between water
341 and land as present in these wetlands and that the effects of herbivory in the riparian zone are
342 reversible.

343

344 *Herbivores*

345 Top-down forces may have increased in relevance over the last decades as populations of
346 aquatic herbivores have increased considerably in both Europe and North America (Van Eerden
347 and others 2005; Bos and Ydenberg 2011). In our study we found a few indications that next to
348 waterfowl, muskrats were important herbivores as their density correlated negatively with the
349 vegetation development over time (Appendix 2). Even though their absolute density was rather
350 low in most study areas (muskrat densities decreased over the last decade; personal
351 communication Anouk Prins, Muskrat control agency, the Netherlands), their preference for
352 wetlands and wetland plants may make them very effective in inhibiting expansion of emergent
353 species (Danell 1979). Whereas mammals, such as beaver (Parker and others 2007), nutria
354 (Evers and others 1998), muskrat (Danell 1979) and moose (Butler and Kielland 2008) or hippo's
355 (Kanga and others 2013) can affect wetland vegetation, we now show that aquatic herbivores not
356 only affect vegetation composition but can also determine ecosystem processes such as plant
357 expansion in open water or species turnover. Our results suggest that the role of herbivorous
358 mammals, such as the muskrat, deserves further investigation as also in a previous study a

359 correlation was found between muskrat density and colonization of open water by emergent
360 vegetation (Sarneel and others 2011).

361

362 *Species turnover and diversity*

363 We found that grazing reduced riparian plant species richness which may be attributed to the
364 observation that grazing increased species extinction but did not affect colonization. The species
365 that arrived in the exclosures had a higher establishment success compared to the same number
366 of new species that arrived in the control plots, which had a higher probability to disappear after
367 one growing season. This is in line with transplant studies that showed that grazers can reduce
368 the establishment success of juvenile riparian plants (Veen and others 2013). Our study therefore
369 implies that the herbivore effects on recruitment found in many other studies in ecotones and
370 other ecosystems (Cadenasso and Pickett 2000; Bakker and others 2004; Kuijper and Bakker
371 2005) can result in differences in species turnover and thereby induce vegetation changes.

372 Species richness generally first increases when empty habitat is colonized and with
373 ongoing succession it may eventually decrease, as standing biomass and competition for
374 resources will increase. Our exclosures, with their low initial cover, were likely still in an early
375 phase of succession, where the species richness is increasing. We indeed observed a positive
376 relation between total cover of the plot (representing succession) and species richness (data not
377 shown). It could be hypothesized that when succession proceeds, the (shallow) ungrazed plots
378 that fill may eventually decrease in species richness. Therefore, it is possible that grazing, like
379 other disturbances such as flooding, can increase diversity on larger spatial scales by locally
380 setting back succession, thereby increasing landscape heterogeneity. In intertidal ecotones, for
381 instance, diversity was found to increase even in heavily grazed marshes when there were low
382 intensity grazing marshes present in the landscape (Wanner and others 2014).

383

384 *Top-down vs bottom-up control*

385 In accordance with our hypothesis, we found that vegetation expansion was (negatively) related
386 to water depth in the absence of herbivores, but not in their presence. We found that grazing

387 effects were small and overall vegetation cover was sparse at a water depth of about 1.5 m,
388 which corresponds to a strongly reduced light availability in our turbid peat systems (Bornette and
389 Pujalon 2011; Sarneel and others 2011). At the other end of the gradient, in shallow water,
390 grazing overruled the effect of improved growing conditions. Herbivores may therefore enforce a
391 narrow riparian zone in shallow water bodies due to a high accessibility of stems and rhizomes,
392 and to high herbivore density as water birds may prefer shallow water for foraging (Tatu and
393 others 2007) or feel safer when staying close to the reed beds (Weisner and others 1997). Likely,
394 bottom-up forces that are related to water depth such as light and oxygen availability increase in
395 importance for the vegetation structure in the transition zone in deeper water, where next to a
396 lower accessibility, grazing pressure may be lower due to a low foliage availability.

397 Whereas vegetation expansion was correlated to water depth but not to vegetation N:P
398 ratio, species richness was negatively related to vegetation N:P ratio, but not to water depth.
399 However, in disagreement with our hypothesis, riparian plant species richness was both in the
400 presence and absence of grazers (negatively) related to the vegetation N:P ratio. Grazers
401 significantly reduced species richness across the gradient of vegetation N:P ratios, which is in line
402 with the results of Gayet and others (2011) on submerged macrophytes in fishponds, who
403 observed that the impact of mute swan grazing was not related to pond nutrient status. The N:P
404 ratio in the vegetation indicated a relative N-limitation for the vegetation in most of our plots (N:P
405 < 14, Koerselman and Meuleman 1996; Gusewell and others 2003), which is most likely due to
406 the anthropogenic P-enrichment of Dutch wetlands (Wassen and others 2005; Lamers and others
407 2014). As herbivores have been shown to affect nutrient availability to plants and may modify the
408 vegetation N:P ratio as well (van den Wyngaert and others 2003; Bai and others 2012), the
409 mechanisms underlying the relationship between the vegetation N:P ratio and riparian plant
410 species richness and herbivores are complex and remain to be further elucidated.

411 Another layer of complexity may appear when top-down effects on vegetation expansion
412 or diversity are modulated by predator densities such as was shown for riparian zones in the
413 Yellowstone national park and algal communities in reef systems and near shore kelps (Estes
414 and Palmisan 1974; Power and others 1985; Marshall and others 2013).

415 *Implications and conclusions*

416 Hillebrand and others (2007) showed that herbivores generally reduced species richness in
417 freshwater but tended to increase richness in terrestrial systems. In our study in the transition
418 between those ecosystems, grazing decreased riparian species richness, resembling aquatic
419 systems in this respect. Herbivores further decreased the width and structure of the riparian
420 vegetation which may have cascading effects for the numerous species that dwell in the riparian
421 ecotone (Naiman and Decamps 1997). Moreover, the riparian width determines interactions
422 between bordering systems such as sediment inputs (from land to water and vice versa) and has
423 complex effects on nutrient cycling (Verhoeven and others 2006; Yuan and others 2009). By
424 enforcing a sharp boundaries between different ecosystems, herbivory in the ecotone may
425 therefore have spatially cascading consequences for the diversity and functioning of its bordering
426 ecosystems.

427 Sharp boundaries under grazing are reported for several ecosystems, but then commonly
428 refer to smaller scales, such as mosaic vegetation patches within an ecosystem. For instance
429 grazing by rabbits inhibits shrub and tree expansion in grasslands, thus maintaining a sharp
430 boundary between grassland and woodland patches (Bakker and others 2004). Similar sharp
431 boundaries have been observed to be created by red deer between heather and grassland
432 patches (Farnsworth and Anderson 2001) and by sea urchins between reefs and sea grass beds
433 (Ogden and others 1973). We demonstrate that herbivores can also inhibit a gradual transition
434 between ecosystems, thereby maintaining a sharp boundary on larger spatial scales.

435 Recently, Silliman and others (2013) emphasized that edges of resource or vegetation
436 patches can be particularly prone to grazing, when high numbers of herbivores aggregate there in
437 so-called consumer fronts. In wetlands, molting Greylag geese may temporarily aggregate and
438 graze intensively on the edges of the vegetation fringe (Vulink and Van Eerden 1998) resembling
439 a consumer front, but in the majority of our study sites there were no consumer fronts. Therefore,
440 our results suggest that also at average herbivore densities, grazing at the edges can induce
441 sharp transitions. Herbivores thereby can enforce sharp boundaries at a small scale between
442 patches or at the large scale between whole ecosystems.

443

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452

453

454 **Figure legends**

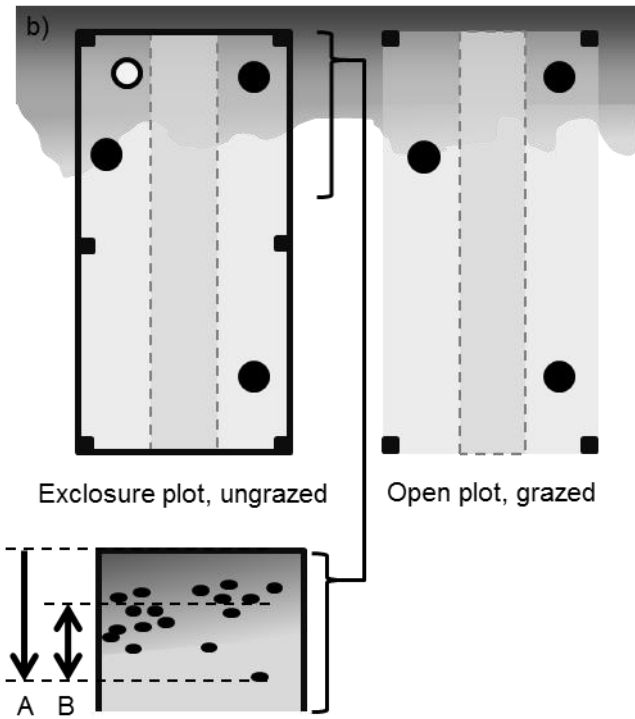
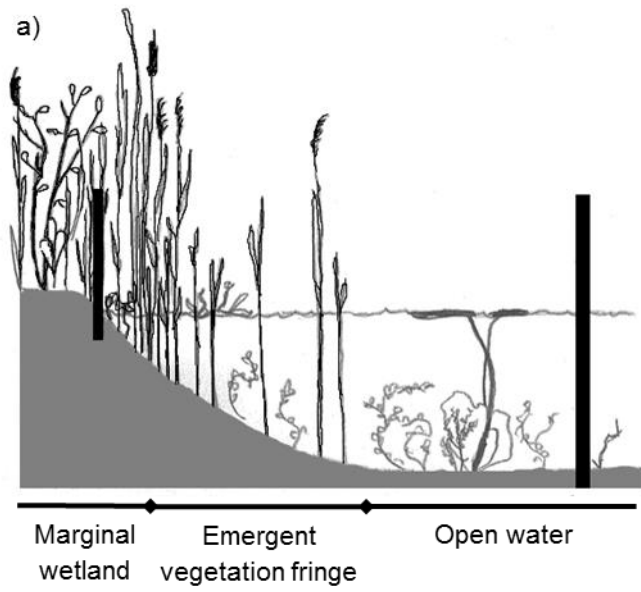
455 **Fig. 1:** a) Schematic cross section of the riparian zone with different vegetation types. b)
456 Schematic top view of an exclosure and control plot in the riparian zone. The dash-lined square
457 indicates the location of the vegetation transect. Circles indicate the location of the biomass
458 samples taken (black taken in 2011 and white in 2012). Arrow A indicates distance of the
459 emergent stem furthest from the bank ward plot end (indicated with black ovals), and arrow B
460 indicates the ten emergent stems that were selected to determine the percentage of stems
461 grazed.

462 **Fig. 2:** a) Mean maximal distance of emergent stems in the water (cm) in the control plots and
463 exclosures in July 2012. b) Mean percentage of damaged stems determined on the ten stems
464 standing most distant from the bank in July 2012. c) Mean emergent vegetation cover increase
465 (% of the transect) over the two growing seasons. Error bars indicate standard errors. Asterisks
466 indicate significant differences between the treatments ($*** = P < 0.001$, $** = P < 0.01$, $* = P < 0.05$).

467 **Fig. 3:** a) Cover percentage, b) species diversity and c) species richness per transect (\pm S.E.) of
468 the control plots and exclosures in July 2011 and 2012. d) Mean proportion of species per
469 transect that were present in 2012 but not in 2011 and thus must have colonized the surveyed
470 area and proportion of species that got extinct from the surveyed area. Differences between
471 control plots and exclosures were tested separately per year and the level of significance is
472 indicated with asterisks ($*** = P < 0.001$, $** = P < 0.01$, $* = P < 0.05$).

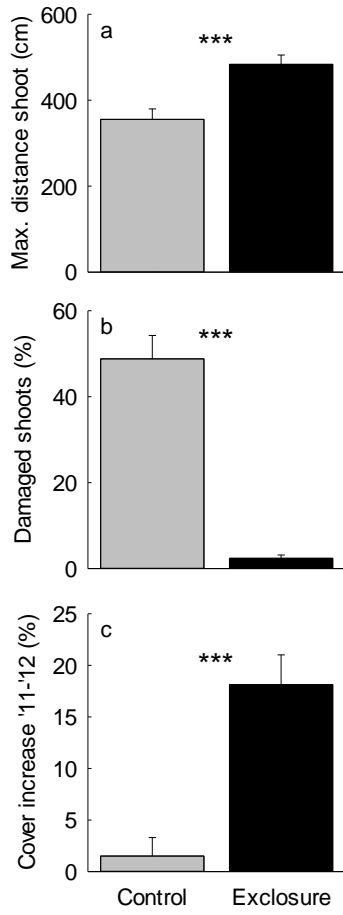
473 **Fig. 4:** a) Total standing biomass and b) total species richness per biomass sample (0.2 m^{-2}) in
474 the different vegetation zones (see Fig 1). Capital letters indicate significant differences between
475 the different spatial sections of the transect, significant difference between exclosure treatments
476 is indicated next to the legend ($*** = P < 0.001$, ns = not significant).

477 **Fig. 5:** Correlation between emergent vegetation cover (a, b) and species richness (c, d) of the
478 transects and vegetation N:P ratio and water depth in July 2012. Each dot represents a single
479 plot.



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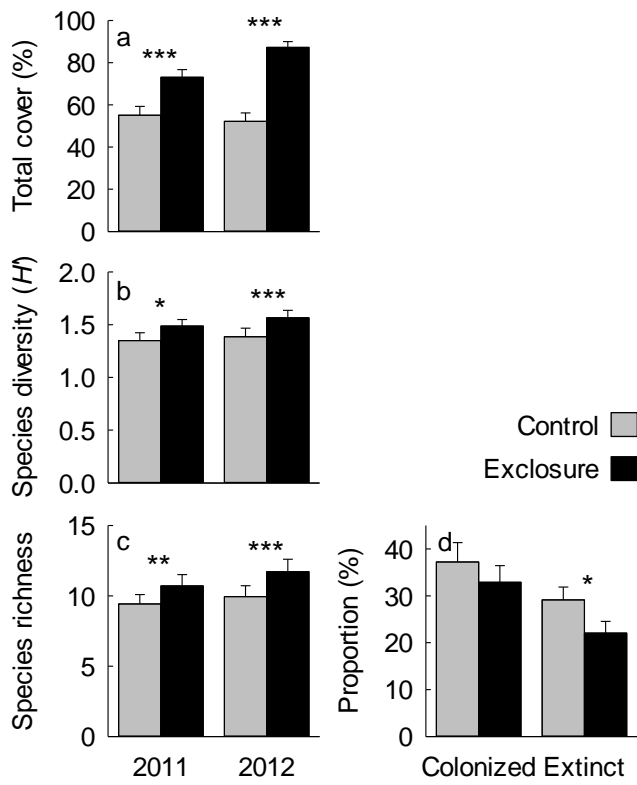
Figure 1



483

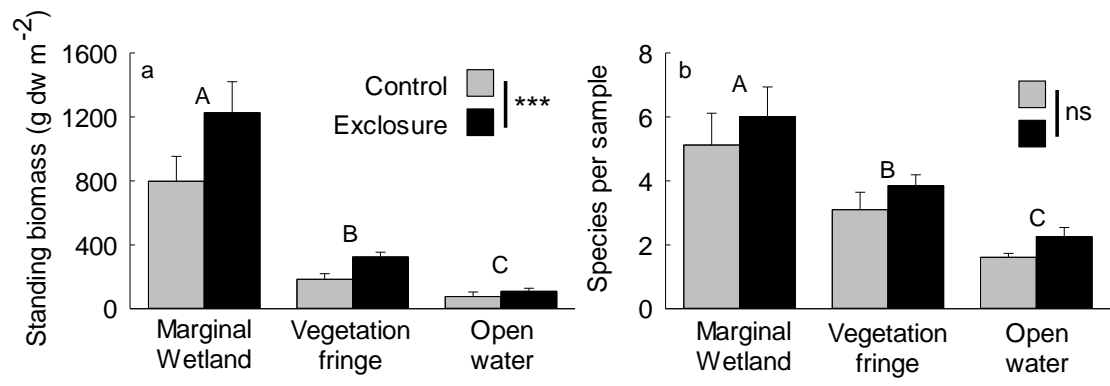
484 **Figure 2**

485



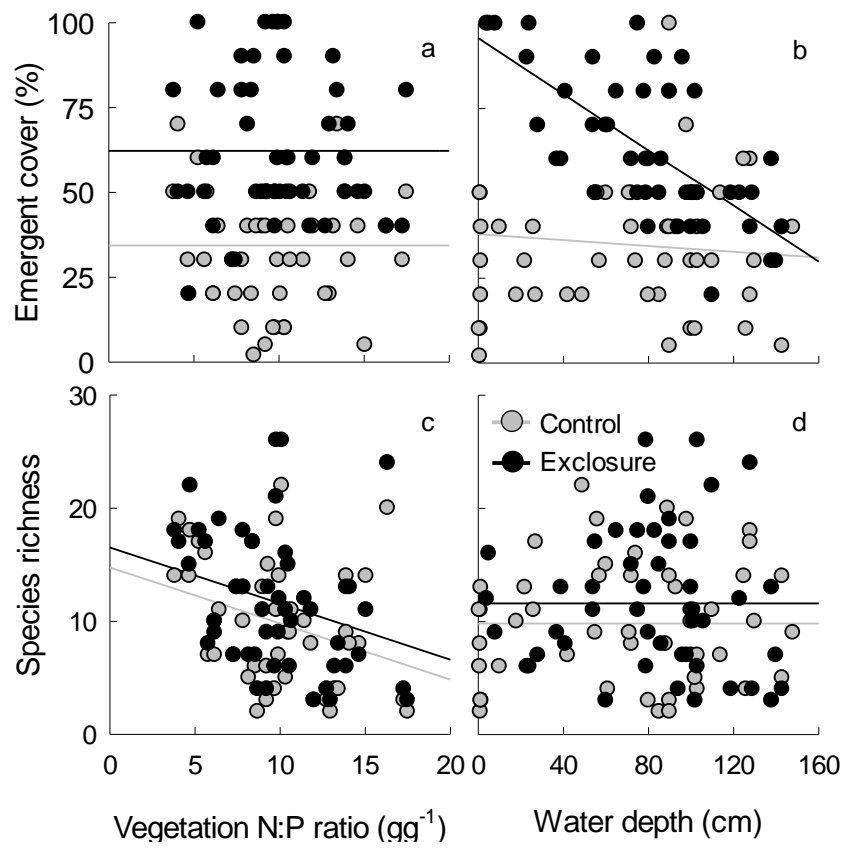
486

487 **Figure 3**



488

489 **Figure 4**



490

491 **Figure 5**

492

493 **Table legends**

494 **Table 1: Characteristics of the 10 study areas.**

495 Type of water body refers to the dominant type of water bodies included. N:P ratio is the
496 vegetation N:P ratio (gg^{-1}) averaged for 2011 and 2012. Water depth (m) is the average water
497 depth at 5 m distance in the enclosure. Water level fluctuations (m) is the difference between the
498 minimum and maximum water level between 10 April 2011 and 1 August 2012. SOM shore is the
499 percentage soil organic matter per gram dry weight of soil, determined by loss on ignition.
500 Waterfowl biomass (kg ha^{-1}) are averages from counts between 1 April and 31 August 2011 and
501 muskrat densities (kg ha^{-1}) are the average of total catches in 2011 and 2012.

502 **Table 2: Statistic results of grazing treatment effects on vegetation characteristics.**

503 Results of separate analyses of July 2011 and 2012. Chi-square values (χ^2) and significance (P)
504 calculated with generalized linear mixed models with paired plot nested within study area as
505 random factor. Degrees of freedom (d.f.) are 1 for all analyses. The transformation used is
506 indicated between brackets. Asin is arcsine transformation of the square root, Sqrt is square root;
507 Nt is not transformed.

508 **Table 3: Statistic effects of environmental conditions and grazing treatment.**

509 Results of the analysis of the effect of grazing treatment and the environmental factors relative
510 nutrient availability (vegetation N:P ratio) and water depth on vegetation characteristics. χ^2 and P -
511 values of the likelihood ratio tests comparing the generalized mixed linear models with and
512 without the variable of interest are indicated. For that reason, degrees of freedom were 1 for all
513 analyses.

514 **Table 1: Characteristics of the 10 study areas.**

515

516	Area	Type of	Vegetation	Water depth	Water level	Waterfowl	Muskrats
517	(Latitude; Longitude)	water body	N:P ratio (gg⁻¹)	(m)	fluctuations (m)	(kgha⁻¹)	(kgha⁻¹)
518	Botshol (52°15'; 4°55')	shallow lake	13.8	1.21	0.21	6	0.08
519	Loenderveen Oost (52°12'; 5°03')	shallow lake	10.3	0.83	0.31	3	0.11
520	Middelpolder (52°18'; 4°53')	ditches	5.2	0.95	0.35	8	0.51
521	Polder Tienhoven (52°10'; 5°05')	turf pond	11.3	1.15	0.13	21	0.20
522	Naardermeer (52°18'; 5°06')	shallow lake	12.1	0.72	0.20	6	>0.01
523	Nieuw Keverdijkse polder (52°17'; 5°05')	shallow lake	10.0	0.34	0.83	10	>0.01
524	Oostelijke binnenpolder (52°10'; 5°06')	turf pond	8.1	0.91	0.27	110	0.02
525	Polder Ronde Hoep (52°16'; 4°54')	ditches	7.1	0.92	0.35	4	0.05
526	Groene Jonker (52°10'; 4°49')	shallow lake	10.5	0.29	0.42	15	0.18
527	Westbroekse zodden (52°10'; 5°07')	turf pond	10.5	1.09	0.32	56	0.04

528 **Table 2: Statistical results of grazing treatment on vegetation characteristics.**

529

530		2011		2012	
531		χ^2	<i>P</i>	χ^2	<i>P</i>
532	Total vegetation				
533	Cover (Asin)	15.679	<0.001	47.226	<0.001
534	Species richness (Sqrt)	6.793	0.009	13.465	<0.001
535	Species diversity (Nt)	6.319	0.012	11.674	0.001
536	Emergent species				
537	Cover (Asin)	13.285	<0.001	33.019	<0.001
538	Species richness (Sqrt)	4.797	0.029	10.534	0.001
539	Species diversity (Nt)	0.595	0.441	2.334	0.127
540	Floating and submerged species				
541	Cover (Asin)	7.228	0.007	16.353	<0.001
542	Species richness (Sqrt)	2.550	0.110	4.549	0.033
543	Species diversity (Nt)	2.456	0.117	1.011	0.315

544 **Table 3: Statistical results of grazing treatment and environment on vegetation characteristics.**

545

546

547 **Variable**

548

549 Emergent vegetation cover 2012 (%)

550

551 Species richness 2012

552

553 Proportion of species colonized between 2011 & 2012 (%)

554

555 Proportion of species extinct between 2011 & 2012 (%)

556

	Environmental	Exclosure		Environmental		Interaction	
	covariate	Treatment (Tr)		covariate (Co)		Tr x Co	
		χ^2	<i>P</i>	χ^2	<i>P</i>	χ^2	<i>P</i>
	Vegetation N:P ratio	37.407	<0.001	0.001	0.981	0.089	0.765
	Water depth	42.044	<0.001	11.668	<0.001	13.633	<0.001
	Vegetation N:P ratio	12.711	<0.001	4.199	0.04	0.369	0.543
	Water depth	12.508	<0.001	1.594	0.207	2.260	0.133
	Vegetation N:P ratio	0.940	0.332	18.093	<0.001	0.084	0.772
	Water depth	1.033	0.310	4.931	0.026	0.987	0.321
	Vegetation N:P ratio	5.605	0.018	16.545	<0.001	1.043	0.307
	Water depth	5.671	0.017	3.291	0.070	3.203	0.074

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