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8 **Habitat management varying in space and time: the effects of grazing and fire**  
9 **management on marshland birds**

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25

26 **Abstract** Freshwater wetlands and marshes with extensive reedbeds are important hotspots of  
27 biological diversity but are subject to biotic homogenisation in the absence of proper  
28 management. We assessed the impact of spatiotemporally variable management by cattle grazing  
29 (for four years) and late-summer burning (one or three years before the study) on both songbirds  
30 and non-passerines in a previously homogeneous reedbed. We surveyed birds by a combination  
31 of line transects and point counts in a quasi-experimental design consisting of six treatment  
32 levels. Management led to a higher diversity of marsh habitats and increased bird diversity. The  
33 species richness and abundance of non-passerines (ducks and geese, wading birds, gulls and  
34 terns, rails, coots and grebes) was higher in recently burned than in unburned or old-burned  
35 patches. The species richness of farmland songbirds was higher in grazed patches than in non-  
36 grazed patches, and reed songbirds had higher richness and abundance in unburned, old-burned  
37 or grazed patches than in recently burned patches. Total Shannon diversity and evenness of birds  
38 was lowest whereas Simpson diversity was highest in the most intensive treatment (patches  
39 grazed and twice-burned). Non-managed patches had fewer species and individuals of all groups  
40 except reed songbirds. The proportion of old reed was low in recently burned and grazed patches  
41 and similarly high in all other treatments. No other property of reed stands was influenced by  
42 management, and both the allocation and the effect of management were independent from water  
43 level. Spatiotemporally variable management by cattle grazing and late-summer burning may  
44 thus simultaneously benefit several groups of birds. The effect of burning alone disappeared in  
45 three years even in the presence of grazing, thus, it needs to be repeated every 2-3 years. We  
46 conclude that both management actions are necessary to establish and maintain a high diversity  
47 of habitats for marshland bird communities.

48

49 **Keywords** · habitat diversity · habitat heterogeneity · Hortobágy National Park · intermediate

50 disturbance hypothesis · mosaic vegetation · salt marsh

51

## 52 **Introduction**

53

54 Habitat management for biodiversity conservation relies on two main principles, the species-area  
55 relationship (SAR) and the intermediate disturbance hypothesis (IDH, Connell 1978). According  
56 to the SAR, the number of species generally increases with area (Connor and McCoy 2001; Pan  
57 2013), thus, management of larger habitat patches should conserve more species. However, the  
58 relationship between the area and number of species is not linear; initially the increment of the  
59 species is fast, but becomes slower as area increases (Báldi and Kisbenedek 2000; Celada and  
60 Bogliani 1993; Paracuellos and Tellería 2004). According to the IDH, species diversity is  
61 maximized when ecological disturbance is at intermediate levels (McCabe and Gotelli 2000;  
62 Schwilk et al. 1997). At low levels of disturbance, the diversity of species often decreases due to  
63 biotic homogenization (Lockwood and McKinney 2001). For example, in reed habitats, the  
64 characteristics and physiognomic structure of habitats becomes homogeneous in the absence of  
65 disturbance by mowing, cutting, flooding, or burning, at both the local and landscape scales  
66 (Lougheed et al. 2008). Under appropriate long-term management, the homogeneous structure of  
67 the reed habitat breaks up and a more heterogeneous structure is formed, which provides more  
68 suitable habitats for a wider spectrum of species through complexity in vegetation structure, and  
69 composition, density and biomass (Wiens 1997; Christensen 1997).

70

71 Freshwater wetlands are of outstanding importance for biodiversity and have become a priority  
72 in conservation (Bobbink et al. 2006; Schweiger et al. 2002). Wetlands have decreased  
73 considerably in size, number and quality in the last century in Europe (and in Hungary,  
74 Vásárhelyi 1995). Although wetlands have been subject to intensive research in conservation and

75 restoration (Wagner et al. 2008; Wheeler et al. 1995), little is known about the appropriate  
76 spatiotemporal allocation and impact of reedbed management in wetlands (Ausden et al. 2005).  
77 The theory of adaptive ecosystem management has been present since the 1980s, but areas  
78 available for management are rarely large enough to accommodate and experiment with different  
79 management regimes (Groom et al. 2006). In temperate grasslands, spatiotemporally variable  
80 management by prescribed fire and by grazing resulted in highly heterogeneous habitats  
81 (Fuhlendorf and Engle 2001; Hartnett et al. 1996; Vinton et al. 1993). In most wetland studies,  
82 sampling areas are too small (under 1 ha) to evaluate the effects of disturbance or the undisturbed  
83 operation of natural ecological processes on higher taxonomic groups (Wagner et al. 2008). In  
84 addition, most studies followed up only one management action and focused on invertebrates  
85 (Ausden et al. 2005; Dithlogo et al. 1992; Schmidt et al. 2005; Hardman et al. 2012). As a result,  
86 we generally know little on how spatiotemporally variable management affects vertebrates,  
87 habitats and ecological processes.

88

89 The management of reedbeds includes various actions such as periodical flooding ( Poulin et al.  
90 2002; Graveland 1998), mowing or cutting (harvesting, Poulin and Lefebvre 2002; Vadász et al.  
91 2008), burning (Moga et al. 2010), grazing/trampling, excavating and herbicide application, or  
92 their combination (e.g. burning and cutting in Báldi and Moskát 1995). While effects such as  
93 grazing, change in water level, and burning may be considered threats under uncontrolled  
94 conditions, they can be important conservation measures as part of a management strategy  
95 aiming to apply these effects as controlled disturbances (Margoluis *et al.* 2009; Salafsky *et al.*  
96 2009). A meta-analysis of 21 European studies on the effect of reed management by Valkama et  
97 al. (2008) found that management by harvesting, burning, mowing and grazing alters the

98 structure of reedbeds, with reed stems becoming shorter and denser in managed sites compared  
99 to non-managed ones. Plant species richness usually increases by management but invertebrate  
100 richness decreases after 1-2 years of management. In birds, the abundance of passerine species  
101 decreases on average by 60% after burning and reed harvesting (Valkama et al. 2008). Many  
102 reedbed-breeding passerines, mainly *Acrocephalus* warblers, actively avoid cut areas, while  
103 others show decreased abundance and diversity (Vadász et al. 2008; Poulin and Lefebvre 2002).  
104 Some reed songbirds, however, use managed areas, for example, the Aquatic Warbler (*A.*  
105 *paludicola*) prefers cut reed stands (Tanneberger et al. 2009), while the Stonechat (*Saxicola*  
106 *torquatus*) and Marsh Warbler (*A. palustris*) prefer burned reed (Moga et al. 2010). We know  
107 much less on how reed management influences non-passerine birds. In addition, little is known  
108 on whether there are interactive or synergistic effects of two different management actions on  
109 birds (Valkama et al. 2008) to maximize their diversity and abundance in reedbeds.

110

111 The aim of this study was to evaluate the impact of spatiotemporally variable management by  
112 grazing and burning on marshland bird communities and functional groups. We addressed the  
113 following questions: (1) Do the responses of the bird community or functional groups to  
114 management differ by the type or regime of management? (2) Do the responses differ among  
115 bird functional groups including both passerines and non-passerines? (3) Is there interaction or  
116 synergy between the impacts of management by grazing and management by burning? To  
117 answer these questions, we apply a quasi-experimental approach in which experimental units  
118 (line transects combined with point counts) were replicated in similarly managed areas along a  
119 gradient of no management, one treatment (grazing), or two treatments (grazing and burning).

120

121 **Methods**

122

123 Management actions

124

125 The study was conducted at the Fekete-rét marsh (600 ha; N 47.559°, E 20.932°), the largest  
126 marsh in the Egyek-Pusztakócs marsh system (Hungary). In order to open up reedbeds, control  
127 reed and increase the diversity of habitats by re-creating the former wetland mosaic, two  
128 management actions were designed in 2004: grazing/trampling by cattle and fire management  
129 (prescribed burning).

130

131 Grazing – Grazing by Hungarian grey cattle was started in spring 2006. Trampling on rhizomes  
132 through controlled grazing has little effect on reed density but long term grazing reduces the  
133 vigour of the reed plant considerably (Cross and Fleming 1989). Grey cattle are highly suitable  
134 for grazing in marshes as they will go after and consume reed even in deep water, up to 1.5 m  
135 (Kelemen 2002). Grazing was conducted by a stock of 180 grey cattle between late April and  
136 late November every year between 2006 and 2009. Cattle were free to roam in the entire  
137 southern half of the marsh (c. 300 ha) to mimic natural disturbance as closely as possible.  
138 However, grazing was concentrated in the SW part of the marsh (c. 200 ha) closest to the fold  
139 (Figure 1, Figure S1) and cattle also used meadows and grasslands (total c. 100 ha) surrounding  
140 the marsh. This resulted in a gradient of grazing intensity from heavily grazed/trampled through  
141 slightly grazed/trampled to ungrazed areas.

142

143 Fire management – Burning took place in early September in both 2007 and 2009, in the non-  
144 breeding period. The late summer is the flowering period of reed (late summer), when most  
145 nutrients are in the shoot/inflorescence of the plant, reed can be controlled effectively through  
146 burning due to damage on the nutrient-poor rhizomes (Cross and Fleming 1989). Fire  
147 management was designed and implemented in cooperation with professional fire crews. In  
148 2007, the fire was started on the E side of the marsh and progressed westwards, whereas in 2009,  
149 the fire progressed from W to E with westerly winds. Although fire intensity varied, as suggested  
150 by flames of different height (generally 2-3 m but sometimes up to 10-12 m), both fires caused a  
151 near-total loss of old and green reed (Figure S2). The total area burned was 110 ha in 2007 and  
152 130 ha in 2009. Although some areas were burned in only one year, there was also a substantial  
153 area that was burned in both years (Figure 1).

154

155 Both management actions were considered as ecological disturbances, which can be  
156 characterised by their regime (duration, size, intensity, frequency, reversibility etc.) (Salafsky et  
157 al. 2009; Salafsky et al. 2008). By allocating two treatment levels of grazing management and  
158 three levels of burning, our experiment involved variability in the duration (grazed never vs. for  
159 four years), the frequency (burned never, once, or twice in four years) and the intensity (the  
160 intensity of grazing and burning were allowed to vary within the marsh as described above) of  
161 disturbance.

162

163 Experimental design and data collection

164



165 The experimental design consisted of an incomplete crossing of the grazing and burning  
166 management with six treatment levels (Table 1). Both cattle and fires were free to roam in the  
167 southern half of the marsh to mimic ancient disturbances as close as possible, which resulted in  
168 managed areas of irregular shapes. We digitized the areas actually grazed and burned in detailed  
169 ground surveys at the end of the vegetation period. We recorded point localities using a hand-  
170 held GPS receiver during walking along the visually identified borderline of regularly  
171 grazed/trampled and un-grazed marsh and burned and unburned reed. A spatial overlay of the  
172 obtained polygons allowed us to identify areas with six different combinations of management  
173 actions (treatment levels, Table 1).

174

175 In each of the six treatment levels, we designated five 100-m-long transects as replicates (total  
176  $n = 30$ ). The transect starting points were selected randomly within similarly treated areas with  
177 the restriction that transects were at least 100 m apart from each other. The orientation of  
178 transects was selected randomly, except where the shape of the treated area restricted the  
179 orientation. We walked transects once in April and once in May in 2010 to maximize the chances  
180 of recording both early-nesting and late-nesting species. Data from the two occasions were  
181 pooled per transect for analysis. We counted birds for 5 min each at 0, 25, 50, 75 and 100 m from  
182 the starting point of the transect and also counted birds when walking between the points  
183 (combination of point counts and the line transect method, Bibby et al. 2000; Gibbons and  
184 Gregory 2006; Gregory et al. 2004). We recorded all birds seen or heard but analysed only those  
185 that were within 25 m on both sides of transects. To avoid double-counting of the singing males  
186 of reed-nesting passerines we mapped their territories. Bird species were classified into  
187 functional groups based on their foraging and nesting characteristics (Perrins and Cramp 1998).

188

189 We measured water depth at each of the five counting points, which were averaged for each  
190 transect. We also quantified reed density and complexity at the three internal counting points to  
191 characterize the effect of management. The number of old and new reed stems were counted in a  
192 circle (diameter 40 cm) positioned at a height of 1 m and 1 m in a randomly selected direction  
193 from each internal counting point. We first estimated reed density (based on the counting at the  
194 three internal points) by (i) the average number of old stems, (ii) the average number of new  
195 stems, (iii) the total number of both old and new stems, and (iv) the average of total number of  
196 stems, and (v) the proportion of old reed stems (per total number of stems in the transect)  
197 because old reed is important for the breeding of early reed-nesting passerines. Second, we  
198 estimated reed complexity by (i) the standard deviation (SD) of the mean number of all stems  
199 and (ii) the coefficient of variation (CV) in the number of all stems (standard deviation per mean  
200 of number of all stems) for each transect. We also recorded two variables that potentially reflect  
201 management, (i) the proportion of reed cover (1 for transects with a continuous cover of reed, 0.9  
202 for transects with reed cover on 90 m etc.), and (ii) the proportion of the length of the transect  
203 where reed had been cut relative to the total length of the transect (e.g. 0.2 indicating that reed  
204 was cut on 20% of the 100-m length). Evidence of reed cutting was found in eight transects or  
205 27% of  $n = 30$  transects. We thus obtained five variables for reed density (mean number of old  
206 and new stems, total number of all stems, mean number of stems, proportion of old stems), two  
207 variables for reed complexity (SD of the mean number of all stems and CV in the number of all  
208 stems), and two additional variables potentially reflecting management effects: reed cover,  
209 proportion of transect length cut in each transect. We thus estimated nine variables for reedbed

210 structure to allow for the possibility that responses of bird functional groups will differ by the  
211 preference of birds to different aspects of reed.

212

213 Statistical analysis

214

215 We used General Linear Models (GLM) to model the responses of the bird assemblage to the  
216 management treatment and various covariates. Response variables in GLMs were species  
217 richness, total abundance, Shannon-Wiener and Simpson diversity and evenness for all birds and  
218 species richness and abundance for bird functional groups. Independent variables were  
219 management, nine variables of reedbed structure, and water depth. Because there was  
220 collinearity among the seven variables describing reed density and complexity (Pearson  
221 correlations,  $r > 0.53$ ,  $p < 0.01$ ), we only considered those three combinations of variables which  
222 were not correlated (number of old reed stems with S.D. of reed density; number of new reed  
223 stems with C.V. of reed density; and proportion of old reed stems with S.D. of reed density). The  
224 proportion of reed cover or proportion of reed cut were not related to the reed density or  
225 complexity variables, therefore, we entered these variables in all full models. Finally, there was  
226 no difference in water depth among the areas with different management actions (one-way  
227 ANOVA,  $F_5 = 0.434$ ,  $p = 0.821$ ). Furthermore, there was no significant correlation between  
228 water depth and either of the nine variables describing reedbed structure (Spearman correlations,  
229  $0.171 < r_s < 0.224$ ,  $p > 0.230$ ).

230

231 We first ran GLMs to select models that best described our data relative to the three  
232 combinations of reed density and complexity variables. We used Akaike's Information Criterion

233 to select the best of the three models for each response variable. In the second step, we ran the  
234 best-fitting full models and applied a backward stepwise algorithm to remove non-significant  
235 variables and interaction terms. The final reduced models were then fitted to estimate  
236 coefficients and compare means.

237

238 The normality of variables was checked by the Shapiro-Wilk test and the homogeneity of  
239 variances was checked by Bartlett tests. One-way ANOVA was used if the assumptions of  
240 parametric tests were met, in other cases, we used Kruskal-Wallis tests to analyse the differences  
241 between the six treatments. We used the R environment 2.15.2 and SPSS 17.0 for statistical  
242 analyses.

243

## 244 **Results**

245

246 We recorded 1063 individuals of 45 bird species (Table S1). The number of species breeding in  
247 the marsh or the surrounding area was 39 (n = 965 individuals), whereas migrants included 6  
248 species (n = 98 individuals). The mean number of individuals per transect was  $35.4 \pm 20.17$ .

249

250 Effects of management on the bird community

251

252 The Shannon and Simpson diversity as well as the evenness of bird communities were  
253 significantly affected by management, whereas total species richness and abundance were not  
254 (Table 2, Figure 2). Shannon diversity and evenness were low in grazed patches burned twice  
255 and were uniformly high in all other treatments (Figure 2C, E), whereas Simpson diversity was

256 highest in grazed patches burned twice and lower in all other treatments (Figure 2D). Species  
257 richness was not affected by any of the factors studied, although the effect of reed complexity  
258 was marginally non-significant (Table 2). Abundance appeared to be higher in grazed patches  
259 with recent burning (burned in 2009 and burned twice), although large variation did not result in  
260 statistically significant differences among treatments (Figure 2B). Rather, bird abundance was  
261 negatively affected both by reed cover and water depth (Table 2), indicating more birds in  
262 transects with more open water and with shallower water.

263

264 Effects of management on bird groups

265

266 The response of birds to management varied greatly in different groups (Figure 3, Table S2).  
267 Ducks and geese had higher abundance in grazed newly-burned patches, followed by grazed  
268 twice-burned and grazed unburned patches (Figure 3B). There was no difference in species  
269 richness by treatment (Figure 3A). Wading birds as well as gulls and terns showed a similar  
270 pattern but both their species richness and abundance were significantly higher in newly-burned  
271 patches than in other treatments (Figure 3C-F). Reed songbirds showed a contrasting pattern in  
272 that both their species richness and abundance were lowest in newly-burned patches and were  
273 significantly higher in old-burned or unburned patches (Figure 3G, H). The species richness of  
274 farmland songbirds was higher in grazed patches with new burning than in non-grazed patches  
275 and was intermediate in other grazed patches regardless of whether patches were burned or not  
276 (Figure 4I), indicating the overall importance of grazing for farmland birds. Finally, the species  
277 richness of rails, coots and grebes was influenced positively by reed complexity (CV) and water  
278 depth and negatively by reed cover but not by management *per se* (Table S2).

279

280 Management effects on reed

281

282 The proportion of old reed differed significantly between the six treatments (Kruskal-Wallis test,  
283  $\chi^2_5 = 18.683$ ,  $p = 0.0022$ ), because newly and twice-burned areas combined with grazing had  
284 little old reed, whereas other treatments had at least 35% on average (Figure 4). Furthermore, the  
285 proportion of old reed was higher in non-managed than in grazed unburned patches, whereas  
286 there was no such difference by grazing between the two old-burned treatment levels (Figure 4).  
287 Finally, there was no difference among treatment levels in either mean reed density (one-way  
288 ANOVA,  $F_5 = 1.77$ ,  $p = 0.156$ ), reed complexity (SD:  $F_5 = 1.02$ ,  $p = 0.425$ ; CV:  $F_5 = 1.30$ ,  $p =$   
289  $0.297$ ) or reed cover ( $\chi^2_5 = 3.748$ ,  $p = 0.586$ ).

290

## 291 **Discussion**

292

### 293 Key findings

294 We found that spatiotemporally variable management by grazing and burning led to a more  
295 heterogeneous landscape structure of marsh habitats (Figure S1), which increased bird diversity  
296 in three main ways. First, there were more species and individuals of non-passerines in recently  
297 burned patches than in unburned or old-burned patches. Second, there were more species and  
298 individuals of reed songbirds in unburned, old-burned or grazed patches than in newly-burned  
299 patches. Finally, there were more species of farmland birds in grazed patches, particularly in  
300 newly-burned ones, than in non-grazed patches. Our results thus indicate that spatiotemporally  
301 variable management may simultaneously benefit several functional groups of birds. Our

302 findings also suggest that this benefit was mediated by management-caused changes in reed  
303 structure and increases in habitat diversity and was independent of the variation in water level,  
304 which further reinforces the importance of management by grazing and burning.

305

#### 306 Effects of cattle grazing

307 Continuous grazing through four vegetation periods led to the establishment of trampled  
308 corridors and areas in the homogeneous reed, where old reed stems were partially destroyed and  
309 the growth of new reed was stunted. Grazing by cattle has been known to efficiently control reed  
310 (van Deursen and Drost 1990), although its effect depends on the type of livestock and grazing  
311 intensity (Vulink et al. 2000) and the duration of grazing (Korner 2013). In our study, grazing  
312 and trampling led to a mosaic-like patch structure of habitats, which was preferred by farmland  
313 birds and several reed songbirds. Although the number of wading birds and waterfowl also  
314 increased in a long-term grazing programme at Lake Neusiedler in eastern Austria (Korner  
315 2013), we did not find such a tendency. In our study, wading birds and waterfowl preferred  
316 partially flooded areas with both grazing and burning, showing that grazing alone was not  
317 enough to create potential breeding, feeding or roosting habitats for these bird groups.

318

319 For most reed songbirds, patches with a high proportion of old reed were preferable as their  
320 species richness and abundance was high relative to patches that were recently burned. The non-  
321 managed reed was characterized by high reed songbird diversity and evenness compared to  
322 managed stands, similarly to the findings in Valkama et al. (2008). For example, Báldi and  
323 Moskát (1995) compared species richness and abundance of reed passerines among cut, burned,  
324 non-managed reed and heterogeneous reed containing bulrush, meadows and trees. The

325 abundance and species richness of reed passerines, a group which encompassed both reed and  
326 farmland songbirds in our study, was significantly higher in the control area than in managed or  
327 heterogeneous areas. Báldi and Moskát (1995) concluded that homogeneous reed stands were  
328 highly suitable for reed passerines, thus, they suggested limited or no management for reed  
329 passerines. Most other studies focusing on reed passerines also found higher diversity in  
330 homogeneous and unmanaged reed (Vadász et al. 2008; Graveland 1999). In several studies, the  
331 area-sensitive reed passerines positively preferred non-managed but heterogeneous reed beds  
332 (Báldi and Kisbenedek 1998; Báldi 2004; Benassi et al. 2009). However, some authors reported  
333 that reed songbirds may differ in their preferences with regard to management (Poulin and  
334 Lefebvre 2002) or to water depth because some species nest exclusively in flooded non-managed  
335 reedbeds, while others have a wider tolerance regarding the absence of water (Neto 2006).

336

### 337 Effects of burning

338 The late-summer burning of reed resulted in shallow pools with low vegetation cover in the next  
339 year, which was attractive to waterfowl and wading birds. This effect largely disappeared  
340 because reed grew back strong in these areas by year 3 after burning, resulting in no difference  
341 between old-burned and non-burned patches for the non-passerine groups. Our results thus  
342 suggest that burning is highly effective at controlling reed but that this effect is temporary at  
343 most. These results suggest that burning needs to be repeated every 2-3 years to reap its full  
344 benefits to non-passerine birds. In contrast, the species richness of passerines in (Moga et al.  
345 2010) was higher in burned areas. However, in Moga et al. (2010) and other studies (e.g. Mérő et  
346 al. 2014) reed was burned in March of the year of the survey. To our knowledge, our study is the  
347 first to report the next-year effects of late-summer burning of reedbeds.



348

349 We found that the proportion of old reed was significantly lower in the two recently burned and  
350 grazed patches than in the other four treatment levels. Experimental studies of spring burning  
351 and mowing of reed resulted in extensive damage to the shoots and differences in reed stem  
352 density and diameter; the reed compensate damages on young shoots due to spring burning by  
353 the growth of several thinner replacement shoots (van der Toorn and Mook 1982). Van Deursen  
354 and Drost (1990) found that reed stands might thus be in equilibrium with grazing pressure, but  
355 also reported that reed production can be reduced to 40% due to grazing compared to an  
356 ungrazed stand. In the spring the following year we still detected the effect of late-summer  
357 burning, furthermore, trampling by cattle in the burned areas throughout the autumn represented  
358 further damage to the reed plants which led to decreased reed productivity in spring. Our results  
359 thus suggest that the combination of burning and grazing leads to long-lasting damage to reed  
360 plants in areas burned in late summer, where non-passerines and farmland songbirds showed  
361 high richness and abundance the next spring.

362

363 Water depth

364 Besides management and reed properties, water depth also significantly influenced the bird  
365 community (in four of the five models) and some functional groups. There were positive  
366 relationships between water depth and Shannon diversity and evenness, and the species richness  
367 of reed songbirds, and rails, coots and grebes, and there were negative relationships between  
368 water depth and total abundance, Simpson diversity, the abundance of gulls and terns, and the  
369 species richness of farmland songbirds. These results are in line with expectations based on the  
370 general vegetation patterns largely determined by water depth and on the feeding and habitat use

371 properties of the functional groups involved. For example, shallow water is more likely to host a  
372 diverse vegetation (bulrushes, *Schoenoplectus* spp., *Typha* spp., grasses e.g. *Alopecurus*,  
373 *Beckmannia*), which gradually gives way to more homogeneous reedbeds in waters of  
374 intermediate depth, whereas very deep water will usually be open water devoid of emergent  
375 vegetation but rich in floating or submerged vegetation (pondweed, e.g. *Potamogeton* spp.,  
376 *Lemna* spp., *Ceratophyllum* spp. etc.). The positive relationship between water depth and the  
377 richness of reed songbirds and rails, coots and grebes can be explained that transects going  
378 through intermediate water depth likely provided better conditions for nesting and feeding for  
379 reed songbirds (mainly *Acrocephalus* spp., plus *Emberiza schoeniclus*, *Locustella luscinioides*,  
380 *Luscinia svecica*, *Motacilla flava*, *Panurus biarmicus*) and rails, coots and grebes (*Fulica atra*,  
381 *Porzana parva*, *Rallus aquaticus*, *Tachybaptus ruficollis*) than transects in shallower water. The  
382 somewhat surprising negative relationship between water depth and gull/tern abundance was  
383 because gulls and terns, which usually nest on floating vegetation in open water, often rested in  
384 cattle-trampled openings in shallow water or because shallower water probably provided better  
385 conditions for feeding. Finally, the negative relationship between water depth and species  
386 richness of farmland songbirds conformed to the expectations because habitats typically required  
387 by these species (*Alauda arvensis*, *Hirundo rustica*, *Miliaria calandra*, *Saxicola rubetra*, *Corvus*  
388 *cornix*) became rarer with increasing water depth.

389

390 Despite the influence of water depth on several response variables, in the transects surveyed,  
391 there was no systematic variation in water depth among the different treatments, and there were  
392 no relationships between water depth and reed structure variables. Moreover, there was no  
393 interaction between management and water depth in any of the models. These findings indicated

394 that the effects of management and water depth were independent from one another. These  
395 observations, however, also suggest that varying the water level as part of a long-term marsh  
396 management programme can be promising as an introduction of further disturbance to increase  
397 the diversity of marsh habitats and to benefit a variety of bird species. For example, many  
398 species such as ducks and geese, storks and herons, and coots and grebes require a minimum of  
399 water for nesting and feeding (Nummi et al. 2013; Pöysä and Vaananen 2014; Causarano and  
400 Battisti 2009). Beyond the pure presence of water, the changes in the water level can also affect  
401 the presence and abundance of these and several other groups of water birds (e.g. Causarano et  
402 al. 2009; Redolfi De Zan et al. 2010; Zacchei et al. 2011).

403

#### 404 Management and the intermediate disturbance hypothesis

405 The results of spatiotemporally variable, combined management by burning and grazing fit the  
406 expectations based on IDH in the study marsh. First, the IDH predicts that high disturbance will  
407 lead to lower diversity because fewer species will tolerate intense or too frequent disturbance.  
408 Our results support this prediction because total Shannon diversity and evenness were lowest  
409 whereas Simpson diversity was highest for the patches with highest disturbance (grazed and  
410 twice-burned). Because Shannon diversity is more affected by rare species while Simpson  
411 diversity is more affected by common species (Magurran 2004), this result suggests that patches  
412 with highest disturbance had disproportionately more of the common rather than the rare species.  
413 Second, the IDH predicts that low disturbance will be tolerated by a few species, leading to  
414 biotic homogenization. The finding that control (non-managed) patches had fewer species and  
415 individuals of all groups but reed songbirds appears to support this prediction because reed

416 songbirds avoided combined, burned and grazed patches. However, because reed songbirds had  
417 many species, this pattern did not show for total diversity.

418

#### 419 Conclusions

420 We conclude that spatiotemporally variable combined management of reedbeds by grazing and  
421 burning positively affects the bird community. Grazing and trampling by cattle led to the  
422 opening up of homogeneous reedbeds, creating habitat patches preferred by farmland songbirds.  
423 Late-summer burning followed by autumn grazing was effective in controlling reed so that  
424 habitats suitable for several non-passerine groups (waterfowl, wading birds, gulls and terns) were  
425 established. Reed control led to the increase of open water surfaces with patchy reed, a habitat  
426 preferred by rails, coots and grebes. Finally, non-managed patches had high proportions of old  
427 reed, which provided habitat for reed songbirds. Many of these changes were mediated by the  
428 availability or proportion of old reed, which was the property of reed most affected by  
429 management. The spatiotemporally variable management thus led to an increased diversity of  
430 habitats and a more heterogeneous marsh landscape, which was reflected in the increased  
431 richness and abundance of bird functional groups.

432

#### 433 Practical implications

434 Wetland managers are often faced with the choice of the hierarchical levels (populations/species  
435 or the entire community) they target with conservation actions. When the goal of conservation  
436 actions is to increase the density of area-sensitive and specialised bird species (e.g. *Acrocephalus*  
437 *scirpaceus*, *Ixobrychus minutus*), then the population/species level is targeted (Benassi *et al.*  
438 2009). In contrast, when the goal is to increase the number of species, managers target the

439 community level and use richness and diversity indices (Magurran and McGill 2011) for follow-  
440 up (e.g. Rácz et al. 2013; Déri et al. 2011). Reedbed management has to be prioritised based on  
441 the local conservation needs and managers need to consider the trade-off between increasing the  
442 size of homogeneous reed stands for reedbed specialist species on one hand and increasing the  
443 diversity of habitats by grazing, burning or water level management on the other. The  
444 exceptionally large spatial scales available for our experiment made it possible to provide an  
445 example for management to benefit the entire avian community without compromising the  
446 habitat requirements of specialists.

447  
448 Our study provided several other practical implications. Grazing by cattle needs to be continuous  
449 and maintained over several years to keep the reedbed loose and heterogeneous. Late-summer  
450 burning can also efficiently control reed but burning in itself causes only a temporary effect that  
451 disappears in three years even in the presence of grazing, thus, it needs to be repeated every two  
452 or three years. Ideally, both actions should be carried out in the non-breeding period of birds or  
453 the inactive period of other animals of conservation importance. The late summer, after breeding  
454 ceases and before migration or wintering begins, offers a good time period. Trampling in burned  
455 areas in the autumn and early spring by cattle leads to the establishment of shallow banks with  
456 little or no vegetation, which is attractive for waterfowl, wading birds and gulls and terns.  
457 Generally we conclude that both management actions, grazing and burning, are needed to  
458 maintain a high diversity of habitats for marshland bird communities.

459

460

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462

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469

470 **Conflict of interest** The authors declare that they have no conflict of interest.

471

#### 472 **Supplementary Material**

473 Additional Supplementary Material may be found in the online version of this article:

474 Supplementary Material Methods: Management needs: previous history, Figure S1

475 Supplementary Material Results: Table S1, Table S2, Figure S2

476

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- 641

642 **Tables**

643

644 Table 1. An overview of treatments in marsh habitat patches and the terminology used in this  
645 study. Grazing was conducted in the SW part of the marsh on 200 ha between late April  
646 and late November every year between 2006 and 2010.

<b>Fire management</b>		<b>Grazing management</b>	
<b>Burned in</b>	<b>Grazed</b>	<b>Non-grazed</b>	
2007	Grazed, old-burned	Non-grazed, old-burned	
2009	Grazed, newly-burned	–	
Both years	Grazed, twice-burned	–	
Never	Grazed, unburned (burning control)	Non-grazed, unburned (overall control)	

647

648

649 Table 2. Results of general linear models testing the effects of management, reed properties and  
 650 water depth on variables describing the marsh bird community. Models shown were obtained by  
 651 backward stepwise removal (function ‘step’ in R) of effects not improving model fit from full  
 652 models specified after a model selection procedure. Significant effects are in Bold.

<b>Response variable</b>	<b>Predictors</b>	<b>Coefficient ± S.E.</b>	<b>F (df<sub>1</sub>, df<sub>2</sub>)</b>	<b>p</b>
Species richness	Reed complexity (CV) <sup>a</sup>	1.87 ± 1.032	3.853 (1, 27)	0.060
	Proportion of reed cut	-2.31 ± 1.430	2.608 (1, 27)	0.118
Abundance	<b>Reed cover</b>	<b>-52.19 ± 24.781</b>	<b>4.451 (1, 26)</b>	<b>0.045</b>
	Proportion of reed cut	-21.24 ± 10.849	3.225 (1, 26)	0.084
	<b>Water depth</b>	<b>-0.60 ± 0.291</b>	<b>4.336 (1,26)</b>	<b>0.047</b>
Shannon diversity	<b>Management</b>	<b>-0.47 ± 0.184</b>	<b>3.324 (5, 21)</b>	<b>0.023</b>
	Reed complexity (CV) <sup>a</sup>	0.19 ± 0.140	2.118 (1, 21)	0.160
	Proportion of reed cut	-0.28 ± 0.223	2.398 (1, 21)	0.136
	<b>Water depth</b>	<b>0.01 ± 0.005</b>	<b>6.137 (1, 21)</b>	<b>0.022</b>
Simpson diversity	<b>Management</b>	<b>0.16 ± 0.051</b>	<b>5.317 (5, 23)</b>	<b>0.002</b>
	<b>Water depth</b>	<b>-0.00 ± 0.001</b>	<b>8.138 (1, 23)</b>	<b>0.009</b>
Evenness	<b>Management</b>	<b>-0.16 ± 0.054</b>	<b>5.347 (5, 23)</b>	<b>0.002</b>
	<b>Water depth</b>	<b>0.00 ± 0.001</b>	<b>7.500 (1, 23)</b>	<b>0.012</b>

653 <sup>a</sup> coefficient of variation in the number of reed stems per transect  
 654  
 655

656 **Figure legends**

657

658 Figure 1. Aerial photograph of Fekete-rét marsh (in 2005), with location of management actions.

659 Source of photograph: Institute of Geodesy, Cartography and Remote Sensing, Budapest,  
660 Hungary.

661

662 Figure 2. Mean  $\pm$  S.E. community parameters in management treatment levels. Groups not  
663 sharing lowercase letters are significantly different (Tukey's HSD test,  $p < 0.05$ ).

664

665 Figure 3. Mean  $\pm$  S.E. species richness and abundance of the five main functional groups in  
666 management treatment levels. Groups not sharing lowercase letters are significantly different  
667 (Tukey's HSD test,  $p < 0.05$ ).

668

669 Figure 4. Mean  $\pm$  S.E. proportion of old reed in management treatment levels.

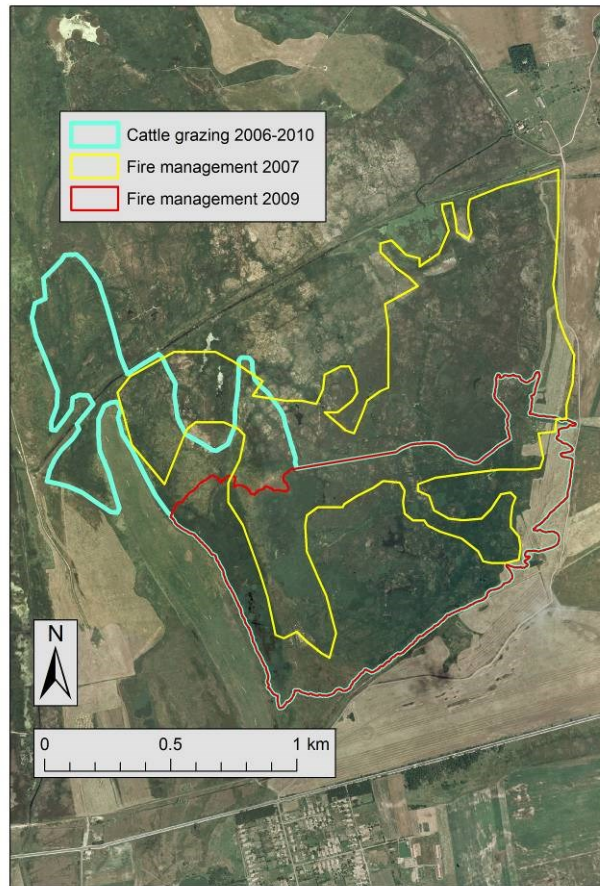
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672 **Figures**

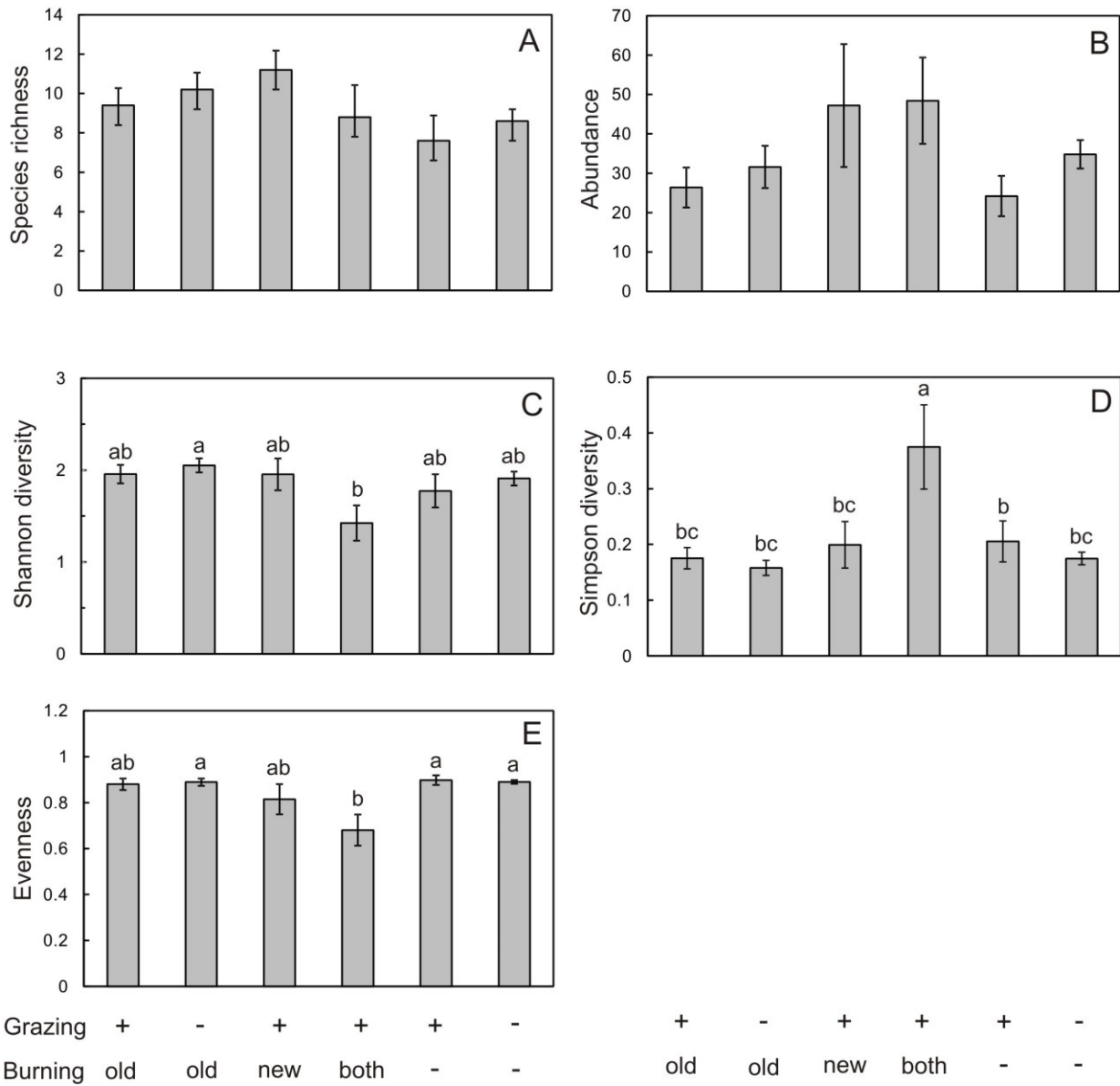
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674 Figure 1



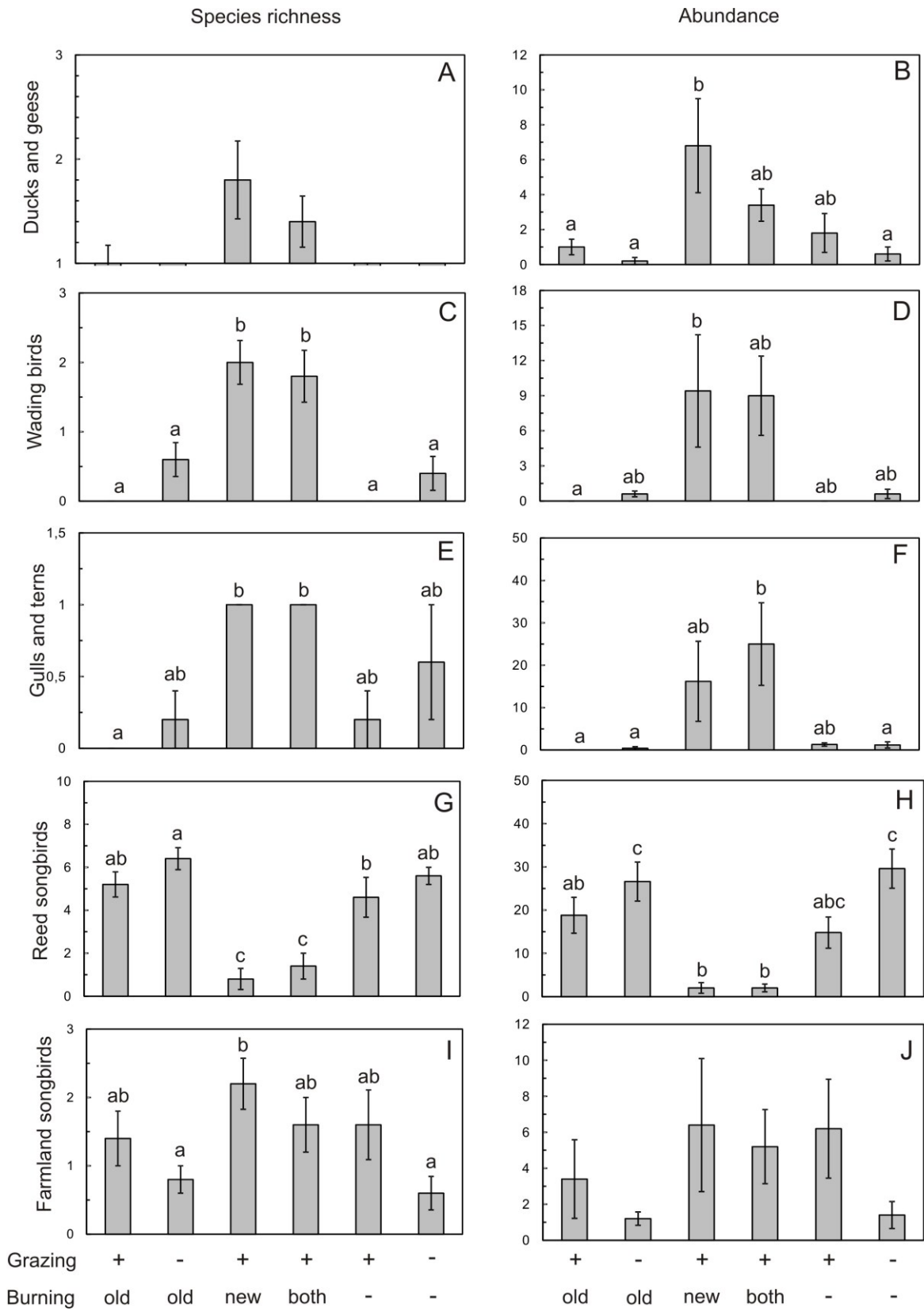
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678 Figure 2



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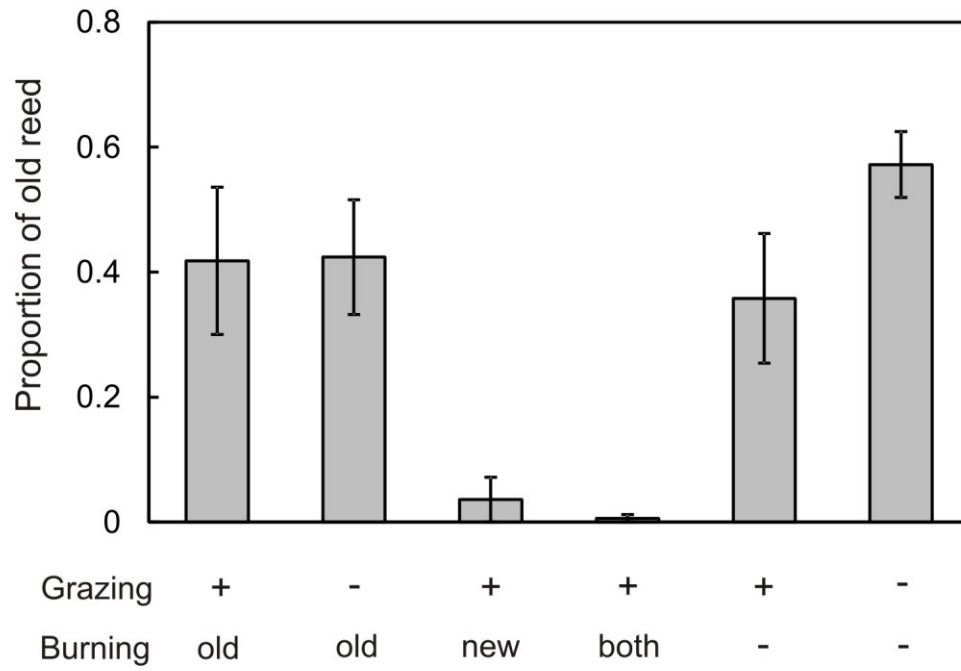
682 Figure 3



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684 Figure 4.



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