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

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

Keywords · habitat diversity · habitat heterogeneity · Hortobágy National Park · intermediate disturbance hypothesis · mosaic vegetation   salt marsh

Introduction

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

Freshwater wetlands are of outstanding importance for biodiversity and have become a priority in conservation (Bobbink et al. 2006; Schweiger et al. 2002). Wetlands have decreased considerably in size, number and quality in the last century in Europe (and in Hungary, Vásárhelyi 1995). Although wetlands have been subject to intensive research in conservation and restoration (Wagner et al. 2008; Wheeler et al. 1995), little is known about the appropriate spatiotemporal allocation and impact of reedbed management in wetlands (Ausden et al. 2005). The theory of adaptive ecosystem management has been present since the 1980s, but areas available for management are rarely large enough to accommodate and experiment with different management regimes (Groom et al. 2006). In temperate grasslands, spatiotemporally variable management by prescribed fire and by grazing resulted in highly heterogeneous habitats (Fuhlendorf and Engle 2001; Hartnett et al. 1996; Vinton et al. 1993). In most wetland studies, sampling areas are too small (under 1 ha) to evaluate the effects of disturbance or the undisturbed operation of natural ecological processes on higher taxonomic groups (Wagner et al. 2008). In addition, most studies followed up only one management action and focused on invertebrates (Ausden et al. 2005; Ditlhogo et al. 1992; Schmidt et al. 2005; Hardman et al. 2012). As a result, we generally know little on how spatiotemporally variable management affects vertebrates, habitats and ecological processes.

The management of reedbeds includes various actions such as periodical flooding (Poulin et al. 2002; Graveland 1998), mowing or cutting (harvesting, Poulin and Lefebvre 2002; Vadász et al. 2008), burning (Moga et al. 2010), grazing/trampling, excavating and herbicide application, or their combination (e.g. burning and cutting in Báldi and Moskát 1995). While effects such as grazing, change in water level, and burning may be considered threats under uncontrolled conditions, they can be important conservation measures as part of a management strategy aiming to apply these effects as controlled disturbances (Margoluis *et al.* 2009; Salafsky *et al.* 2009). A meta-analysis of 21 European studies on the effect of reed management by Valkama et al. (2008) found that management by harvesting, burning, mowing and grazing alters the structure of reedbeds, with reed stems becoming shorter and denser in managed sites compared to non-managed ones. Plant species richness usually increases by management but invertebrate richness decreases after 1-2 years of management. In birds, the abundance of passerine species decreases on average by 60% after burning and reed harvesting (Valkama et al. 2008). Many reedbed-breeding passerines, mainly *Acrocephalus* warblers, actively avoid cut areas, while others show decreased abundance and diversity (Vadász et al. 2008; Poulin and Lefebvre 2002). Some reed songbirds, however, use managed areas, for example, the Aquatic Warbler (*A. paludicola*) prefers cut reed stands (Tanneberger et al. 2009), while the Stonechat (*Saxicola torquatus*) and Marsh Warbler (*A. palustris*) prefer burned reed (Moga et al. 2010). We know much less on how reed management influences non-passerine birds. In addition, little is known on whether there are interactive or synergistic effects of two different management actions on birds (Valkama et al. 2008) to maximize their diversity and abundance in reedbeds.

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

Methods

Management actions

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

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

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

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

Experimental design and data collection

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

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

We measured water depth at each of the five counting points, which were averaged for each transect. We also quantified reed density and complexity at the three internal counting points to characterize the effect of management. The number of old and new reed stems were counted in a circle (diameter 40 cm) positioned at a height of 1 m and 1 m in a randomly selected direction from each internal counting point. We first estimated reed density (based on the counting at the three internal points) by (i) the average number of old stems, (ii) the average number of new stems, (iii) the total number of both old and new stems, and (iv) the average of total number of stems, and (v) the proportion of old reed stems (per total number of stems in the transect) because old reed is important for the breeding of early reed-nesting passerines. Second, we estimated reed complexity by (i) the standard deviation (SD) of the mean number of all stems and (ii) the coefficient of variation (CV) in the number of all stems (standard deviation per mean of number of all stems) for each transect. We also recorded two variables that potentially reflect management, (i) the proportion of reed cover (1 for transects with a continuous cover of reed, 0.9 for transects with reed cover on 90 m etc.), and (ii) the proportion of the length of the transect where reed had been cut relative to the total length of the transect (e.g. 0.2 indicating that reed was cut on 20% of the 100-m length). Evidence of reed cutting was found in eight transects or 27% of n = 30 transects. We thus obtained five variables for reed density (mean number of old and new stems, total number of all stems, mean number of stems, proportion of old stems), two variables for reed complexity (SD of the mean number of all stems and CV in the number of all stems), and two additional variables potentially reflecting management effects: reed cover, proportion of transect length cut in each transect. We thus estimated nine variables for reedbed structure to allow for the possibility that responses of bird functional groups will differ by the preference of birds to different aspects of reed.

Statistical analysis

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

We first ran GLMs to select models that best described our data relative to the three combinations of reed density and complexity variables. We used Akaike's Information Criterion to select the best of the three models for each response variable. In the second step, we ran the best-fitting full models and applied a backward stepwise algorithm to remove non-significant variables and interaction terms. The final reduced models were then fitted to estimate coefficients and compare means.

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

Results

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

Effects of management on the bird community

The Shannon and Simpson diversity as well as the evenness of bird communities were significantly affected by management, whereas total species richness and abundance were not (Table 2, Figure 2). Shannon diversity and evenness were low in grazed patches burned twice and were uniformly high in all other treatments (Figure 2C, E), whereas Simpson diversity was highest in grazed patches burned twice and lower in all other treatments (Figure 2D). Species richness was not affected by any of the factors studied, although the effect of reed complexity was marginally non-significant (Table 2). Abundance appeared to be higher in grazed patches with recent burning (burned in 2009 and burned twice), although large variation did not result in statistically significant differences among treatments (Figure 2B). Rather, bird abundance was negatively affected both by reed cover and water depth (Table 2), indicating more birds in transects with more open water and with shallower water.

Effects of management on bird groups

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

Management effects on reed

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

Discussion

Key findings

We found that spatiotemporally variable management by grazing and burning led to a more heterogeneous landscape structure of marsh habitats (Figure S1), which increased bird diversity in three main ways. First, there were more species and individuals of non-passerines in recently burned patches than in unburned or old-burned patches. Second, there were more species and individuals of reed songbirds in unburned, old-burned or grazed patches than in newly-burned patches. Finally, there were more species of farmland birds in grazed patches, particularly in newly-burned ones, than in non-grazed patches. Our results thus indicate that spatiotemporally variable management may simultaneously benefit several functional groups of birds. Our findings also suggest that this benefit was mediated by management-caused changes in reed structure and increases in habitat diversity and was independent of the variation in water level, which further reinforces the importance of management by grazing and burning.

Effects of cattle grazing

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

For most reed songbirds, patches with a high proportion of old reed were preferable as their species richness and abundance was high relative to patches that were recently burned. The non-managed reed was characterized by high reed songbird diversity and evenness compared to managed stands, similarly to the findings in Valkama et al. (2008). For example, Báldi and Moskát (1995) compared species richness and abundance of reed passerines among cut, burned, non-managed reed and heterogeneous reed containing bulrush, meadows and trees. The abundance and species richness of reed passerines, a group which encompassed both reed and farmland songbirds in our study, was significantly higher in the control area than in managed or heterogeneous areas. Báldi and Moskát (1995) concluded that homogeneous reed stands were highly suitable for reed passerines, thus, they suggested limited or no management for reed passerines. Most other studies focusing on reed passerines also found higher diversity in homogeneous and unmanaged reed (Vadász et al. 2008; Graveland 1999). In several studies, the area-sensitive reed passerines positively preferred non-managed but heterogeneous reed beds (Báldi and Kisbenedek 1998; Báldi 2004; Benassi et al. 2009). However, some authors reported that reed songbirds may differ in their preferences with regard to management (Poulin and Lefebvre 2002) or to water depth because some species nest exclusively in flooded non-managed reedbeds, while others have a wider tolerance regarding the absence of water (Neto 2006).

Effects of burning

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

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

Water depth

Besides management and reed properties, water depth also significantly influenced the bird community (in four of the five models) and some functional groups. There were positive relationships between water depth and Shannon diversity and evenness, and the species richness of reed songbirds, and rails, coots and grebes, and there were negative relationships between water depth and total abundance, Simpson diversity, the abundance of gulls and terns, and the species richness of farmland songbirds. These results are in line with expectations based on the general vegetation patterns largely determined by water depth and on the feeding and habitat use properties of the functional groups involved. For example, shallow water is more likely to host a diverse vegetation (bulrushes, *Schoenoplectus* spp., *Typha* spp., grasses e.g. *Alopecurus*, *Beckmannia*), which gradually gives way to more homogeneous reedbeds in waters of intermediate depth, whereas very deep water will usually be open water devoid of emergent vegetation but rich in floating or submerged vegetation (pondweed, e.g. *Potamogeton* spp., *Lemna* spp., *Ceratophyllum* spp. etc.). The positive relationship between water depth and the richness of reed songbirds and rails, coots and grebes can be explained that transects going through intermediate water depth likely provided better conditions for nesting and feeding for reed songbirds (mainly *Acrocephalus* spp., plus *Emberiza schoeniclus*, *Locustella luscinioides*, *Luscinia svecica*, *Motacilla flava*, *Panurus biarmicus*) and rails, coots and grebes (*Fulica atra*, *Porzana parva*, *Rallus aquaticus*, *Tachybaptus ruficollis*) than transects in shallower water. The somewhat surprising negative relationship between water depth and gull/tern abundance was because gulls and terns, which usually nest on floating vegetation in open water, often rested in cattle-trampled openings in shallow water or because shallower water probably provided better conditions for feeding. Finally, the negative relationship between water depth and species richness of farmland songbirds conformed to the expectations because habitats typically required by these species (*Alauda arvensis*, *Hirundo rustica*, *Miliaria calandra*, *Saxicola rubetra*, *Corvus cornix*) became rarer with increasing water depth.

Despite the influence of water depth on several response variables, in the transects surveyed, there was no systematic variation in water depth among the different treatments, and there were no relationships between water depth and reed structure variables. Moreover, there was no interaction between management and water depth in any of the models. These findings indicated that the effects of management and water depth were independent from one another. These observations, however, also suggest that varying the water level as part of a long-term marsh management programme can be promising as an introduction of further disturbance to increase the diversity of marsh habitats and to benefit a variety of bird species. For example, many species such as ducks and geese, storks and herons, and coots and grebes require a minimum of water for nesting and feeding (Nummi et al. 2013; Pöysa and Vaananen 2014; Causarano and Battisti 2009). Beyond the pure presence of water, the changes in the water level can also affect the presence and abundance of these and several other groups of water birds (e.g. Causarano et al. 2009; Redolfi De Zan et al. 2010; Zacchei et al. 2011).

Management and the intermediate disturbance hypothesis

The results of spatiotemporally variable, combined management by burning and grazing fit the expectations based on IDH in the study marsh. First, the IDH predicts that high disturbance will lead to lower diversity because fewer species will tolerate intense or too frequent disturbance. Our results support this prediction because total Shannon diversity and evenness were lowest whereas Simpson diversity was highest for the patches with highest disturbance (grazed and twice-burned). Because Shannon diversity is more affected by rare species while Simpson diversity is more affected by common species (Magurran 2004), this result suggests that patches with highest disturbance had disproportionately more of the common rather than the rare species. Second, the IDH predicts that low disturbance will be tolerated by a few species, leading to biotic homogenization. The finding that control (non-managed) patches had fewer species and individuals of all groups but reed songbirds appears to support this prediction because reed songbirds avoided combined, burned and grazed patches. However, because reed songbirds had many species, this pattern did not show for total diversity.

Conclusions

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

Practical implications

Wetland managers are often faced with the choice of the hierarchical levels (populations/species or the entire community) they target with conservation actions. When the goal of conservation actions is to increase the density of area-sensitive and specialised bird species (e.g. *Acrocephalus scirpaceus*, *Ixobrychus minutus*), then the population/species level is targeted (Benassi *et al.* 2009). In contrast, when the goal is to increase the number of species, managers target the community level and use richness and diversity indices (Magurran and McGill 2011) for follow-up (e.g. Rácz et al. 2013; Déri et al. 2011). Reedbed management has to be prioritised based on the local conservation needs and managers need to consider the trade-off between increasing the size of homogeneous reed stands for reedbed specialist species on one hand and increasing the diversity of habitats by grazing, burning or water level management on the other. The exceptionally large spatial scales available for our experiment made it possible to provide an example for management to benefit the entire avian community without compromising the habitat requirements of specialists.

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

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

Supplementary Material

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

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

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

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Tables

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

Fire management	**Grazing management**	
Burned in	**Grazed**	**Non-grazed**
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)

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

Response variable	**Predictors**	**Coefficient ± S.E.**	**F (df_1, df_2)**	**p**
Species richness	Reed complexity (CV)[a]	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	**Reed cover**	**-52.19 ± 24.781**	**4.451 (1, 26)**	**0.045**
	Proportion of reed cut	-21.24 ± 10.849	3.225 (1, 26)	0.084
	Water depth	**-0.60 ± 0.291**	**4.336 (1,26)**	**0.047**
Shannon diversity	**Management**	**-0.47 ± 0.184**	**3.324 (5, 21)**	**0.023**
	Reed complexity (CV)[a]	0.19 ± 0.140	2.118 (1, 21)	0.160
	Proportion of reed cut	-0.28 ± 0.223	2.398 (1, 21)	0.136
	Water depth	**0.01 ± 0.005**	**6.137 (1, 21)**	**0.022**
Simpson diversity	**Management**	**0.16 ± 0.051**	**5.317 (5, 23)**	**0.002**
	Water depth	**-0.00 ± 0.001**	**8.138 (1, 23)**	**0.009**
Evenness	**Management**	**-0.16 ± 0.054**	**5.347 (5, 23)**	**0.002**
	Water depth	**0.00 ± 0.001**	**7.500 (1, 23)**	**0.012**

[a] coefficient of variation in the number of reed stems per transect

Figure legends

Figure 1. Aerial photograph of Fekete-rét marsh (in 2005), with location of management actions. Source of photograph: Institute of Geodesy, Cartography and Remote Sensing, Budapest, Hungary.

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

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

Figure 4. Mean ± S.E. proportion of old reed in management treatment levels.

Figures

Figure 1

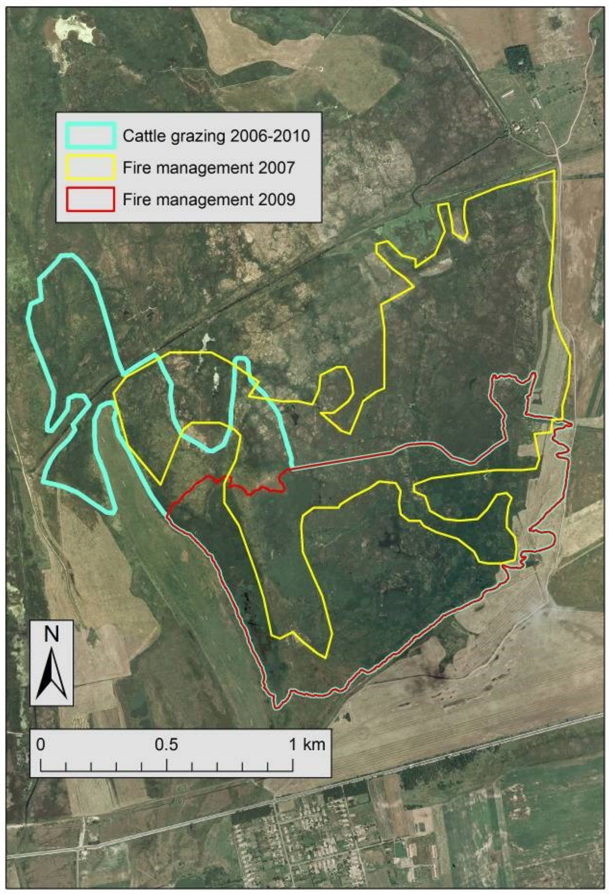
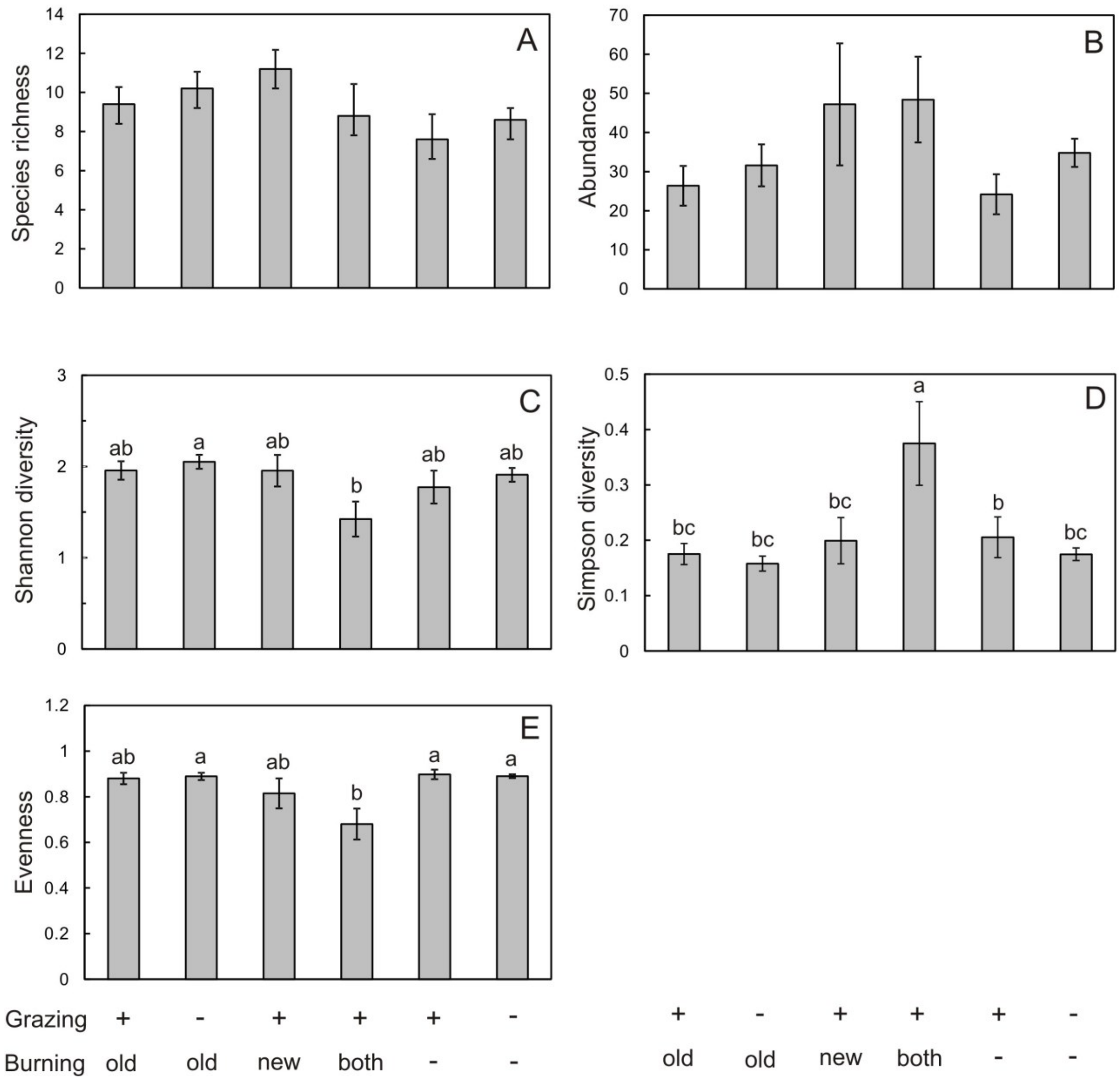
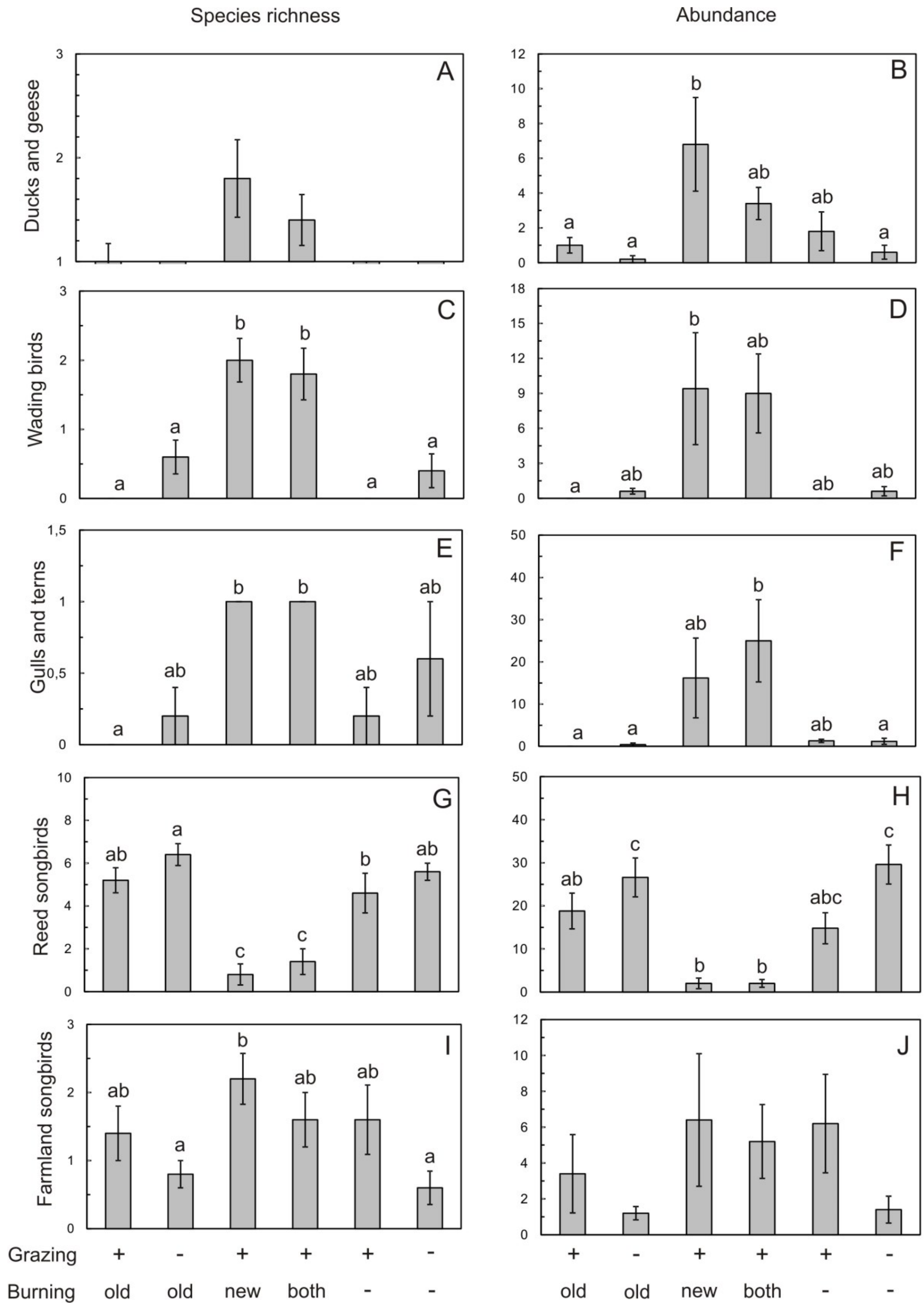


Figure 2



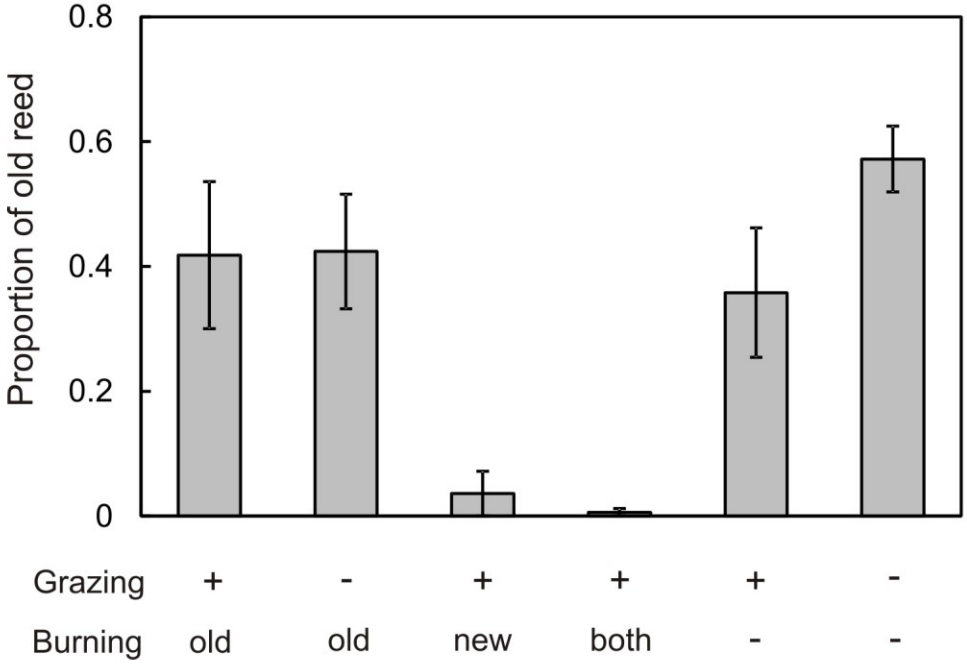
A
B
C
D
E
Species richness
Abundance
Shannon diversity
Simpson diversity
Evenness
0
2
4
6
8
10
12
14
0
10
20
30
40
50
60
70
0
1
2
3
0
0.1
0.2
0.3
0.4
0.5
0
0.2
0.4
0.6
0.8
1
1.2
ab a ab b ab ab
bc bc bc a b bc
ab a ab b a a
Grazing + - + + + -
Burning old old new both - -
+ - + + + -
old old new both - -

Figure 3



Species richness
Abundance
Ducks and geese
Wading birds
Gulls and terns
Reed songbirds
Farmland songbirds
A
B
C
D
E
F
G
H
I
J
Grazing + - + + + -
Burning old old new both - -

Figure 4.



0.8
0.6
0.4
0.2
0
Proportion of old reed
Grazing + - + + + -
Burning old old new both - -