Title

Spatiotemporally variable management by grazing and burning increases marsh diversity and benefits amphibians: a field experiment

Authors

Béla Mester[1*], Mónika Szalai[2], Thomas Oliver Mérő[3], Miklós Puky[4], Szabolcs Lengyel[1]

Affiliations

[1] Hungarian Academy of Sciences (HAS), Centre for Ecological Research (CER), Danube Research Institute (DRI), Department of Tisza River Research, 4026 Debrecen, Bem tér 18/c., Hungary; mester.bela@okologia.mta.hu; lengyel.szabolcs@okologia.mta.hu

[2] Körös-Maros National Park Directorate, Department of Nature Conservation and Grants Coordination, 5540 Szarvas, Anna-liget 1., Hungary; monika.szalai@kmnp.hu

[3] Nature Protection and Study Society - NATURA, Sombor, Serbia; thomas.oliver.mero@gmail.com

[4] HAS CER DRI, Department of Restoration and Animal Ecology, 1113 Budapest, Karolina út 29., Hungary; puky.miklos@okologia.mta.hu

*Corresponding author

BM, E-mail: mester.bela@okologia.mta.hu, Phone/Fax: +36 52 509-200 / 11270

Abstract

Ecosystem management often aims to maintain a diversity of habitats to benefit a large number of species within a landscape. We studied the effects of wetland management by low-intensity cattle-grazing and late-summer burning on marsh vegetation and globally declining anuran amphibians (frogs and toads) in a previously homogeneous reedbed. Burning effectively removed old reed and increased the variability of reed cover and marsh vegetation by the next spring. However, reed grew back strong in areas burned 2 or 3 years before the study, indicating that fire rejuvenates reedbeds. In contrast, cattle-grazing kept reed cover homogeneously low and created open water surfaces. The number of amphibian species and individuals decreased with mean reed cover and old reed density, and increased with variability in reed cover. Correspondingly, amphibian richness and counts were greatest in newly burned areas the next spring. In contrast, a year later, richness and counts were greatest in grazed-only areas, with large decreases in newly burned and control areas. Our results suggest that combined management with grazing and burning can create different habitat patches, some of which will be optimal for amphibians in one year, whereas other patches may become suitable in a subsequent year when successional changes alter previously optimal patches. To maximize optimal habitats, mosaic management should repeat burning once every 2 or 3 years in a rotational manner, and also maintain low-intensity cattle-grazing, which controls reeds and benefits amphibians more sustainably. Our study supports spatiotemporally varied management to facilitate habitat heterogeneity and complexity in dynamic landscapes.

1. Introduction

One of the most important principles of ecosystem management is to create and maintain a diversity of habitat types within the landscape to maximise species diversity (Christensen 1997). Ideal ecosystem management should mimic natural disturbance regimes as far as possible because these enable the maintenance of ecological integrity and near-natural ecological processes in dynamic ecosystems (Mori 2011). Management, when considered as disturbance, can be characterised by its type, temporal frequency, duration, spatial extent and local intensity or specificity (White et al. 1999). The optimal implementation of management requires knowledge of the necessary intensity of disturbance in time and space in light of the resiliency of the ecosystem to be managed (Groom et al. 2006). Ecological theory suggests that species diversity is maximised when ecological disturbance is at intermediate levels in terms of temporal frequency, spatial extent and local intensity (intermediate disturbance hypothesis or IDH, Connell 1978). Despite the overall relevance of the IDH to ecosystem management (e.g. McCabe and Gotelli 2000; Schwilk et al. 1997), intermediate levels of disturbance are rarely known. It is therefore essential that we know the optimal levels of frequency and spatial extent of habitat management if we are to increase habitat diversity to provide for as many species as possible and to mimic natural ecosystems as far as possible. When ecological disturbance is at low levels compared to historically occurring natural disturbances, biotic homogenisation occurs, leading to decreasing species diversity (Lockwood and McKinney 2001). For instance, in many temperate wetlands, when disturbance by grazing/trampling, mowing, cutting, flooding or burning is absent, habitats often become homogeneous in character and physiognomy due to the spread of Common Reed (*Phragmites australis*), a process that can be detected both at the local and landscape scales (Lougheed et al. 2008). In such cases, management should be directed at mimicking

3

natural disturbances. Spatiotemporally variable management may break up habitat homogeneity, leading to more heterogeneous habitat structure and a range of habitat types accessible for a wider pool of species (Christensen 1997; Wiens 1997). Spatiotemporally variable management by grazing and prescribed fire leads to heterogeneous habitats in temperate grasslands (Fuhlendorf and Engle 2001; Hartnett et al. 1996; Vinton et al. 1993) and in wetlands (Mérő et al. 2015).

The global decline of amphibians presents a major challenge in conservation and natural resource management (Nyström et al. 2007; Pittman et al. 2014; Stuart et al. 2004). One of the main reasons for the decline is the loss, fragmentation and degradation or pollution of freshwater wetlands (Cushman 2006; Dodd and Smith 2003; Van Den Bos and Bakker 1990), which also are important centres of biodiversity for plants and animals other than amphibians (Zedler and Kercher 2005). The restoration and management of freshwater wetlands have thus become an urgent and global priority in conservation (Bobbink et al. 2006; Schweiger et al. 2002). Despite the increasing attention to the restoration and management of freshwater wetlands (Wagner et al. 2008), we know little of the appropriate spatiotemporal allocation of management (Ausden et al. 2005; Perry et al. 2012) and of the impact of such management on amphibians (Smith and Sutherland 2014). Habitat management for amphibians includes creating or restoring breeding ponds, increasing the connectivity between ponds, and establishing and maintaining shallow open water habitats by grazing or fire management (Bisson et al. 2003; Hazell et al. 2004; Pilliod et al. 2003). Although there is a growing body of knowledge on how controlled and natural fires affect amphibian communities, the issue is far from settled due to the complexity of species-specific effects that depend on the local habitat structure and populations (Hossack and Corn 2007). Short-term negative effects include increased solar and UV-B radiation, high surface temperatures, aridification, and

increased predation (Pilliod et al. 2003). In contrast, some studies reported minor negative effects, mostly at mid to long-term time intervals, such as the maintenance of mosaic habitat structure and landscape heterogeneity (Perry et al. 2012; Russell et al. 1999). Amphibians have various behavioural and physiological adaptations that enable them to survive the direct effects of burning in wet habitats. Open water surfaces and unburned wet patches provide refuges for amphibians during burning, whereas underground burrows can also protect them from fires (Pilliod et al. 2003; Roznik and Johnson 2007; Russell et al. 1999). Bufonids and Pelobatids also may show an evolutionary adaptation to escape fire by digging burrows (Nomura et al. 2009), whereas hylid frogs are known to avoid an approaching headfire by detecting its crackling sounds (Grafe et al. 2002).

Although livestock grazing can benefit amphibians by removing vegetation from shallow waters, several studies found that amphibians are negatively affected by grazing (Burton et al. 2009; Hoverman et al. 2012; Jansen and Healey 2003). However, these studies were conducted in forest and grassland ponds and we know little about the separate or combined effects of grazing and fire management on amphibians in marshes and reedbeds. The combined effects of grazing and burning have been studied only in grasslands of northern Argentina (Cano and Leynaud 2009). All other studies of wetlands followed only one management action and focused on plants or invertebrates (Ausden et al. 2005; Ditlhogo et al. 1992; Hardman et al. 2012; Schmidt et al. 2005), likely because the restored/managed areas were too small (under 1 hectare) to evaluate the impacts of disturbance on taxonomic groups such as vertebrates (Wagner et al. 2008). It is thus not surprising that a recent meta-analysis of European studies on the effects of reedbed management on wildlife found no study of amphibians (Valkama et al. 2008).

In this study we examine whether and how spatiotemporally variable management by low-intensity cattle-grazing and prescribed late-summer burning of reedbeds affect reed habitats and anuran amphibians (frogs and toads). Grazing and burning were conducted to increase the diversity of marshes that had become homogeneously overgrown by Common Reed due to invariable management (constant water supply and winter reed harvesting) in the past. In a unique large-scale field experiment (Mérő et al. 2015), we quantified reed cover, plant species richness, anuran species richness and counts over two years to address five questions: (i) Does management reduce reed cover, influence vegetation structure and increase the diversity of habitats? (ii) Do changes in reedbed properties due to management benefit anuran amphibians? (iii) Is there a direct link between management and benefits to the amphibian community? (iv) Do grazing and burning differ in their impacts on the reed habitats and on amphibians? (v) Does management intensity influence anuran species richness and counts?

2. Materials and methods

2.1. Study area

The experiment was implemented in Fekete-rét (N47°33'38.60", E20°56'4.07"; 88 m a.s.l.), the largest (600 ha) alkali marsh in the Egyek-Pusztakócs marsh and grassland system (EPMS, 4073 ha). The entire EPMS is included in the Natura 2000 network, is an Important Bird Area in Europe, is listed in the Ramsar Convention on Wetlands of International Importance and is a World Heritage Site as part of Hortobágy National Park (E-Hungary) (Aradi et al. 2003). Paleoecological studies indicate that the region was frequently burned by wildfires in pre-human times and that these fires were important in maintaining the open steppe and wooded steppe landscape prior to the appearance of pastoralism c. 1000 yrs B.C., which led to a further increase in open habitats (Magyari et al. 2010). The area was an active floodplain of the Tisza river until its regulation in the 1850s. Military maps from 1855-1866

and aerial photographs from 1959-1965 (**Fig. S1**) show the marsh as a complex of open water surfaces, bare alkali shorelines, and small patches of bulrushes (*Typha* spp.) and reed in the lower-lying parts of the marsh (Aradi et al. 2003). Low vegetation cover was maintained by extensive grazing by cattle and sheep. For example, in the eastern Hortobágy region, the area covered by reed was 0.04% in 1892, which increased to more than 2% by 1975 with the decline of grazing (Tóth 2003). The marshes were drained and became completely dry by the early 1970s. In the first and largest (>4000-ha) habitat restoration programme in Hungary (1976-1997), a new water supply system was built that again brought water from the Tisza river to the marshes, which have recovered spectacularly. However, a constant water supply and intensive winter reed-harvesting led to the establishment of homogeneous reedbeds by the mid-2000s. Reed management by cattle-grazing and burning was implemented between 2006 and 2009 as part of a landscape-scale rehabilitation project (Lengyel et al. 2012) (http://life2004.hnp.hu).

2.2. Marsh management by cattle-grazing and prescribed burning

Management aimed to increase the diversity of marsh habitats by creating openings in homogeneous reedbeds to ultimately recover the mosaic structure of habitats that once characterised the area. Based on historical land use and previous experience elsewhere (Aradi et al. 2003; Kelemen 2002), cattle-grazing and burning were chosen for reedbed management. Paleoecological studies and accounts from shorter time scales indicate that both these disturbances were part of the ecosystem's evolutionary history (see above). To mimic natural disturbances (grazing by large herbivores and wildfire) as closely as possible, cattle were free to roam and fire was not contained within the southern half of the marsh (**Fig. S2**). Grazing infrastructure was established in the SW part of the marsh in early 2006. Grazing was conducted between April and November each year between 2006 and 2011 by 180 head of

Hungarian grey cattle, an ancient breed highly suitable for marsh management as they consume reed even in deep (up to 1.5 m) water (Kelemen 2002). Cattle regularly used 200 hectares of the marsh and c. 100 ha of meadows and grasslands surrounding the marsh; grazing pressure was thus 0.6 livestock units (LUs) per hectare.

Prescribed burning was implemented by professional firefighters and national park rangers early in September 2007 and 2009 (**Fig. S3**). This is the peak flowering period of the reed plant, and we predicted that burning at this time, when much of the nutrients available to the plant are in the shoots and inflorescences, will cause the greatest damage to the plant (Cross and Fleming 1989; Engloner 2009; Hazell et al. 2004). Furthermore, this period is well after the breeding season but before the autumn migration to wintering sites for amphibians and is less likely to cause harm to amphibians than spring burning, a usual practice in reed management. Fires lasted for two (2007) or three (2009) days and were relatively thorough, with flames usually reaching 2-3 m high but sometimes much higher (10-12 m). The fire caused a nearly complete loss of old and green reed on 110 ha (in 2007) and 130 ha (in 2009) (**Fig. S3**).

2.3. Experimental design

The implementation of the principle of mimicking natural disturbances as closely as possible resulted in differently managed areas of irregular shape (**Fig. 1**). The actual areas that were grazed and burned were determined during detailed ground surveys in which we walked and recorded the borderlines between managed (regularly grazed/trampled or burned) and unmanaged areas by hand-held GPS units (accuracy: 2-3 m). Field measurements were then entered in a geographical information system (GIS) and similarly managed areas were delineated as polygons. The experimental design was an incomplete crossing of the grazing

8

management (two levels: grazed, ungrazed) and the burning management (four levels: unburned, burned only in 2007, burned only in 2009 and burned twice). Most of the areas burned in 2009 were subsequently grazed by cattle, thus, two treatment combinations (ungrazed and burned in 2009, and ungrazed and burned twice) were not replicated. The final six treatment combinations, in the order of increasing disturbance intensity, were: (i) not managed (overall control), (ii) grazed and unburned (burning control), (iii) ungrazed, old-burned (burned only in 2007), (iv) grazed, old-burned, (v) grazed, newly burned (burned only in 2009), and (vi) grazed, twice-burned (in both 2007 and 2009). After identifying similarly treated areas (polygons in the GIS), we randomly selected five transects as experimental/sampling units within each treatment level (total n = 30). We first randomly selected the starting points (X, Y coordinates) of the transect and then randomly determined the orientation of the transects (length: 100 m) except where the shape of the treated area inhibited random placement. To reduce spatial non-independence arising from the proximity of the experimental units, transects were designated at least 100 m from each other.

2.4. Sampling methods

We sampled anurans by visual and call detection surveys while walking along the transects. In visual surveys, we recorded individuals observed visually within 2 m or heard within 25 m either left or right from the transect (Dodd et al. 2012). Call surveys also served to identify the three water frog species of the *Pelophylax* complex (Anthony and Puky 2001). Surveys were conducted in mid-April at the peak mating and vocalising period for most species. The order in which transects were surveyed was determined randomly.

To evaluate the effect of management on reedbed properties, we recorded four variables. We estimated reed cover as the proportion of transect length covered by reed along the four 25 m

sections of each transect and averaged the four values for the entire transect length to obtain mean reed cover. Mean reed cover (%) was arcsine-transformed for analysis. To estimate reedbed complexity, we used the coefficient of variation (CV) in reed cover, i.e., the standard deviation divided by the mean reed cover of the transect. For more detailed information on reed properties after the last burning (2009), we also measured reed density in April 2010 by counting the number of old (dry) and new (green) reed stems in a circle (diameter 40 cm, area ~ 0.126 m^2) held at 1 m height and 1 m away in a randomly chosen direction at three equally spaced internal points of each transect (at 25, 50 and 75 m). These measurements were also averaged for each transect.

We recorded several additional environmental variables that could influence the number and activity of anuran amphibians (water depth, water temperature and three variables for weather). We measured water depth (accuracy: 5 cm) and water temperature at five internal points (0, 25, 50, 75, and 100 m) along each transect. Finally, we measured air temperature and wind speed and estimated cloud cover (on a scale of 1 to 5) for the duration of the survey of each transect. For each environmental variable recorded, we averaged values measured at several points along the transect for analysis and we used one transect as one datapoint.

To evaluate changes in the marsh vegetation after management, we sampled vegetation at 56 randomly selected points in the marsh before the first burning (June 2007). At each sampling point, we recorded all flowering plants, determined every species and estimated their cover in a randomly placed 2 m x 2 m plot. Thirty of the 56 plots were burned in Sep 2007 and subsequently grazed in autumn 2007 and spring 2008; we resurveyed these plots using the same methods in June 2008 for before-after comparisons.

Sampling of amphibians along the transects was conducted in the early spring (April) in both 2010 and 2011. In 2012, a year of extreme drought, the national park authority allowed the marsh to dry completely in order to mimic weather-driven dynamics in the EPMS, whereas in 2013, the eastern part of the marsh was reconstructed for ecotourism development. Sampling in 2012 and 2013 would thus not have resulted in data that could be compared meaningfully with data from previous years. Furthermore, management effects were already weak in year 2 after management due to the rapid regrowth of reed by the third spring (2012), indicating that continued sampling was not likely to add much to the evaluation of management effects on amphibians.

The expected outcome of burning and grazing was to control reed vegetation, which may bear on the detection probability of amphibians if increasing vegetation cover is associated with decreasing detectability. We carried out two additional surveys to test such an association. First, in the early summer of 2010, we surveyed 12 transects (length 40 m each, total 480 m) other than the 100 m study transects for a total of 124 minutes in unmanaged dense reed to make sure that we did not miss anurans due to lower detection probability. Intensive searching resulted in only nine individuals of two species (1 adult Edible Frog *Pelophylax esculentus* and 5 juvenile *Pelophylax* spp., and 3 adult Fire-bellied Toads *Bombina bombina*, the most abundant amphibian of the marsh system). Second, we performed nighttime call monitoring (Dodd et al. 2012) in 2011 in conjunction with the regular transect survey. If detection probability was lower in dense reed, there should be no correlation or there should be a negative correlation betwen the number of visually found individuals and call intensity. The widely used Wisconsin index for call intensity showed positive correlations with the number of visually found individuals (Spearman rank correlations, n = 30 transects; all species: r = 0.384, p = 0.036; Fire-bellied Toads, r = 0.451, p = 0.012), although the correlation was

positive but not significant for *Pelophylax* water frogs (r = 0.225, p = 0.232). In addition, the number of visually recorded individuals and the number of individuals detected by their calls in the regular transect surveys showed positive correlations (Spearman rank correlations, n = 30 transects; all species: r = 0.432, p = 0.017; Fire-bellied Toads, r = 0.478, p = 0.007), again with a non-significant positive correlation for *Pelophylax* water frogs (r = 0.255, p = 0.175). *Pelophylax* water frogs, however, are much larger and easier to detect visually than Fire-bellied Toads, other toads or Tree Frogs, therefore, detection probability is less of an issue with this group. Finally, a recent study of detection probability of amphibians in ponds covered by an average of 40% vegetation (Petitot et al. 2014) found high rates of detection for all amphibians even in one visit if the date of the survey was carefully chosen and if the observer was familiar with the species and the study area (both conditions apply in our study). These observations suggest that detection probability was not likely to be lower in dense reed than in more open habitats.

2.5. Data processing and analysis

We performed statistical analyses in three steps. First, we studied whether management affected reedbed properties (mean cover, CV reed cover, number of old and new reed stems) by fitting general linear mixed-effects models (GLME). For mean and CV reed cover (available for two years), the model included the three management treatments (grazed vs. ungrazed, burned in 2007 vs. unburned in 2007, burned in 2009 and unburned in 2009) as predictors and year as fixed effects, whereas transect identity was used as the random effect. To test whether the effect of management treatments differed between the years, we included all interactions between the management variables and year. For the number of old and new reed stems (available from 2010 only), GLMEs included the three management treatments as fixed effects. GLMEs were built using the 'lme' function of the R package 'lme4'. In

addition, we compared the species richness and total cover of flowering plants before and after the first burning by Wilcoxon's matched pairs tests to more closely evaluate the effect of burning on vegetation diversity.

In the second step, we studied the effect of reedbed properties on the anuran amphibian community. Response variables were species richness (number of species), total counts (number of individuals), and the counts of *Pelophylax* water frogs (three species combined) and Fire-bellied Toads. For each of the four response variables, we built GLMEs with the two reed cover variables, year and five environmental variables as fixed effects, the management*year interactions, and transect identity as the random effect. We fitted GLMEs using the 'glmer' function of R, specifying Poisson error distribution and log link function, as recommended for count data (R Core Team 2014).

In the third step, we directly analyzed the effect of management treatments on amphibian anuran richness and counts. Again, we fitted GLMEs ('glmer', Poisson errors and log link function) for four response variables (species richness, total counts, counts of *Pelophylax* water frogs and Fire-bellied Toads) to explain their variation based on the three management treatment variables, year, interactions between treatment and year, and the five environmental variables.

In each GLME, the full model included all main effects and biologically meaningful interactions. In models fitted by function 'glmer', we used Wald Z-statistic and its associated level of significance for each parameter in the model summary. We then removed non-significant (p > 0.05) effects and interactions in a backward stepwise fashion to obtain the minimal adequate model (Crawley 2007), which was then used to test the effects of

13

management and to calculate coefficients. In cases when management significantly ($p < 0.05$) influenced response variables, we compared means by performing t-tests using Welch's adjustment of the degrees of freedom when variances were unequal. All statistical analyses were carried out in the R statistical environment (version 3.1.1., R Core Team 2014).

3. Results

In 2010, we detected 537 individuals of six anuran amphibian species (118 individuals of the three *Pelophylax* water frogs, 359 Fire-bellied Toads, 39 Common Toads (*Bufo bufo*) and 21 Green Toads (*Pseudepidalea viridis*). In 2011, we recorded 630 individuals of five species (290 individuals of the three water frogs, 329 Fire-bellied Toads, and 11 European Tree Frogs *Hyla arborea*). Common or Green Toads were detected only in 2010 and only in newly burned or twice-burned areas, whereas Tree Frogs were observed only in 2011, with seven individuals in grazed newly burned areas and four individuals scattered in three other treatments.

3.1. Effects of management on reed properties

Mean reed cover was high in transects with no management and in ungrazed, old-burned transects, lowest in grazed-only transects and intermediate in grazed, old-burned transects (**Fig. 2A**). In newly burned transects, mean reed cover was low in 2010 but increased at least two-fold and returned to intermediate levels by 2011 (**Fig. 2A**). Mean reed cover was influenced positively by year as it increased from 2010 to 2011 and was influenced negatively by grazing as it remained low only in grazed-only areas (**Fig. 2A**, **Table 1**). CV reed cover was positively influenced by burning in 2009, and was greater in newly burned areas (0.61 ±

S.E. 0.105, n = 20 transects) than in unburned areas (0.31 ± 0.050, n = 40; $t_{27.93}$ = 2.566, p = 0.016; **Fig. 2B**, **Table 1**).

Mean reed cover in the before-after comparison study plots decreased significantly from 55.6 ± 37.71% (S.D.) before management to 35.7 ± 22.58% the next year (Wilcoxon's matched pairs test, z = 3.617, n = 30, p < 0.001). We detected 10 plant species before and 18 after the management. Nine taxa appeared (*Atriplex hastata*, *Bidens tripartitus*, *Chenopodium chenopodioides*, *Galium palustris*, *Inula britannica*, *Persicaria* spp., *Rumex stenophyllus*, *Schoenoplectus lacustris* and *Sonchus arvensis*) and one species (*Salix caprea*) disappeared. The mean number of plant species increased from 2.9 ± 1.46 before to 4.0 ± 2.40 after the management (z = 3.264, n = 30, p = 0.001). In addition, several species increased their cover considerably after management (*Epilobium tetragonum*, *Lycopus europaeus* and *Rumex palustris*).

In 2010, there were hardly any old reed stems in areas burned in 2009 (0.4 ± 0.30 stems per 0.126 m^2, or c. 3.2 stems·m^{-2}, n = 10 transects), whereas the mean number of old reed stems was much greater (14.1 ± 2.15 or c. 113 stems·m^{-2} , n = 20) in other areas ($t_{19.73}$ = 6.309, p < 0.0001; **Fig. 2C**), indicating a significant negative effect of recent burning on the number of old reed stems (**Table 1**). The number of old stems in areas burned in 2007 was comparable to those in non-managed control and grazed-only areas (**Fig. 2C**).

The number of new reed stems in 2010 indicated increased regrowth of reed in newly burned areas, whereas the number of old and new reed stems was similar in old-burned areas (**Fig. 2C**). Burning in 2007 positively influenced the number of new reed stems (**Table 1**), because the number of new reed stems in 2010 was significantly greater in areas burned in 2007 (17.9

± 1.78, n = 15) than in other areas (12.9 ± 1.38, n = 15; $t_{26.34}$ = 2.193, p = 0.037; **Table 1**). Such regrowth of new reed was particularly pronounced in the twice-burned transects (**Fig. 2C**).

3.2. Effects of reed properties on amphibians

When data from both years were analyzed, mean reed cover was the only factor significantly influencing species richness (**Table 2**), and its effect was negative, indicating fewer species in transects with greater reed cover (**Fig. 3A**). Total counts were influenced by significant interactions between mean reed cover and year and between CV reed cover and year (**Table 2**). The former interaction was because total counts decreased faster with mean reed cover in 2011 than in 2010 (**Fig. 3B**). The latter interaction was because total counts increased with CV reed cover in 2010 but not in 2011, although the range of CV reed cover in 2011 was also roughly half of what it was in 2010, indicating more homogeneous reed in the transects (**Fig. 3C**).

In 2010, the number of old reed stems had strong negative effects on both species richness and total counts (**Table 2**, **Fig. 3D-E**). Two rare toads were detected only in newly burned areas (n = 39 Common Toads) or in newly burned areas and ungrazed, old-burned areas (n = 21 Green Toads). Total counts were positively related to the number of new reed stems (**Table 2**, **Fig. 3F**), likely because the latter was particularly high in areas burned in 2009 (**Fig. 2C**) that were preferred by amphibians.

3.3. Effects of management on amphibians

Analyses of the direct effects of management on amphibians showed that species richness was influenced by significant interactions between grazing and year and between recent burning

and year (**Table 3**). The former interaction was mostly because species richness increased significantly from 2010 to 2011 in grazed-only areas and in old-burned areas with grazing, but decreased in non-managed areas and in newly burned areas (**Fig. 4A**). The latter interaction was because species richness in 2010 was greater in newly burned areas than in other areas but not in 2011 (**Fig. 4A**). Species richness was also positively influenced by cloud cover (**Table 3**).

Total counts was similarly influenced by significant interactions between grazing and year and between recent burning and year (**Table 3**). The former interaction was because counts increased considerably in grazed-only transects from 13.8 ± 8.61 individuals (range 0-47) in 2010 to 73.4 ± 27.32 individuals (range: 27-177) in 2011, whereas it did not change much in ungrazed areas (**Fig. 4B**). The increase in counts in grazed-only areas was observed both for the three species of *Pelophylax* water frogs and the Fire-bellied Toad (**Fig. 5**). The latter interaction was because counts decreased by more than half from 2010 to 2011 in areas burned in 2009 (**Fig. 4B**), likely due to the regrowth of reed. The decrease in these areas was greater for Fire-bellied Toads than for water frogs (**Fig. 5**). Finally, total counts were also influenced negatively by water depth and positively by wind intensity and cloud cover (**Table 3**).

4. Discussion

We used a field experiment to simultaneously measure the effects of cattle-grazing and controlled fire on the diversity of marsh habitats and on post-metamorphic anuran amphibians. Our results demonstrated that management by low-intensity cattle-grazing and high-intensity burning can reduce reed cover and increase the plant and amphibian diversity

of marsh habitats. Late-summer burning effectively destroyed old reed, reduced reed cover, increased the variability in reed cover and facilitated the appearance of plants other than reed the next spring. However, burning did not completely destroy reed because it grew back readily from rhizomes. Mean reed cover in 2010 and 2011 was either high or intermediate in areas burned in 2007 and it increased back to intermediate levels by 2011 in areas burned in 2009. In addition, the number of new reed stems was positively related to burning in 2007 and increased regrowth was observed in twice-burned areas. These findings suggest that the disturbance effect of burning disappears in 2-3 years and thus it provides only short-term benefits to reedbed habitats and amphibians. In contrast, mean reed cover remained low in cattle-grazed areas, and low values of CV reed cover indicated low reed cover throughout the transect length in grazed areas. Regular trampling and grazing by cattle effectively controlled reed, increased the diversity of habitats (**Fig. S4**), including the shallow, open water surfaces and mudflats preferred by amphibians (**Fig. S5**).

The increased diversity of marsh habitats, principally the greater availability of shallow, open water surfaces with little or no reed, became suitable for amphibian reproduction the following spring. This conclusion was supported by (i) more species and individuals of water frogs and rare toads in newly burned areas, which had little or no reed cover, (ii) the negative relationships between anuran richness or counts and mean reed cover or the number of old reed stems, and (iii) the positive relationship between total counts and CV reed cover. One explanation for the greater counts of anurans in newly burned areas is that these areas had almost no old reed in spring 2010 and their water probably warmed faster than water with old reed cover (Puky et al. 2005). Open water surfaces can provide better exposure of water frogs to the sun to warm up their bodies, especially on cold (April) days. Earlier warming results in more time available for feeding and reproduction, thus, open water is likely a key factor for

18

amphibians in this community. Taken together, these results suggest that the changes in reed properties due to management benefitted anuran amphibians.

We also found direct links between grazing and anuran richness or counts. Species richness increased from 2010 to 2011 only in grazed-only and old-burned grazed areas, but decreased in newly burned areas and control transects. Similarly, in 2010, total counts were greatest in newly burned areas, whereas in 2011, they were greatest in grazed-only areas, with a large decrease in newly burned and control areas. These results provide evidence that burning and cattle-grazing have different impacts on amphibians (**Fig. 6**). Whereas the primary effect of recent burning was to eliminate old reed stems, the primary effect of old burning was to facilitate the regrowth of reed, indicating that fire enables the rejuvenation of reed (Valkama et al. 2008). In contrast, the primary effect of cattle-grazing was to keep mean reed cover homogeneously low over the entire transect length. Because lower mean reed cover was associated with greater amphibian richness and counts, these observations suggest that cattle-grazing may have a more fundamental effect than fire in controlling reed and in providing benefits to amphibians. A likely explanation is that cattle not only consume the shoots throughout the year but also damage the underwater plant parts through their trampling (Hamer and McDonnell 2008). Although this effect likely depends on grazing intensity (Jansen and Healey 2003), our observations suggest that over longer terms (i.e., four years), even low-intensity cattle-grazing can effectively control reed and maintain low reed cover. Taken together, our results support the view that management combining grazing and burning can create different habitat patches, some of which will be optimal for anuran amphibians in one year, while other patches becoming suitable in a subsequent year when successional changes decrease the suitability of the previously optimal patches in the dynamically changing marsh landscape (**Fig. 5**).

Finally, our results also demonstrate that management intensity influenced amphibian richness and counts (cf. order of increasing intensity from left to right on the x-axis in Figs. 4 and 5). This is because the greatest species richness and counts were found for high-intensity treatments in 2010 (grazed and burned in 2009 or in both years) and for a low-intensity treatment in 2011 (grazed only). Intermediate levels of management intensity (ungrazed and burned in 2007, or grazed and burned in 2007) did not have more species or individuals than either low-intensity or high-intensity treatments. Therefore, our results do not support the predictions of the IDH.

To our knowledge, our study is the first to provide both direct and indirect evidence of beneficial effects of cattle-grazing and fire management on amphibians in non-forest habitats, and thus it fills a gap in wetland management for biodiversity conservation (Valkama et al. 2008). Surveys of the bird community in the study area also demonstrated that management resulted in a higher diversity of habitats and it increased bird diversity in various ways (Mérő et al. 2015). Our results agree with those of Perry et al. (2012), who found greater abundance of toads after a short-rotation controlled burning in forests, and suggest that burning can also benefit toads in marshes. Our findings, however, differ from the results of a similar study conducted in grasslands in northern Argentina, which found that prescribed burning, combined with intensive grazing, had large negative effects on amphibians (Cano and Leynaud 2009). Likely explanations for these differences are that burning may cause considerably more direct damage to amphibians in grasslands than in wet marshes and that grazing in our study was implemented at a low intensity and in wet habitats, which may better tolerate grazing than grasslands.

Cattle-grazing of marshes can increase habitat diversity by removing old reed, reducing reed density, creating openings and open water surfaces in reedbeds (Jansen and Healey 2003; Verga et al. 2012). Despite these benefits, previous studies reported lower species richness, abundance or diversity of amphibians in cattle-grazed wetlands, due to direct mortality from trampling, increased predation and solar and UV-B radiation in more open habitats, increased desiccation, deterioration of water quality through increased nitrogen levels or eutrophization, or the presence of *Ranavirus* (Burton et al. 2009; Hoverman et al. 2012; Jansen and Healey 2003; Schmutzer et al. 2008). We did not observe any of these effects in our study, likely because the intensity of grazing was low. The impact of grazing on amphibians is known to depend on its timing, intensity and local history, and can vary by species (Burton et al. 2009; Verga et al. 2012). Our results suggest that low-intensity grazing does not directly harm post-metamorphic anurans or that the potential negative effects are counter-balanced by the habitat-level benefits of grazing. Further studies are required to evaluate whether cattle had adverse effects on tadpole survival and development through their trampling or the nitrification/eutrophication of the wetland habitats (Gray et al. 2007).

We conclude that reedbed management by low-intensity cattle-grazing and late-summer burning can lead to habitats preferred by post-metamorphic anurans. Low-intensity grazing controls reed and has little negative effects on anurans, but it needs to be maintained over longer periods to benefit amphibians. Late-summer burning also effectively controls reed by eliminating old reed, but it needs to be repeated once every 2-3 years to benefit amphibians because its effect disappears soon due to the regrowth of reed. Our results support the view that habitat management varying in space and time can lead to a mosaic of reed marsh habitats that benefits anuran amphibians. The results of our study thus support previous calls

for spatiotemporally varied management to facilitate habitat heterogeneity and complexity in dynamic landscapes (Christensen 1997; Parr and Andersen 2006).

5. Management implications

We recommend the joint use of grazing and fire management to increase the habitat and species diversity of reed marshes as the two are complementary rather than supplementary. Controlled fires should be carried out in late-summer to minimize direct mortality to amphibians, and patchy burning or patch mosaic burning is considered more favourable as it leaves suitable refuges to species (Parr and Andersen 2006). Our results further show that if the objective of management is to completely destroy the reed plant, the rhizome must be drowned by flooding the next winter/spring. Otherwise, reed will vigorously regrow in burned areas (Valkama et al. 2008). In long-term marsh management by controlled burning, local fire intervals should be carefully established, particularly if periodic flooding or cattle-grazing is planned (Coops and Hosper 2002; Hackney and de la Cruz 1981; Matthews et al. 2010; Parr and Andersen 2006). Ideally, patch mosaic burning should be implemented in a rotational manner; for example, if the fire interval is set at three years, one-third of the area should be burned every year to maximize the continuity of optimal habitats. Finally, the direct negative effects of cattle-grazing to amphibians can be minimized and the indirect, habitat-level benefits to amphibians can be maximized if grazing is conducted at low stocking intensity (likely not much more than the 0.6 LUs per hectare applied here). A mosaic management of fire and grazing is recommended in large extensive reedbeds to best mimic the natural disturbances and to maintain diverse habitats and vegetation.

7. References

Anthony, B., Puky, M., 2001. Kétéltűek hang alapján történő monitorozása [Call monitoring of amphibians]. Central European University and Varangy Akciócsoport Egyesület, Budapest.

Aradi, C., Győri, S., Lengyel, S., 2003. Az Egyek-Pusztakócsi mocsárrendszer (Hortobágy) [The Egyek-Pusztakócs marsh system], In River Tisza and its Hydrological System II. Strategic Studies at the Hungarian Academy of Sciences. ed. I. Teplán, pp. 277-306. Hungarian Academy of Sciences, Budapest.

Ausden, M., Hall, M., Pearson, P., Strudwick, T., 2005. The effects of cattle grazing on tall-herb fen vegetation and molluscs. Biological Conservation 122, 317-326.

Bisson, P.A., Rieman, B.E., Luce, C., Hessburg, P.F., Lee, D.C., Kershner, J.L., Reeves, G.H., Gresswell, R.E., 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. Forest Ecology and Management 178, 213-229.

Bobbink, R., Beltman, B., Verhoeven, J.T.A., Whigham, D.F., 2006. Wetlands: Functioning, Biodiversity Conservation and Restoration. Springer, Berlin.

Burton, E.C., Gray, M.J., Schmutzer, A.C., Miller, D.L., 2009. Differential responses of postmetamorphic amphibians to cattle-grazing in wetlands. Journal of Wildlife Management 73, 269-277.

Cano, P.D., Leynaud, G.C., 2009. Effects of fire and cattle grazing on amphibians and lizards in northeastern Argentina (Humid Chaco). European Journal of Wildlife Research 56, 411-420.

Christensen, N.L., 1997. Managing for heterogeneity and complexity on dynamic landscapes, In The Ecological Basis for Conservation: Heterogeneity, Ecosystems, and Biodiversity. eds S.T.A. Pickett, R.S. Ostfeld, M. Shachak, G.E. Likens, pp. 167-186. Chapman & Hall, New York.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199, 1302-1310.

Coops, H., Hosper, S.H., 2002. Water-level management as a tool for the restoration of shallow lakes in the Netherlands. Lake and Reservoir Management 18, 293-298.

Crawley, M.J., 2007. The R Book. John Wiley & Sons, Ltd., Chichester.

Cross, D.H., Fleming, K.L., 1989. Control of *Phragmites* or Common Reed, In Waterfowl Management Handbook. eds D.H. Cross, P. Wohs, pp. 1-5. U.S. Fish and Wildlife Service, Fort Collins.

Cushman, S.A., 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128, 231-240.

Ditlhogo, M.K.M., James, R., Laurence, B.R., Sutherland, W.J., 1992. The effects of conservation management of reed beds. I. The invertebrates. Journal of Applied Ecology 29, 265-276.

Dodd, C.K., Jr., Loman, J., Cogălniceanu, D., Puky, M., 2012. Monitoring amphibian populations, In Conservation and Decline of Amphibians: Ecological Aspect, Effect of Humans and Management. eds H. Heatwole, J.L. Wilkinson, pp. 3577-3635. Surrey Beatty & Sons, Baulkham Hills, Australia.

Dodd, C.K., Jr., Smith, L.L., 2003. Habitat destruction and alteration: historical trends and future prospects for amphibians, In Amphibian Conservation. ed. R.D. Semlitsch, pp. 94-112. Smithsonian Institution Press, Washington, D.C.

Engloner, A.I., 2009. Structure, growth dynamics and biomass of reed (*Phragmites australis*): a review. Flora 204, 331-346.

Fuhlendorf, S.D., Engle, D.M., 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. Bioscience 51, 625-632.

Grafe, T.U., Döbler, S., Linsenmair, K.E., 2002. Frogs flee from the sound of fire. Proceedings of the Royal Society of London 269, 999-1003.

Gray, M.J., Miller, D.L., Schmutzer, A.C., Baldwin, C.A., 2007. Frog Virus 3 prevalence in tadpole populations inhabiting cattle-access and non-access wetlands in Tennessee. Diseases of Aquatic Organisms 77, 97-103.

Groom, M.J., Meffe, G.K., Carroll, C.R., 2006. Principles of Conservation Biology. Sinauer Associates, Sunderland.

Hackney, C.T., de la Cruz, A.A., 1981. Effects of fire on brackish marsh communities: management implications. Wetlands 1, 75-86.

Hamer, A.J., McDonnell, M.J., 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation 141, 2432-2449.

Hardman, C.J., Harris, D.B., Sears, J., Droy, N., 2012. Habitat associations of invertebrates in reedbeds, with implications for management. Aquatic Conservation 22, 813-826.

Hartnett, D.C., Hickman, K.R., Fischer, W.L.E., 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49, 413-420.

Hazell, D., Hero, J.-M., Lindenmayer, D., Cunningham, R., 2004. A comparison of constructed and natural habitat for frog conservation in an Australian agricultural landscape. Biological Conservation 119, 61-71.

Hossack, B.R., Corn, P.S., 2007. Responses of pond-breeding amphibians to wildfire: short-term patterns in occupancy and colonization. Ecological Applications 17, 1403-1410.

Hoverman, J.T., Matthew, J.G., Debra, L.M., Nathan, A.H., 2012. Widespread occurrence of *Ranavirus* in pond-breeding amphibian populations. EcoHealth 9, 36-48.

Jansen, A., Healey, M., 2003. Frog communities and wetland condition: relationships with grazing by domestic livestock along an Australian floodplain river. Biological Conservation 109, 207-219.

Kelemen, J., 2002. Legeltetés (Grazing), In Védett és érzékeny természeti területek mezőgazdálkodásának alapjai (Fundamentals of agriculture on protected and sensitive natural areas). eds J. Ángyán, J. Tardy, A. Vajnáné Madarassy, pp. 380-394. Mezőgazda Kiadó, Budapest.

Lengyel, S., Varga, K., Kosztyi, B., Lontay, L., Déri, E., Török, P., Tóthmérész, B., 2012. Grassland restoration to conserve landscape-level biodiversity: a synthesis of early results from a large-scale project. Applied Vegetation Science 15, 264-276.

Lockwood, J.L., McKinney, M.L., 2001. Biotic homogenization: a sequential and selective process, In Biotic Homogenization. eds J.L. Lockwood, M.L. McKinney, pp. 1-17. Kluwer Academic/Plenum Publishers, New York.

Lougheed, V.L., McIntosh, M.D., Parker, C.A., Stevenson, J.R., 2008. Wetland degradation leads to homogenization of the biota at local and landscape scales. Freshwater Biology 53, 2402-2413.

Magyari, E.K., Chapman, J.C., Passmore, D.G., Allen, J.R.M., Huntley, J.P., Huntley, B., 2010. Holocene persistence of wooded steppe in the Great Hungarian Plain. Journal of Biogeography 37, 915-935.

Matthews, C.E., Moorman, C.E., Greenberg, C.H., Waldrop, T.A., 2010. Response of reptiles and amphibians to repeated fuel reduction treatments. Journal of Wildlife Management 74, 1301–1310.

McCabe, D.J., Gotelli, N.J., 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia 124, 270-279.

Mérő, T.O., Lontay, L., Lengyel, S., 2015. Habitat management varying in space and time: the effects of grazing and fire management on marshland birds. Journal of Ornithology In press.

Mori, A.S., 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. Journal of Applied Ecology 48, 280-292.

Nomura, F., Rossa-Feres, D.D., Langeani, F., 2009. Burrowing behavior of *Dermatonotus muelleri* (Anura, Microhylidae) with reference to the origin of burrowing behavior of Anura. Journal of Ethology 27, 195–201.

Nyström, P., Hansson, J., Mansson, J., Sundstedt, M., Reslow, C., Broström, A., 2007. A documented amphibian decline over 40 years: possible causes and implications for species recovery. Biological Conservation 138, 399-411.

Parr, C., Andersen, A., 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. Conservation Biology 20, 1610–1619.

Perry, R.W., Rudolph, D.C., Thill, R.E., 2012. Effects of short-rotation controlled burning on amphibians and reptiles in pine woodlands. Forest Ecology and Management 271, 124-131.

Petitot, M., Manceau, N., Geniez, P., Besnard, A., 2014. Optimizing occupancy surveys by maximizing detection probability: application to amphibian monitoring in the Mediterranean region. Ecology and Evolution 4, 3538-3549.

Pilliod, D.S., Bury, R.B., Hyde, E.J., Pearl, C.A., Corn, P.S., 2003. Fire and amphibians in North America. Forest Ecology and Management. 178, 163-181.

Pittman, S.E., Osbourn, M.S., Semlitsch, R.D., 2014. Movement ecology of amphibians: a missing component for understanding population declines. Biological Conservation 169, 44-53.

Puky, M., Schád, P., Szövényi, G., 2005. Magyarország herpetológiai atlasza [Herpetological Atlas of Hungary]. Varangy Akciócsoport Egyesület, Budapest.

R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Roznik, E.A., Johnson, S.A., 2007. *Rana capito* (Gopher frog). Refuge during fire. Herpetological Review 38, 442.

Russell, K.R., Van Lear, D.H., Guynn, D.C., 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 27, 374-384.

Schmidt, M.H., Lefebvre, G., Poulin, B., Tscharntke, T., 2005. Reed cutting affects arthropod communities, potentially reducing food for passerine birds. Biological Conservation 121, 157-166.

Schmutzer, A.C., Gray, M.J., Burton, E.C., Miller, D.L., 2008. Impacts of cattle on amphibian larvae and the aquatic environment. Freshwater Biology 53, 2613-2625.

Schweiger, E.W., Leibowitz, S.G., Hyman, J.B., Foster, W.E., Downing, M.C., 2002. Synoptic assessment of wetland function: a planning tool for protection of wetland species biodiversity. Biodiversity and Conservation 11, 379-406.

Schwilk, D.W., Keeley, J.E., Bond, W.J., 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. Biodiversity and Conservation 11, 379-406.

Smith, R.K., Sutherland, W.J., 2014. Amphibian Conservation: Global Evidence for the Effects of Interventions. Pelagic Publishing, Exeter.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783-1786.

Tóth, C., 2003. A Hortobágy negyedidőszak végi felszínfejlődésének főbb természeti és antropogén vonásai [Major natural and anthropogenic aspects of late Quaternary surface development of Hortobágy]. University of Debrecen, Debrecen.

Valkama, E., Lyytinen, S., Koricheva, J., 2008. The impact of reed management on wildlife: a meta-analytical review of European studies. Biological Conservation 141, 364-374.

Van Den Bos, J., Bakker, J.P., 1990. The development of vegetation patterns by cattle grazing at low stocking density in the Netherlands. Biological Conservation 51, 263-272.

Verga, E.G., Leynaud, G.C., Lescano, J.N., Bellis, L.M., 2012. Is livestock grazing compatible with amphibian diversity in the High Mountains of Córdoba, Argentina? European Journal of Wildlife Research 58, 823-832.

Vinton, M.A., Hartnett, D.C., Finck, E.J., Briggs, J.M., 1993. Interactive effects of fire, bison (*Bison bison*) grazing, and plant community composition in tallgrass prairie. American Midland Naturalist 129, 10-18.

Wagner, K.I., Gallagher, S.K., Hayes, M., Lawrence, B.A., Zedler, J.B., 2008. Wetland restoration in the new millennium: do research efforts match opportunities? Restoration Ecology 16, 367-372.

White, P.S., Harrod, J., Romme, W.H., Betancourt, J., 1999. Disturbance and temporal dynamics, In Ecological Stewardship: a Common Reference for Ecosystem Management. eds N.C. Johnson, A.J. Malk, W.T. Sexton, R. Szaro, pp. 281-305. Oxford University Press, Oxford.

Wiens, J.A., 1997. The emerging role of patchiness in conservation biology, In The Ecological Basis for Conservation: Heterogeneity, Ecosystems, and Biodiversity. eds S.T.A. Pickett, R.S. Ostfeld, M. Shachak, G.E. Likens, pp. 93-107. Chapman & Hall, New York.

Zedler, J.B., Kercher, S., 2005. Wetland resources: status, trends, ecosystem services, and restorability. Annual Reviews in Environment and Resources 30, 39-74.

Tables

Table 1. Minimal adequate generalised linear mixed-effects models testing the effects of management on four variables describing reed properties.

Response variable	Effect	Coefficient	S.E.	df	t	p
Mean reed cover (both years)	(Intercept)	1.03	0.082	29	12.545	< 0.0001
	Grazing	-0.49	0.090	28	-5.454	< 0.0001
	Year	0.16	0.070	29	2.330	0.027
CV reed cover (both years)	(Intercept)	0.31	0.059	30	5.286	< 0.0001
	Fire 2009	0.30	0.103	28	2.916	0.007
Number of old reed stems (2010)	(Intercept)	14.07	1.776	28	7.924	< 0.0001
	Fire 2009	-13.70	3.075	28	-4.455	< 0.0001
Number of new reed stems (2010)	(Intercept)	12.91	1.599	28	8.074	< 0.0001
	Fire 2007	4.96	2.262	28	2.193	0.037

Table 2. Minimal adequate generalised linear mixed-effects models testing the effects of reed properties and environmental variables on species richness and counts of anuran amphibians in both years and in 2010 only, when more detailed data on reed density was available.

Response variable	Effect	Coefficient	S.E.	z	p
Species richness	(Intercept)	1.25	0.180	6.924	< 0.0001
(both years)	Mean reed cover	-0.66	0.231	-2.863	0.004
Total counts	(Intercept)	2.74	0.354	7.737	< 0.0001
(both years)	Mean reed cover	-1.31	0.278	-4.725	< 0.0001
	Year	3.85	0.323	11.922	< 0.0001
	CV reed cover	0.32	0.204	1.545	0.122
	Cloud cover	0.30	0.028	10.673	< 0.0001
	Mean reed cover*Year	-2.90	0.305	-9.516	< 0.0001
	CV reed cover*Year	-4.36	0.372	-11.718	< 0.0001
Species richness	(Intercept)	1.39	0.148	9.387	< 0.0001
(2010 only)	Number of old reed stems	-0.07	0.017	-4.278	< 0.0001
Total counts	(Intercept)	1.29	0.698	1.847	0.065
(2010 only)	CV reed cover	0.99	0.464	2.137	0.033
	Number of old reed stems	-0.09	0.024	-3.611	< 0.001
	Number of new reed stems	0.07	0.033	2.099	0.036

Table 3. Minimal adequate generalised linear mixed-effect models testing the effects of grazing, burning in 2007 and 2009, year and environmental variables on species richness and total counts of anuran amphibians.

Response variable	Effect	Coefficient	S.E.	z	p
Species richness	(Intercept)	0.72	0.259	2.759	0.006
	Grazing	-0.71	0.396	-1.784	0.074
	Year	-0.61	0.401	-1.518	0.129
	Fire2009	1.81	0.369	4.896	< 0.001
	Water depth	-0.02	0.009	-1.952	0.051
	Cloud cover	0.13	0.050	2.591	0.010
	Grazing*Year	1.48	0.538	2.757	0.006
	Fire2009*Year	-1.94	0.492	-3.949	< 0.0001
Total counts	(Intercept)	1.86	0.358	5.198	0.000
	Grazing	-0.74	0.483	-1.532	0.126
	Year	-0.60	0.195	-3.094	0.002
	Fire2009	2.64	0.481	5.482	< 0.001
	Water depth	-0.05	0.006	-7.554	< 0.001
	Wind intensity	0.24	0.066	3.673	< 0.001
	Cloud cover	0.39	0.037	10.397	< 0.0001
	Grazing*Year	2.23	0.230	9.673	< 0.0001
	Fire2009*Year	-3.40	0.208	-16.334	< 0.0001

Figure legends

Figure 1. Aerial image of the study site in 2007, with location of management actions. Source of image: Institute of Geodesy, Cartography and Remote Sensing, Budapest, Hungary.

Figure 2. Mean reed cover and the coefficient of variation (CV) in reed cover per transect in two years (A-B), and the number of old and new reed stems per $0.126 \, \text{m}^2$ in 2010 (C) in transects with different management (means ± S.E.s shown from n = 5 transects for each datapoint; 0: no management, 1: management). Results of generalised linear mixed-effects models are in Table 1.

Figure 3. Species richness and total counts of anuran amphibians as a function of mean and CV of reed cover (both years, A-C) and number of old and new reed stems (2010 only, D-F) per transect. Least-squares regression lines are for visual guidance only; statistics such as parameter estimates from generalised linear mixed-effects models are in Table 2.

Figure 4. Mean ± S.E. species richness and total counts of anuran amphibians in transects with different management (n = 5 transects for each datapoint; 0: no management, 1: management).

Figure 5. Mean ± S.E. counts of Pelophylax spp. water frogs (A) and Fire-bellied Toads (B) in transects with different management (n = 5 transects for each datapoint; 0: no management, 1: management).

Figure 6. Schematic summary of the effects of burning and grazing on marsh vegetation and
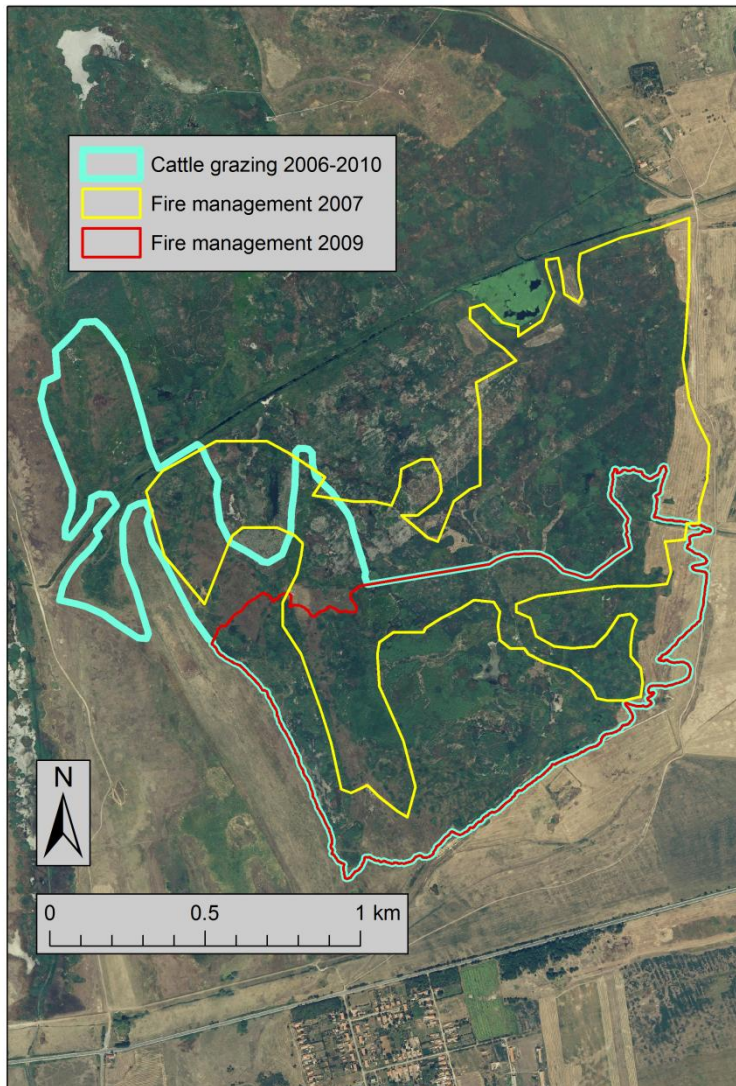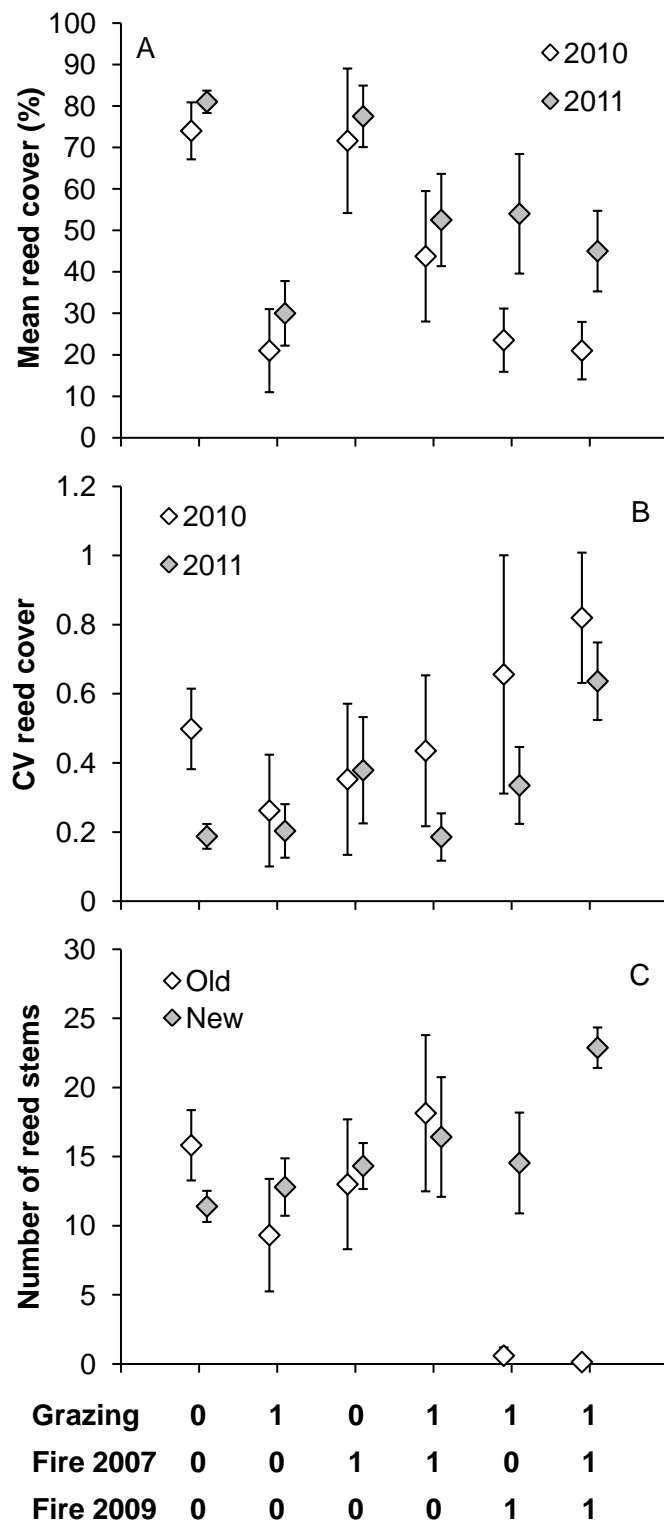
anuran amphibians (green - new reed, orange- old reed).
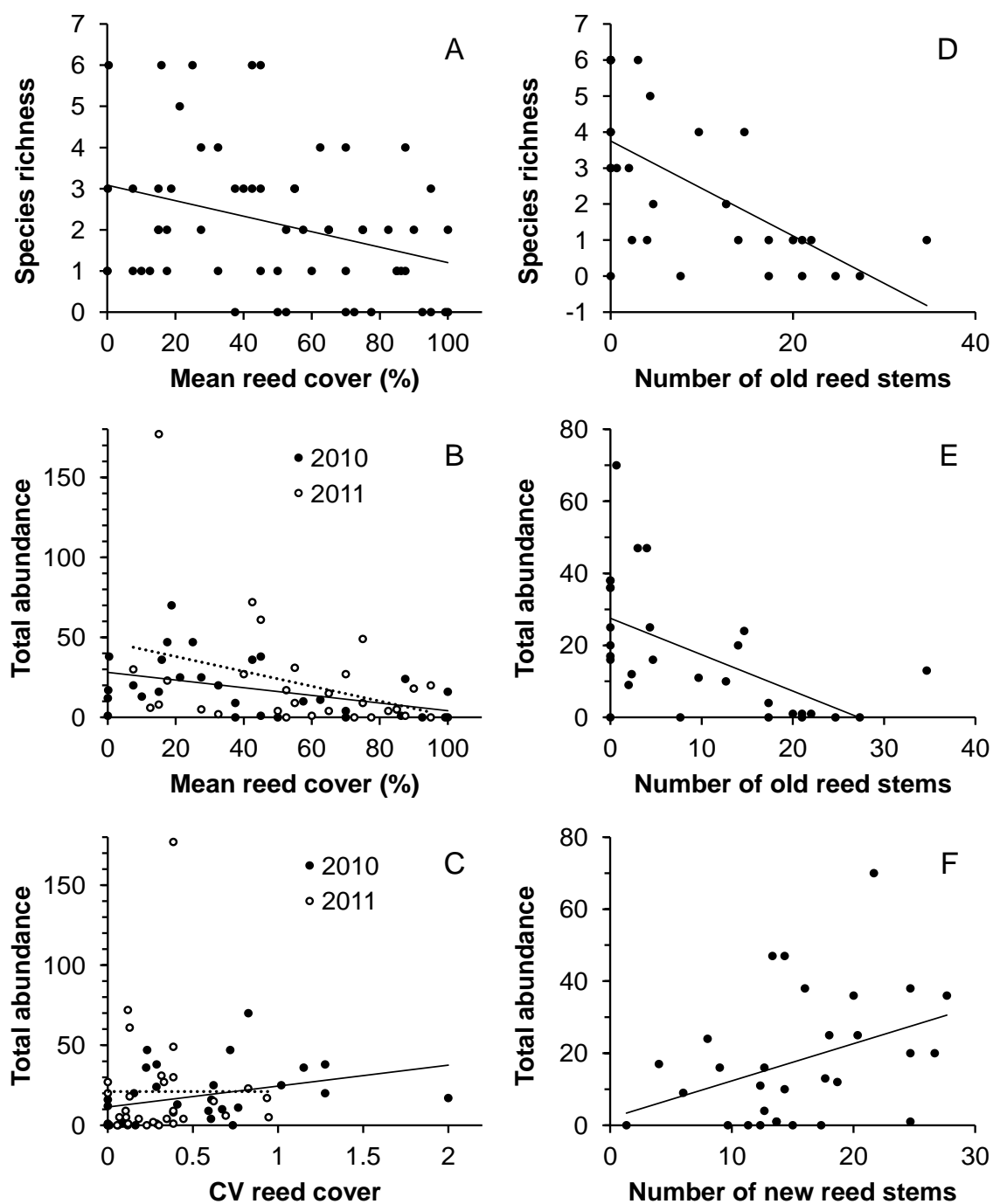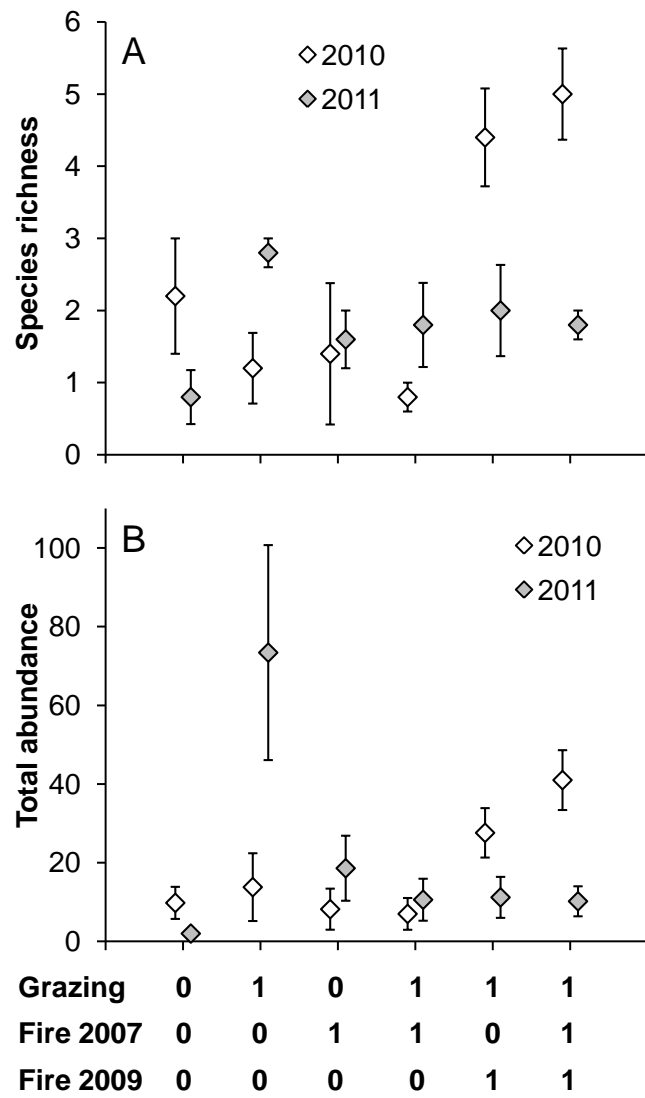
Figures

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

Year 0	Year 1	Year 2

Late-summer fire

Old reed eliminated
More open water
High amphibian
richness and counts

New reed growth
Less open water
Low amphibian
richness and counts

Low-intensity
cattle grazing
(for 3 years)

Low cover of mixed reed
Medium open water
Low amphibian
richness and counts

Low cover of mixed reed
Medium open water
High amphibian
richness and counts