



Salvaging bycatch data for conservation: Unexpected benefits of restored grasslands to amphibians in wetland buffer zones and ecological corridors



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ABSTRACT

The degradation and loss of habitats are one of the major causes of the recent global decline of amphibian populations, and wetland ecosystems are increasingly restored to counter these effects. However, there is little information on how restoration of non-wetland habitats such as grasslands affect amphibians in wet-terrestrial habitat complexes. We studied the spatial and temporal impacts of large-scale grassland restoration in wetland buffer zones and ecological corridors on amphibians in Hortobágy National Park (E-Hungary). We used bycatch data on amphibians inadvertently collected over seven years by Barber pitfall trapping in a post-restoration monitoring of invertebrates in restored and natural grasslands. Repeated measures analyses revealed higher abundance and species richness of amphibians from year 2 to 6 after restoration than in years 7 to 10. Early phases of restoration, dominated by weedy and dicotyledonous plants, provided suitable microclimatic refuges and foraging areas to amphibians. The availability of such microhabitats decreased in later phases of restoration, dominated by grasses and a few dicotyledonous plants. Legacy effects were important because fine-scale differences in crop history and seed mixture resulted in variation in total abundance and species richness. Space-for-time substitution analyses two and seven years after restoration also confirmed the temporal differences between early and late phases of restoration. Restored grasslands did not differ from natural grasslands in total abundance, species abundances or species richness of amphibians. Our study demonstrates that increasing the area of grasslands around and among lowland marshes can be an effective tool for conservation because amphibians readily use these areas as refuges or for foraging, movement, migration and dispersal. Restoration of non-wetland habitat can benefit amphibians at the local scale by extending suitable terrestrial habitats and at the landscape scale by establishing functional connectivity between wetlands.

1. Introduction

Habitat loss is one of the major threats to biodiversity and is a fundamental cause of the global decline of amphibian populations (Rinella et al., 2016). A major component of global habitat loss is the decreasing area and the deteriorating quality of natural grasslands due to increasing anthropogenic habitat disturbances (Bakker and Berendse, 1999). Grasslands harbor high species diversity (Pärtel et al., 2005), and provide a wide range of ecosystem services (Isbell et al., 2011). Grasslands can serve both as core terrestrial habitats and terrestrial buffer zones for amphibians in their terrestrial life stages (Gibbons, 2003; Semlitsch and Bodie, 2003). Grasslands also function as elements of green infrastructure as they connect wetlands and marshes (Manton

et al., 2016).

Although habitat restoration can, in theory, counter habitat loss, restoring habitats for amphibians has received increased attention only recently (Clauzel et al., 2015; Klaus and Noss, 2016; Rowe and Garcia, 2014). Because the primary targets of habitat restoration and construction for amphibians are wetlands (Drayer and Richter, 2016; Kolář et al., 2017), grassland restorations are rarely implemented specifically for amphibians (Smith and Sutherland, 2014). Two studies that followed the effects of grassland restoration on amphibians found that reseeded grasslands in former coal mines can be beneficial to local amphibians (Galán, 1997; Lannoo et al., 2009).

Lowland grasslands, especially those that surround wetlands, may provide suitable sites for the foraging, aestivation and hibernation of

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Table 1

Number of individuals of amphibian species captured in pitfall traps on restored and natural grasslands, the number of trap-days and number of individuals per trap-day by study year.

Grassland type	Year	Number of individuals									Number of	
		<i>L. vulgaris</i>	<i>T. dobrogicus</i>	<i>B. bombina</i>	<i>P. fuscus</i>	<i>B. bufo</i>	<i>B. viridis</i>	<i>Pelophylax</i> spp.	<i>H. arborea</i>	All species	Trap-days	Individuals /trap-day
Restored	2010	43	596	856	112	3	0	0	7	1617	26,726	0.061
	2011	154	94	103	85	0	0	2	0	438	16,006	0.027
	2012	28	53	69	15	0	0	0	0	165	7084	0.023
	2013	3	10	32	215	3	0	0	0	263	1812	0.145
	2015	0	0	5	38	0	0	0	0	43	8192	0.005
	Total	228	753	1065	465	6	0	2	7	2526	59,820	0.042
Natural	2010	27	161	295	5	1	0	6	0	495	15,190	0.033
	2013	38	629	562	607	2	2	31	11	1882	12,684	0.148
	2016	3	100	103	214	0	0	0	0	420	13,104	0.032
	Total	68	890	960	826	3	2	37	11	2797	40,978	0.068

amphibians and in maintaining the terrestrial connectivity of wetland amphibian populations (Balas et al., 2012; Searcy et al., 2013). However, in many cases grassland restorations are limited in space and time and typically aim to benefit taxon groups other than amphibians (Bond and Lake, 2003). Nevertheless, grasslands can be important as buffer zones around or corridors between wetlands that are fundamental for local amphibians (Harper et al., 2008). The proper restoration of terrestrial habitats, and grasslands in particular, can thus be important in amphibian conservation (Sutherland et al., 2019). However, there is little information on whether and how grassland restoration affects amphibian species, populations, and assemblages in lowland grassland and wetland complexes (Sutherland et al., 2019).

The aim of this study was to evaluate the effects of large-scale grassland restoration on amphibians in their post-breeding terrestrial stage. Specifically, we addressed three questions: (i) How do local restoration conditions and landscape structure affect amphibians in restored grasslands? (ii) Do these effects differ between the early and the later phases of restoration? (iii) Do the number and abundance of amphibian species differ between restored and natural grasslands? To address these questions, we used rarely reported bycatch data collected in a long-term post-restoration monitoring program of invertebrates on restored and natural grasslands.

2. Materials and methods

2.1. Study site and grassland restoration

We implemented the study in the Egyek-Pusztakócs Marsh System (EPMS; 4073 ha) in Hortobágy National Park (E-Hungary, 47°34'N, 20°55'E, Fig. A1 in Supplementary Material), a World Heritage site in the Cultural Landscapes category, between 2010 and 2016. The EPMS is a diverse mixture of marshes, meadows, alkali and loess grasslands, arable lands and wooded areas. The marshes are separated by alkali steppes and by loess grasslands on higher (1–3 m) plateaus, which had been used for agriculture since the 1860s (Aradi et al., 2003).

Seven large marshes were revitalized in a long-term landscape-scale restoration between 1976 and 1997 (Aradi et al., 2003) and are now managed for biodiversity conservation (Mester et al., 2015b). The low frequency of morphological anomalies in amphibians showed that the marshes hold healthy populations of several amphibian species (Mester et al., 2015a). Between 2005 and 2008, alkali steppes and loess grasslands were restored on 760 ha of former alfalfa, cereal or sunflower fields, mostly in potential ecological corridors between and buffer zones around the marshes (Lengyel et al., 2012). Restoration was started by plowing and sowing 20–25 kg/ha of two kinds of seed mixture. Seeds of two grass species were sown on lower-lying, wetter and more compact alkali soils (*Festuca pseudovina*, *Poa angustifolia*) and seeds of three grass species were sown on higher-lying, drier and less compact loess soils (*Festuca rupicola*, *Poa angustifolia*, *Bromus inermis*) (Lengyel et al., 2012).

2.2. Study design

To follow changes in animal assemblages after restoration, we implemented a long-term monitoring program consisting of three studies (Fig. A2): (i) monitoring of restored grasslands in a repeated-measures design every year for five years after restoration, (ii) monitoring of restored grasslands in a space-for-time substitution design once every five years, and (iii) a baseline monitoring of natural grasslands as reference once every three years (Fig. A2). In each study, we surveyed invertebrates using Barber pitfall traps and amphibians, reptiles and small mammals were inadvertently captured as bycatch. Traps were white plastic cups (0.5 l, width 10 cm, height 13 cm) containing c. 100 ml of 25% ethylene-glycol mixed with water and detergent as preservative, as used e.g. in the National Ecological Observatory Network of the U.S. (Hoekman et al., 2017). Bycatch of non-targeted animals, especially small vertebrates, is well-known in field studies that use pitfall traps (Thompson and Thompson, 2008). Several modifications were proposed to minimize such bycatch (Jung et al., 2015; Lange et al., 2011; Weary et al., 2019), including the use of a cover close to the ground surface, which can dramatically decrease bycatch (Hohbein and Conway, 2018). Accordingly, we installed a plywood cover (20 × 20 cm) 1–2 cm above the ground to minimize vertebrate bycatch (Hohbein and Conway, 2018). We did not use a funnel, another modification proposed to minimize vertebrate bycatch (Lange et al., 2011), as it is known to reduce the capture probability of carabids and other arthropods (Pearce et al., 2005), which were the original targets of monitoring. Pitfall traps were operated between May and October, i.e., during almost the entire post-breeding period, when all local species show terrestrial activity (Mester et al., 2017; Speybroeck et al., 2016). The traps were checked once every three weeks between late May and early October for invertebrates and vertebrate bycatch. Live vertebrate individuals were cleaned and released nearby. Dead individuals were safely discarded to avoid accidental poisoning of predators. We replaced missing or damaged traps, and filled traps with new preservative at every check.

Response variables were total abundance (number of all individuals of all species), species richness (number of species), and the number of individuals captured per species, calculated for four species with more than 50 captured individuals in the seven years: smooth newt (*Lissotriton vulgaris*), Danube crested newt (*Triturus dobrogicus*), fire-bellied toad (*Bombina bombina*), and common spadefoot (*Pelobates fuscus*). We pooled data from sampling occasions within a year, resulting in one datapoint for one trap per year. This was possible because exposure (trap-days, i.e., the number of days a trap was active) was similar for all traps within a year.

Predictor variables were local restoration conditions and landscape structure. Restoration conditions were (i) type of the last crop before restoration (alfalfa, cereal, sunflower), (ii) seed mixture used in restoration (alkali, loess) and (iii) restoration age (number of years passed

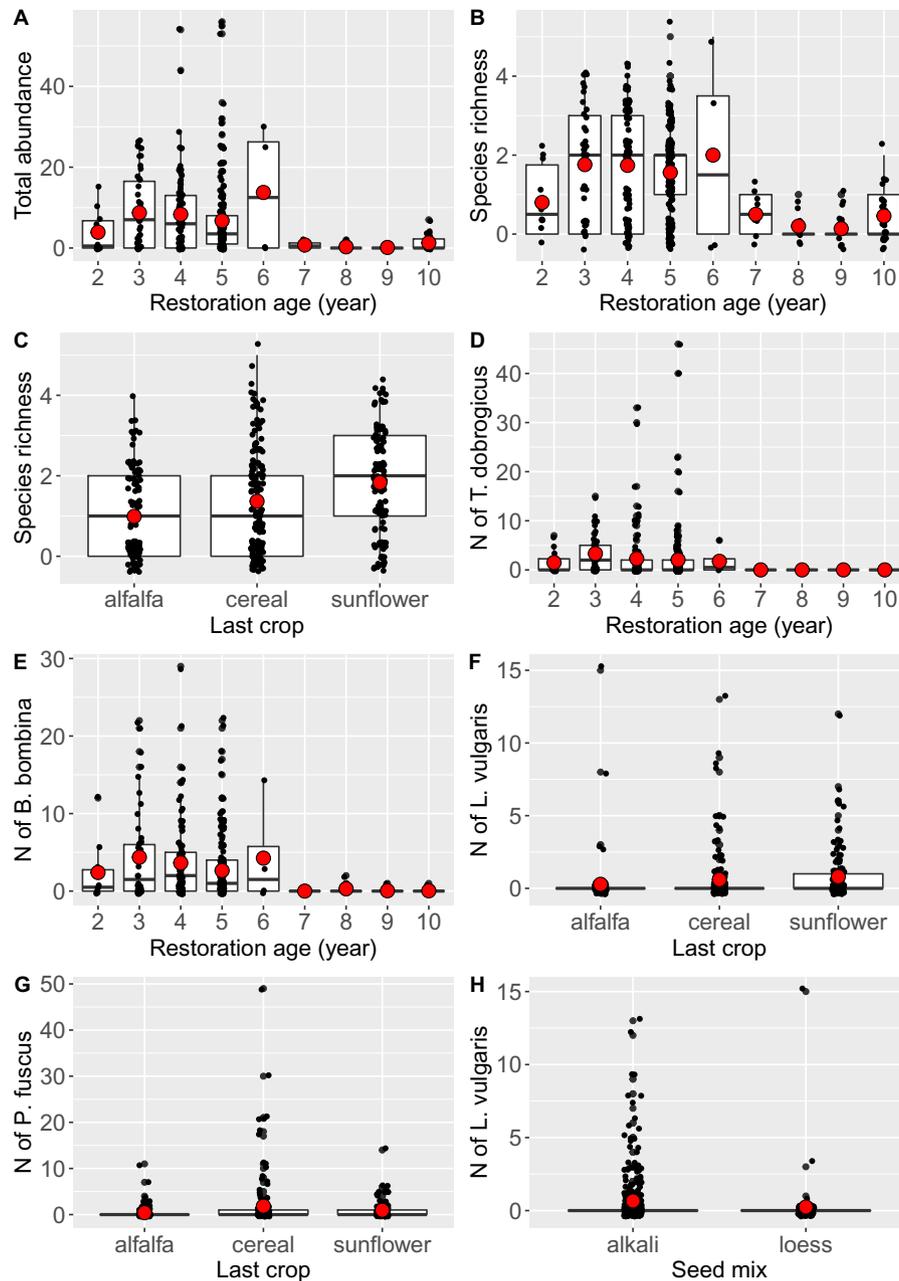


Fig. 1. Response variables as a function of local restoration conditions identified as significant ($p < .05$) by repeated-measures GLMMs (Analysis 1) in Table 2. Boxplots show the median (thick horizontal line), upper and lower quartiles (box), minimum and maximum values (whiskers), original datapoints (black dots), including outliers, jittered for clarity, and means (red dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

since seed-sowing). To characterize landscape structure, we calculated the proportion of eight habitats (marshes, meadows, grasslands, wooded areas, arable lands, residential areas, artificial ponds, canals) in circular buffers of 500 m radius around each trap based on a habitat map (Mérő et al., 2015). This radius was chosen to correspond with the average distance of post-breeding movements of amphibians (Semlitsch, 2008; Sinsch et al., 2012; Smith and Green, 2005). We used QGIS (version 2.16.3) for spatial calculations. To minimize multicollinearity, we reduced the eight variables into uncorrelated principal components in two PCAs, one for restored grasslands (PCA 1: Analyses 1 and 2, see below) and one for restored and natural grasslands combined (PCA 2: Analysis 3). In PCA 1, the first three components explained 63.9% of the total variance, and were identified as ‘Elevation’, ‘Farms’, and ‘Dryness’, whereas in PCA 2, they explained 67.8% of the

variance, and were identified as ‘Naturalness’, ‘Elevation’, and ‘Farms’ (Table A1).

2.3. Statistical analyses

We addressed the research questions in three analyses. In each analysis, we used a model selection approach based on an information theoretic framework (Burnham and Anderson, 2002). Each analysis was started from the full model that contained all relevant predictor variables, and models with all possible combinations of predictor variables were calculated using function ‘dredge’ in the R package ‘MuMIn’. We describe the starting full models below in more detail for Analyses 1 to 3 separately. We then identified the best model (lowest AIC value) and the models with substantial empirical support ($\Delta AIC < 2$ from the best

Table 2

Model-averaged parameter estimates for fixed effects in generalized linear mixed-effects models with repeated measures testing the effects of local restoration conditions and landscape structure on response variables (Analysis 1). Variables with *p*-value below 0.1 are listed.

Response variable	Fixed effect	Estimate ± S.E.	z	p
Total abundance	Restoration age	-0.35 ± 0.129	-2.701	0.0069
Species richness	Restoration age	-0.17 ± 0.052	-3.325	0.0008
	Last crop _{alfalfa}	-0.58 ± 0.194	-2.957	0.0031
	Last crop _{cereal}	-0.43 ± 0.171	-2.488	0.0128
	PC1 Elevation	-0.2 ± 0.066	-3.087	0.002
	PC2 Farms	0.16 ± 0.049	3.251	0.0011
<i>L. vulgaris</i>	Last crop _{alfalfa}	-2.37 ± 1.175	-2.011	0.0443
	Seedmix _{alkali}	2.29 ± 0.697	3.269	0.001
	PC1 Elevation	-1.37 ± 0.283	-4.821	< 0.0001
<i>T. dobrogicus</i>	Restoration age	-0.8 ± 0.232	-3.459	0.0005
	Last crop _{alfalfa}	-0.09 ± 0.736	-0.118	0.9056
	PC1 Elevation	-0.94 ± 0.224	-4.189	< 0.0001
	PC2 Farms	0.43 ± 0.151	2.833	0.0046
<i>B. bombina</i>	PC3 Dryness	-0.27 ± 0.144	-1.857	0.0633
	Restoration age	-0.69 ± 0.209	-3.31	0.0009
<i>P. fuscus</i>	Last crop _{alfalfa}	-1.53 ± 0.765	-1.997	0.0458

model) (Tables A2–4). Finally, we calculated parameter estimates (\pm S.E.) averaged over the models with substantial support. We used the R version 3.6.1 statistical environment for all analyses and graphs (R Core Team, 2019).

2.3.1. Analysis 1

In Analysis 1, we studied the effects of grassland restoration and landscape structure on amphibians using generalized linear mixed-effects models (GLMM) (function ‘glmer’ in package ‘lme4’ in R, Poisson error distribution with logit link). Data used here were from the repeated-measures monitoring of 33 sampling sites on 22 restored fields in five years (2010–2013, 2015; total $n = 166$ traps). Because the area restored was 178, 225, 92, and 265 ha in the four years between 2005 and 2008, respectively, and because monitoring lasted for five years at each site (Fig. A2), the number of traps was highest in 2010 and decreased afterwards, resulting in an unbalanced dataset and the need to use GLMMs that are robust to such designs and heterogeneous variances. We used two nested random effects in GLMMs: sampling site within restored field to control for spatial non-independence, and field within years to control for temporal non-independence due to repeated measurements (Bates, 2010).

2.3.2. Analysis 2

In Analysis 2, we compared short and long-term impacts of grassland restoration using data from 2010 and 2015, when all restored fields were sampled in a space-for-time substitution (chronosequence) design. The data used here were collected at the 33 sites in 2010 ($n = 166$ traps). We re-sampled 32 of these sites on restored fields in 2015 (Fig. A2) with two traps per site (total $n = 64$ traps). We built GLMMs (function ‘lme’ in package ‘nlme’) separately for the two years, with sampling site within restored field as a nested random factor.

2.3.3. Analysis 3

Finally, in Analysis 3, we compared restored and natural grasslands using data from 2010 and 2013, when restored and natural grasslands were both sampled. Here we used data from restored fields (see above) and from the baseline monitoring of natural grasslands (1500 ha) in 2010 and 2013 (Fig. A2). In each year, two pitfall traps were installed in each of 49 natural grassland patches (total $n = 98$ traps) (Lengyel et al., 2016). We built GLMMs (function ‘lme’ in package ‘nlme’) separately for the two years, with habitat type (restored vs. natural) and landscape structure as fixed effects and sampling site within restored field or natural grassland patch as a nested random factor.

Because the number of traps and trap-days varied between years

and habitat types, we repeated each analysis after dividing response variables by the number of trap-days. These results were qualitatively similar to those obtained with the original response variables. In addition, because some traps were damaged or destroyed by large animals, we also repeated each analysis by excluding data from damaged traps. These results were qualitatively identical to those obtained by the full dataset.

3. Results

In 100,798 trap-days in restored and natural grasslands combined, pitfall traps captured 5323 individuals of eight amphibian taxa, corresponding to 0.05 individuals captured per trap-day as bycatch (Table 1). Most (99%) of the individuals belonged to four species (*L. vulgaris*, *T. dobrogicus*, *B. bombina*, *P. fuscus*). Most of the individuals were terrestrial juveniles in *L. vulgaris* (95%) and *T. dobrogicus* (93%), juveniles in *Pelophylax* spp. water frogs (100%), the green toad (*Bufo viridis*) (100%), the common toad (*Bufo bufo*) (100%), and adults in the common tree frog (*Hyla arborea*) (100%), *B. bombina* (96%), and *P. fuscus* (85%).

3.1. Effects of grassland restoration and landscape structure: analysis 1

In 59,820 trap-days in restored grasslands, pitfall traps captured 2526 individuals of seven taxa (Table 1). Total abundance was significantly influenced only by restoration age because the number of individuals was higher in three to six-year-old restorations than in seven to ten-year-old ones (Fig. 1A, Table 2). Species richness was also higher in younger than in older restorations (Fig. 1B, Table 2) and was higher in former sunflower fields than in former alfalfa and cereal fields (Fig. 1C, Table 2).

Species-level GLMMs showed that the numbers of *T. dobrogicus* and *B. bombina* were higher in younger than in older restorations (Figs. 1D, E; Table 2). Last crop type influenced numbers of two species. First, there were more *L. vulgaris* individuals in former sunflower than in alfalfa fields (Fig. 1F, Table 2). Second, the number of *P. fuscus* decreased from former cereal through sunflower to alfalfa fields (Fig. 1G, Table 2). Seed mixture influenced only the number of *L. vulgaris*, which was higher in alkali than in loess restorations (Fig. 1H, Table 2).

At the landscape scale, ‘Elevation’ negatively influenced species richness and the number of *T. dobrogicus* and *L. vulgaris* (Figs. 2A, C, E, Table 2). ‘Farms’ positively influenced species richness and the number of *T. dobrogicus* individuals (Figs. 2B, D, Table 2).

3.2. Restoration effects soon after and long after restoration: analysis 2

In 26,726 trap-days in restored grasslands in 2010, pitfall traps captured 1617 individuals of six species (Table 1). Restoration age positively influenced only the number of *B. bombina* individuals (Fig. 3A, Table 3). Total abundance and the number of *B. bombina* were higher on former sunflower fields than on alfalfa or cereal fields (Figs. 3B, C, Table 3).

In 8192 trap-days at the same sites in 2015, pitfall traps captured 43 individuals of two species (5 *B. bombina*, 38 *P. fuscus*). Species richness was higher on former cereal fields than on alfalfa or sunflower fields (Fig. 3D, Table 3). Total abundance and species richness were higher in loess restorations than in alkali restorations (Figs. 3E, F, Table 3). This was largely because the number of *P. fuscus* was higher in loess restorations (adjusted mean $1.45 \pm$ S.E. 0.304) than in alkali restorations (0.26 ± 0.198) (Fig. 3G, Table 3).

3.3. Comparison of restored and natural grasslands: analysis 3

In 40,978 trap-days in natural grasslands, pitfall traps captured 2797 individuals of eight taxa (Table 1). While we found more individuals of *L. vulgaris* in restored than in natural grasslands, there were

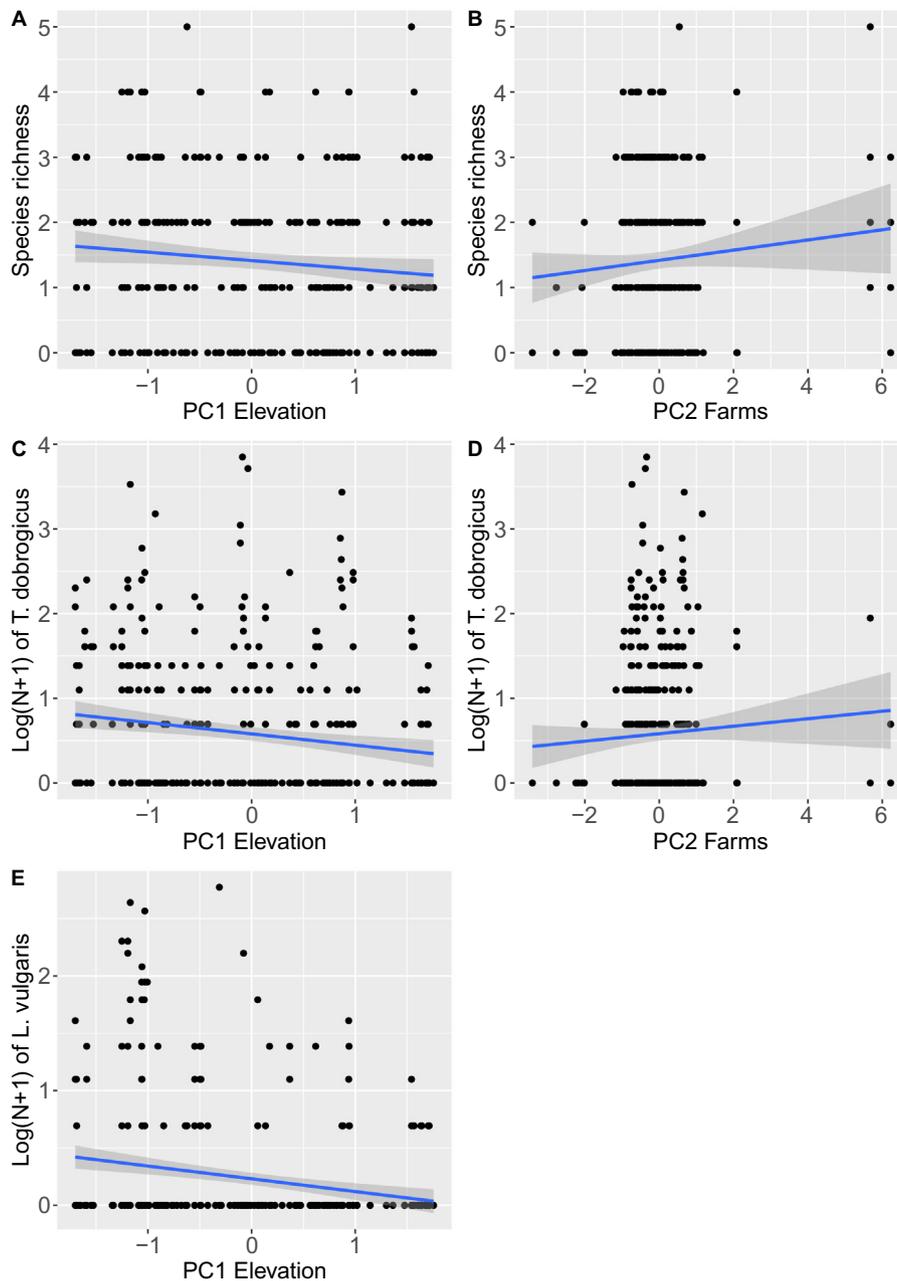


Fig. 2. Response variables as a function of landscape structure variables identified as significant ($p < .05$) by repeated-measures GLMMs (Analysis 1) in Table 2. Regression lines and 95% confidence intervals (shaded area) from simple linear regression are given for visual guidance only; conclusions are drawn from GLMM results.

more individuals of *P. fuscus*, *Pelophylax* spp. and *H. arborea* in natural than in restored grasslands, and two *B. viridis* individuals were found only in natural grasslands (Table 1). The total number of individuals per trap-day, pooled across years, was slightly higher in natural (0.068) than in restored grasslands (0.042) (Table 1).

In 2010, the number of individuals per trap-day was almost two times higher in restored (0.061) than in natural grasslands (0.033) (Table 1). Although model selection identified several models with substantial support for each response variable (Table A4), none of the parameter estimates were significant, indicating that restored and natural grasslands did not differ in either total abundance, species richness or number of individuals of species. In 2010, the number of *T. dobrogicus* individuals was influenced, negatively, by 'Elevation' (Fig. 4A; estimate \pm S.E., -0.94 ± 0.432 , $z = -2.169$, $p = .03$).

In 2013, high numbers of amphibians were captured, however, the

number of individuals per trap-day was very similar in restored and natural grasslands (0.144 vs. 0.148, respectively) (Table 1). The lack of significant parameter estimates suggested that total abundance, species richness and the number of individuals of all but one species did not differ between restored and natural grasslands. The only difference between habitat types was that the number of *P. fuscus* individuals was higher in restored than in natural grasslands (Fig. 4E; -10.24 ± 3.831 , $z = -2.149$, $p = .032$). 'Elevation' negatively influenced the number of *T. dobrogicus* individuals (Fig. 4B; -4.79 ± 1.666 , $z = -2.798$, $p = .005$), total abundance (Fig. 4C; -0.34 ± 0.121 , $z = -2.729$, $p = .006$), and species richness (Fig. 4D; -0.58 ± 0.155 , $z = -3.683$, $p < .001$).

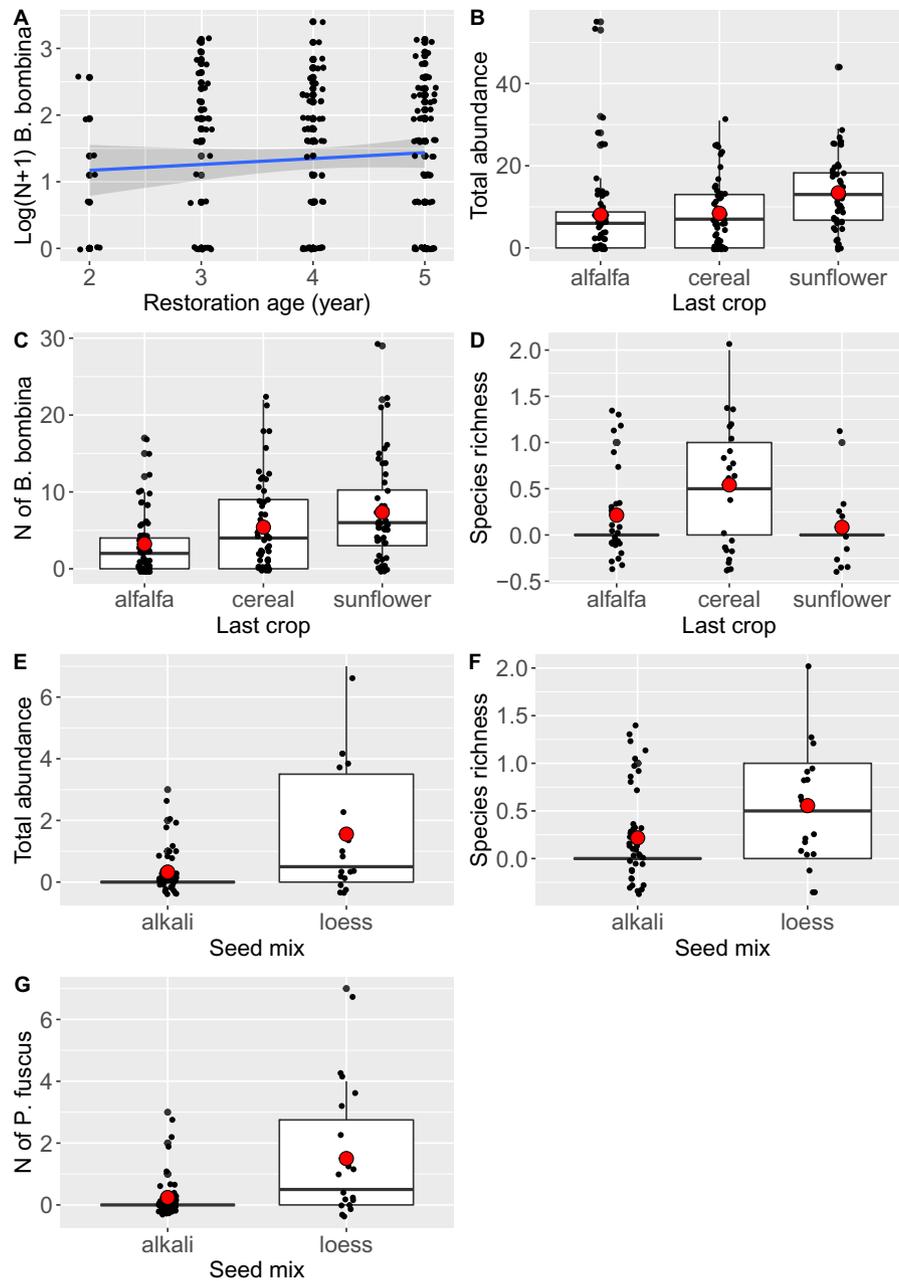


Fig. 3. Response variables as a function of local restoration conditions identified as significant ($p < .05$) by the short-term analysis (Analysis 2 based on data from 2010, A-C) and by the long-term analysis (Analysis 2, data from 2015, D-G) of GLMMs in Table 3. For plot details, please refer to Figs. 1 and 2.

4. Discussion

Our study is one of the first ones to reveal the importance of grassland restoration in establishing terrestrial habitats for amphibians, and it provides three key findings. First, restored and natural grasslands were similar in total abundance, species richness and number of individuals of species, which implies that restored and natural grasslands play similar roles as habitats for amphibians during their terrestrial life stages and pre- and post-breeding movements among the wetlands (Jehle and Arntzen, 2000; Searcy et al., 2013; Smith and Green, 2005). This finding appears to contradict the results of Balas et al. (2012) who reported that the rate of occupancy of amphibian species in wetlands on restored grasslands was higher than in wetlands in farmlands but lower in wetlands in natural prairie grasslands. However, Balas et al. (2012) focused on amphibians in wetlands and did not directly compare amphibians in restored and natural grasslands.

Second, we found that early phases of grassland restoration can be more suitable for amphibians than older phases of restoration. Early phases of grassland restoration are often characterized by diverse vegetation with many early-successional weedy plant species and by high vegetation cover (Lengyel et al., 2012). High vegetation cover can hide amphibians from predators and can also serve as refugia from weather extremes as it provides a more humid microclimate (Török et al., 2010). For example, higher vegetation effectively hides amphibians from avian predators such as *Falco vespertinus* and *Ciconia ciconia* (Larson, 2014), which are common bird species at our study site (Nagy and Lengyel, 2008). In later phases of restoration, grass species dominate, vegetation height and cover decrease and vegetation structure becomes simpler (Lengyel et al., 2012; Mérő et al., 2015; Rinella et al., 2016). These changes may explain the lower number of amphibians in later phases of restoration.

Finally, our findings showed that the impact of restoration on

Table 3

Model-averaged parameter estimates for fixed effects in general linear mixed-effects models based on space-for-time substitution testing the effects of local restoration conditions and landscape structure on response variables based on data from 2010 (short-term) and 2015 (long-term) (Analysis 2). Variables with p-value below 0.1 are listed.

Time scale	Response variable	Fixed effect	Estimate \pm S.E.	z	p
Short-term	Total abundance	Restoration age	2.86 \pm 1.584	1.686	0.0918
		Last crop _{alfalfa}	-10.16 \pm 3.511	-2.703	0.0069
	Species richness	Restoration age	0.36 \pm 0.197	1.687	0.0915
		Last crop _{alfalfa}	-0.99 \pm 0.488	-1.915	0.0554
		Seedmix _{alkali}	-3.25 \pm 1.669	-1.933	0.0532
		Restoration age	2.17 \pm 0.699	2.902	0.0037
Long-term	Total abundance	Last crop _{alfalfa}	-6.34 \pm 1.469	-4.026	0.0057
		Last crop _{cereal}	0.9 \pm 0.47	1.777	0.0755
	Species richness	Seedmix _{alkali}	-1.14 \pm 0.371	-2.747	0.006
		Last crop _{cereal}	0.06 \pm 0.162	2.468	0.0136
		Seedmix _{alkali}	-0.32 \pm 0.14	-2.02	0.0433
		<i>P. fuscus</i>	Last crop _{cereal}	0.81 \pm 0.447	1.676
	Seedmix _{alkali}	-1.2 \pm 0.353	-3.031	0.0024	

amphibians depended on time. A comparison of results (e.g. Figs. 1 and 4) shows that the short-term effects (2010 data, Analysis 2) were similar to those found by repeated measures (Year 1 to 5, Analysis 1), and that both supported the importance of restoration age and last crop type. In the long-term analysis (2015 data, Analysis 2), the effect of restoration age became less important and legacy effects (last crop, seed mixture) became restricted to cereal fields and loess restorations because 88% of the individuals found were *P. fuscus*. This species prefers loose soils for digging its burrows (Vitt and Caldwell, 2014), and such soils in our study area are found on higher-lying, non-inundated loess plateaus that were traditionally used as cereal fields. Burrowing toads, such as *Epidalea calamita* are known to cover distances three times larger on compact soils than on loose soils (Sinsch et al., 2012). *P. fuscus* also uses mammal-made burrows (Vitt and Caldwell, 2014), thus, the higher abundance of *P. fuscus* in loess restorations may also be related to the higher abundance of small mammals in loess than in alkali restorations (Mérő et al., 2015).

The results of analyses 1 and 2 showed that legacy effects (last crop type, seed mixture used) were relevant factors for amphibians. In most cases, former alfalfa fields had fewer amphibians than cereal and sunflower fields. Vegetation studies show that annual weed cover declines faster and grass dominance is reached earlier in former alfalfa fields than in cereal and sunflower fields (Lengyel et al., 2012). This is because alfalfa is a perennial plant usually cultivated for 3 to 5 years without plowing, and its continuous cover effectively reduces the seed bank of weedy species. Alfalfa also produces allelopathic compounds that suppress annual weeds and is thus a potent competitor. Finally, the natural senescence of alfalfa may create microhabitats that are suitable for the germination and establishment of grass species, that can thus develop a seed bank in old alfalfa fields. As a result, restorations on former alfalfa fields pass through the weedy phase faster than restorations on former cereal or sunflower fields (Lengyel et al., 2012). Former cereal and sunflower fields can thus provide good conditions for amphibians for a longer time, which may explain why restorations starting from alfalfa contained fewer amphibians.

Although the seed mixture used explained less variability and appeared less important than last crop type, loess restorations often had more amphibians (newts, and *P. fuscus*, see above) than alkali restorations. For newts, especially juvenile individuals, loess plateaus were important as these were between nearby marshes, and thus they functioned as migration or dispersal corridors between the marshes (Aradi et al., 2003). Newts leave the water early during seasonal droughts to avoid desiccation, to move to foraging areas in deeper water or to suitable climatic refuges on land (Jehle and Arntzen, 2000; Marty et al., 2005). Loess grasslands usually also have taller vegetation than alkali grasslands (Lengyel et al., 2016) and are non-inundated refuges for small mammal species that dig burrows (Mérő et al., 2015), which

provide better microclimate and hiding place from predators for amphibians during their post-breeding movements (Jehle and Arntzen, 2000). In contrast, small-sized amphibians such as *L. vulgaris* and *B. bombina* are known to use soil cracks as refuges in alkali grasslands, which also explains the higher abundance of *L. vulgaris* in alkali restorations. In grasslands grazed by cattle, cow dung may also act as refuges for amphibians (Tihen, 1937). Abandoned burrows of the european mole cricket (*Gryllotalpa gryllotalpa*) and the european field cricket (*Gryllus campestris*) can also be used as refuges by small amphibians.

Our study found benefits for amphibians both at the local and the landscape scale. At the local scale, restored grasslands may contribute to maintaining hydrological supply because restored areas function as the water catchment and reservoir for the marshes. If so, the hydroperiod of local marshes may be extended, which can benefit several amphibian species (Baldwin and Calhoun, 2006; Hamer et al., 2016; Semlitsch, 2000). For example, drainage of surface runoff water for agricultural purposes has been found to lead to the almost complete local extinction of amphibian populations in a wetland-grassland complex in the Prairie Pothole Region (Lannoo et al., 1994). Balas et al. (2012) concluded that during arid weather, grassland restoration supplies water to the marshes, which extends their hydroperiods and maintains suitable breeding sites for amphibians.

At the landscape scale, 'Elevation' negatively affected several response variables (Figs. 2 and 4), indicating more amphibians in lower-lying, wetter areas. This effect was most pronounced in the case of the newts *L. vulgaris*, *T. dobrogicus* and the toad *B. bombina*, which species are more strongly associated with water and aquatic habitats than the others (Mester et al., 2015b; Vitt and Caldwell, 2014). These results emphasize the importance of wetlands and grassland restorations adjacent to them for post-breeding amphibians.

Grassland restoration may simultaneously benefit amphibians by increasing the spatial extent of grasslands and by ensuring connectivity between marshes at the landscape level. The EPMS, a spatially isolated protected area surrounded by agricultural areas, is known to hold large and healthy populations of several amphibian species (Mester et al., 2015a; Mester et al., 2017). Regarding the average spatial scale of amphibian metapopulations (Semlitsch, 2008; Smith and Green, 2005; Zamudio and Wicczorek, 2007), the EPMS is likely to maintain separate metapopulations of several amphibian species. Grassland restoration thus creates corridors that maintain connectivity among the amphibian (sub)populations in the EPMS but it may also increase the permeability of the landscape to establish and maintain connections to other nearby metapopulations (Fig. A1). Grassland restoration can thus also have an effect of minimizing genetic erosion of populations induced by isolation, which is one of the major causes of global amphibian decline (Allentoft and O'Brien, 2010; Cushman, 2006; Dixo et al., 2009).

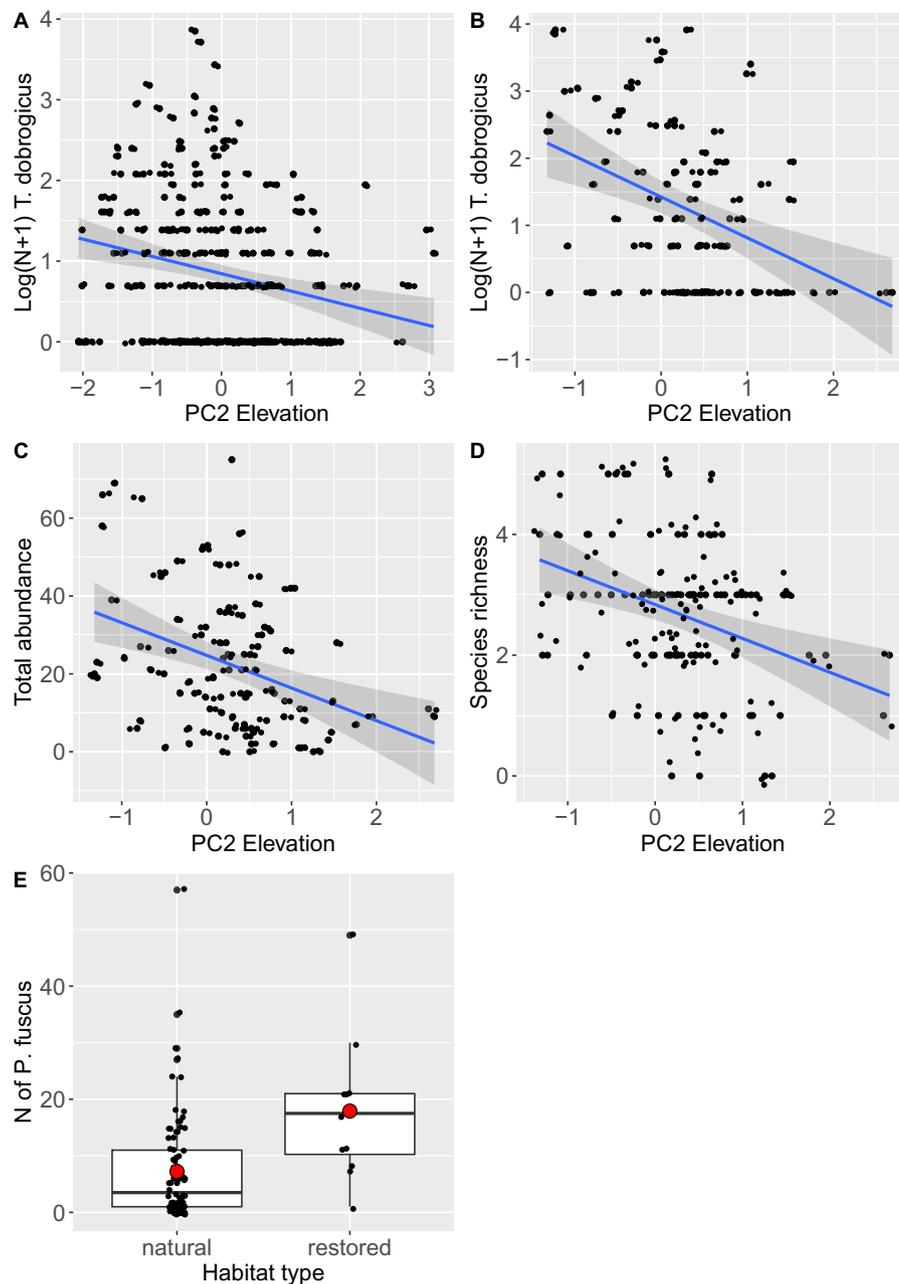


Fig. 4. Response variables as a function of landscape and local variables identified as significant ($p < .05$) by the GLMMs comparing restored and natural grasslands in 2010 and 2013 (Analysis 3). For plot details, please refer to Figs. 1 and 2.

Bycatch data are rarely published and used for analyses in ecological studies (Buchholz et al., 2011), even though bycatch data collected in monitoring programs with adequately high spatial and temporal effort are highly valuable in conservation studies (Hung et al., 2015; Wieten et al., 2012). Our study provides an example for analysing bycatch data to interpret the habitat use of several amphibian species of conservation importance and it also provides practical knowledge relevant to restoration efforts (see Implications and Conclusions). While the mortality of amphibians due to pitfall trapping is regrettable (see Ethics statement), our rate of bycatch of amphibians (0.05 individuals per trap-day) was not much higher than those reported in similar carabid sampling studies that explicitly aimed to mitigate bycatch by using modified pitfall traps (e.g. 0.025 vertebrates per trap-day in Lange et al. (2011), 0.073 in Pearce et al. (2005)). Beyond the trap cover applied in this study and the funnel mentioned above, further measures for mitigating bycatch include installing wire mesh around sampling sites

(Skvarla et al., 2014) or using other trap types (Brown and Matthews, 2016). Finally, if wetland invertebrates are not the target of monitoring, pitfall traps could also be placed farther than 50 m from the edge of the wetland to minimize the bycatch of amphibians, reptiles and small mammals of wetland habitats.

Although pitfall trapping may have caused a decline in local amphibian populations, several results showed that this was not likely in our study. First, the number of amphibians caught per trap-day showed no declining trend, rather, a year-by-year fluctuation (Table 1). Such interannual fluctuation in amphibian numbers is typical at our study site. For example, the number of amphibians killed by car traffic in the spring breeding period on a 14-km section of Main Road 33 bordering our study site varied between few hundred and more than 4000 between 2013 and 2019 (Fig. A3A, Mester et al., unpubl. data). Although comparable data were available from only three years, the number of amphibians caught as bycatch correlated positively with the number of

road-killed amphibians (Fig. A3B). Finally, a strong positive correlation between amphibian bycatch numbers and the amount of spring precipitation (Fig. A3C, $r = 0.992$, $n = 5$ years, $p < .001$) suggested that interannual fluctuations are probably driven mainly by weather rather than by pitfall trapping.

Pitfall trapping can lead to biased estimates of population size if the pitfall traps are size-selective (Lange et al., 2011; Work et al., 2002) or if the preservative used in them attracts individuals. Size selectivity was not likely a problem in our study as the pitfall traps caught large adult specimens of *T. dobrogicus* and *P. fuscus*. Adults of *Pelophylax* spp. green frogs rarely leave water (Speybroeck et al., 2016), whereas juveniles do, which can explain why we caught only *Pelophylax* juveniles. Similarly, the ethylene-glycol preservative was unlikely to attract amphibians. For example, the total abundance of amphibians in the wetlands of the study area can reach 20,000 individuals per hectare in good years (Mester et al., 2015b) and pitfall traps close (30–50 m) to the wetland edges probably would have caught much more individuals than found here if the traps had been attractive to amphibians.

Finally, standardised amphibian surveys based on drift fencing, visual encounter or call surveys may have resulted in different estimates of amphibian abundance and richness than reported here. On one side, a certain number of traps operating in grasslands for several weeks or months probably represent higher temporal sampling effort than a similar number of standard surveys (e.g. line transects) restricted to a finite number of days. Trapping is also more robust to seasonal, daily or weather-driven variation in the activity of amphibians and less affected by tall and dense grassland vegetation than standard surveys, resulting in higher detection probability of amphibians. On the other side, trapping probably has lower spatial sampling effort than standard methods and suffers from shortcomings in study design. For example, distance to the nearest wetland or water body, which is probably relevant in explaining amphibian abundance and richness in grasslands, was not considered a priori in this study. Nevertheless, our extensive bycatch dataset from trapping allowed detailed insights into community-level (richness) and species-level (abundance) patterns of amphibians, which are highly relevant in conservation and ecosystem restoration.

5. Conclusions

We conclude that grassland restoration can be an effective tool to enhance habitats for amphibians in their terrestrial stages as it can provide positive impacts on several species simultaneously at both local and landscape scales. If suitable sources of amphibians (e.g. wetlands, marshes) exist in the landscape, restored grasslands quickly reach abundance and richness levels typical in natural grasslands. Restoration can benefit amphibians by increasing the area of grasslands available for a variety of life activities such as foraging, burrowing, dispersal/migration, or hiding from predators, aestivation and hibernation in the non-breeding period and by ensuring functional connectivity between wetlands both in the breeding and non-breeding periods. The use of restored areas by amphibians, however, can be locally influenced by legacy effects arising from the type of habitat before restoration and the restoration method itself, thus, a proper application needs to consider these effects. Finally, restoration is more likely to benefit amphibians in lower-lying, wetter areas, which supports the importance of landscape structure.

6. Implications

Our study demonstrates that increasing the area of grasslands around and among lowland marshes can be an effective tool in conservation both at the local and the landscape scales. Restoration should focus on (i) areas near marshes/wetlands to facilitate their use by amphibians for various life activities, (ii) areas in potential ecological corridors between wetland/marsh fragments to enhance connectivity,

and (iii) areas in lower-lying, wetter catchment areas to extend the hydroperiod of the marsh/wetland fragment. These measures are essential for ensuring the long-term persistence of amphibian populations in dynamically changing landscapes.

Ethics statement

Monitoring was part of the After-LIFE program (2009–2014) of LIFE-Nature project [LIFE04NAT/HU/000119] and was co-developed with Hortobágy National Park Directorate (HNPD), the main beneficiary of the project. The field data collection protocol, including pitfall trapping, was permitted by the Tiszántúl Environmental Protection, Nature Conservation and Water Management Inspectorate [permit no. 7901/3/2009]. After learning about the high amphibian bycatch rate in pitfall traps in 2010, HNPD reviewed the protocol and left it unchanged to continue monitoring as started. While the high amphibian bycatch rate was regrettable, we decided to use the data available to obtain scientific knowledge for the greater goal of informing the conservation community on the effects of grassland restoration on amphibians.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2020.105916>.

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