



Original research article

Effectiveness of wetland restoration on amphibians in a drying grassland habitat losing its breeding sites

Bálint Wenner^{a,b,*} , Boldizsár Botond Lestyán^c, Attila Móréd^d, Csaba Vadász^d,
András Kelemen^{c,e}, Edvárd Mizsei^{b,d,f}

^a Department of Systematic Zoology and Ecology, Eötvös Loránd University, H-1117, Pázmány Péter sétány 1/A, Budapest, Hungary

^b Institute of Aquatic Ecology, HUN-REN Centre For Ecological Research, H-1113, Karolina road 29., Budapest, Hungary

^c Department of Ecology, University of Szeged, H-6726, Közép fasor 52., Szeged, Hungary

^d Kiskunság National Park Directorate, H-6000, Liszt Ferenc str. 19., Kecskemét, Hungary

^e 'Lendület' Seed Ecology Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány str. 2–4, Vácrátót 2163, Hungary

^f Institute of Metagenomics, University of Debrecen, H-4032, Nagyerdei körút 98., Debrecen Hungary

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ABSTRACT

Amphibians are one of the most threatened taxa globally, partly due to habitat loss, including the loss of suitable breeding sites. This problem is severe in the Hungarian Great Plain (Central Europe), which has lost the majority of its wetlands due to excessive draining. The remaining wetlands are further threatened by climate change, as the increasing intensity of summer droughts significantly decreases the length of the hydroperiod, threatening wetland communities. To mitigate the impacts of climate change on wetland communities, 23 wetland pools were restored at 13 sites in the „Felső-kiskunsági turjánvidék” Natura 2000 site in Central Hungary. In this study we compared amphibian occupancy in restored and near-natural wetlands and artificial ditches, tested the effects of hay and mud transfer on amphibian occupancy and assessed the habitat requirements of the different species. We surveyed amphibians at all 13 restoration sites, 6 nonrestored wetlands as controls and 8 ditches in the spring of 2024. We used multispecies occupancy models to estimate occupancy in the study sites and to investigate the effects of different wetland parameters and restoration techniques on amphibian occupancy. Amphibian occupancy was higher in restored wetlands compared to nonrestored controls, with both hay and mud transfer having positive effects on amphibian occupancy. While the different species had different habitat preferences, generally water depth had a positive effect on amphibian occupancy. Our study highlights the importance of wetland restorations for amphibians in drying landscapes and provides insight into the habitat preferences of multiple amphibian species.

1. Introduction

Wetlands cover about 3–6 % of Earth's surface (Hook, 1993), and account for about 40 % of global ecosystem services (Costanza et al., 2014). Wetlands are severely threatened ecosystems, as their unsustainable use has led to the loss of up to 64–71 % of wetlands in the twentieth century globally (Gardner et al., 2015), with more conservative estimations suggesting a minimum global wetland loss of

* Corresponding author at: Institute of Aquatic Ecology, HUN-REN Centre For Ecological Research, H-1113, Karolina road 29., Budapest, Hungary.
E-mail address: wennerbalint2001reg@gmail.com (B. Wenner).

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33 %, with the greatest loss of wetlands occurring in Europe and Asia (Hu et al., 2017). The loss of wetlands is also severe in Hungary, with some wetland ecosystems having lost up to 90 % of their area (Biró et al., 2018). Temporary wetlands are intermittently inundated wetlands that function as Small Natural Features, similarly to keystone species but on an ecosystem scale (Calhoun et al., 2017). Like other wetlands, temporary wetlands are severely threatened by human alterations, climate change and invasive species (Calhoun et al., 2017).

Amphibians are considered the most threatened vertebrate taxa globally (Catenazzi, 2015), as over one third of extant amphibian species are threatened with extinction (Wake and Vredenburg, 2008). This trend is likely to accelerate as most species live in the tropics with a limited geographic range, making them more vulnerable (Stuart et al., 2004; Wake and Vredenburg, 2008). The main factors contributing to the decline of amphibians are habitat alteration (loss, degradation and fragmentation) (Cushman, 2006; Gallant et al., 2007), the global amphibian pandemic chytridiomycosis and other diseases (Berger et al., 2016; Fisher et al., 2009; Kilpatrick et al., 2010), climate change (Li et al., 2013) and invasive species (Falaschi et al., 2020). Habitat loss impacts several amphibian communities, such as tropical and wetland communities (Lehtinen et al., 1999; Stuart et al., 2004). As a consequence of the loss of suitable breeding sites or terrestrial habitat (Homan et al., 2004; Storfer, 2003), decreased habitat connectivity can have detrimental effects on amphibian populations as well (Cushman, 2006). The main factors threatening amphibian populations worldwide can also interact, e.g. in some regions climate change can facilitate the spread of *Batrachochytrium dendrobatidis*, the fungus responsible for amphibian extinctions (Bosch et al., 2006), while warm, dry spells associated with climate change can further accelerate the loss of amphibian breeding sites (Carey and Alexander, 2003; Li et al., 2013).

The loss and fragmentation of wetlands as breeding sites contribute significantly to global amphibian declines (Gallant et al., 2007). Increasing efforts have been made in recent decades in restoring wetlands to mitigate the impacts of habitat loss on amphibian populations (Brown et al., 2012). Wetland restorations can effectively slow down or reverse amphibian declines locally or regionally across different ecosystems (Clauzel et al., 2015; Deoniziak et al., 2017; O'Brien et al., 2021). Several approaches have been implemented in wetland restoration, such as ditch blocking, restoring the natural flow of rivers, pond creation or deepening existing temporary waterbodies to increase the length of the hydroperiod to make them suitable amphibian breeding sites (Deoniziak et al., 2017; Kolozsvary and Holgerson, 2016; Magnus and Rannap, 2019; O'Brien et al., 2021; Soomets et al., 2023). Generally, restored wetlands can be important breeding places for amphibians and are able to mitigate habitat loss, however, some species utilize restored wetlands to a lesser extent (Magnus and Rannap, 2019; O'Brien et al., 2021), and in some cases, even though a species appears or even breeds in the restoration sites, its breeding success does not increase (Clauzel et al., 2015; Soomets et al., 2023). While designing wetland restorations for amphibian breeding, it is crucial to consider the demands of the target species (Brown et al., 2012; O'Brien et al., 2021). While different species have different needs, generally it can be said that a hydroperiod sufficient for the development of larvae, the presence of preferred plant species, a slightly sloping bank for better accessibility and the absence of predatory fish (which usually occur in permanent waterbodies) are important for most amphibian species (Brown et al., 2012). Higher habitat connectivity is also important to consider during restoration planning (Brown et al., 2012; Clauzel et al., 2015). It is also necessary to incorporate the terrestrial habitat needs of the target species into restoration planning besides the breeding sites (Brown et al., 2012; Magnus and Rannap, 2019; Schmidt et al., 2019; O'Brien et al., 2021).

While evidence-based approaches are used more and more often in ecological restoration, such practices are still not omnipresent in restoration projects (Cooke et al., 2018). Informed restoration is often more effective in reaching restoration targets, determining the effectiveness of different approaches and assessing the feasibility of the interventions (Cooke et al., 2018). When restoring wetlands for amphibian breeding, evidence-based approaches can help in designing suitable habitats for the target species and can result in faster colonisation by amphibians and an overall faster reaching of conservation targets (O'Brien et al., 2021). Monitoring restoration success and assessing the importance of different wetland parameters for amphibian use can provide important insight for future restoration projects (Shulze et al., 2012). Despite their importance, evidence-based practices and postrestoration monitoring of the impacts of the interventions are still scarce in wetland restoration as well (Browne et al., 2018).

The Hungarian Great Plain has lost a significant proportion, up to 80 % of its wetlands due to excessive draining (Fluet-Chouinard et al., 2023; Ujházy and Biró, 2018). These ecosystems are further threatened by droughts, the severity and frequency of which have been increasing significantly due to climate change (Timár et al., 2024). In the wet meadows of the Upper Kiskunság in Central Hungary soil water levels can decrease to only a fraction of their historical minima during drought events. With decreasing soil water levels wetland ecosystems such as temporarily flooded wet meadows and ephemeral wetlands can eventually disappear (Havril et al., 2018). The disappearance of breeding sites is followed by a decline in amphibian population sizes, especially in late-breeding species (Hamer et al., 2023).

To counterbalance the disappearance of amphibian breeding sites and to enhance habitat heterogeneity, we restored several extant or historic temporary wetlands in a grassland mosaic within the frameworks of the HUNVIPHAB LIFE project (LIFE18 NAT/HU/000799). In this study we tested if the restored waterbodies are appropriate replacements for natural amphibian breeding sites by comparing amphibian site occupancy among natural and restored waterbodies as well as artificial ditches, and assessed which properties of the wetlands are important for each amphibian species. We hypothesized that restored wetlands are suitable replacements for disappearing natural waterbodies in the area and that site occupancy of amphibians will be similar among naturally occurring, artificial and restored waterbodies in the area. Of the measured wetland parameters, we predicted that water depth and the coverage and species richness of submerged vegetation will positively influence amphibian site occupancy. We also predicted that additional restoration methods such as hay and mud transfer have a positive effect on amphibian occupancies.

2. Material and methods

2.1. Study site

The studied wetlands are located in the Northern part of the Felső-kiskunsági turjánvidék Natura 2000 site in Central Hungary (HUKN20003). The site itself is characterised by a mosaic of dry (Pannonic sand steppes (6260)) and mesophilic/wet (Molinia meadows on calcareous, peaty or clayey-silt-laden soils (Molinion caeruleae) (6410) and Alluvial meadows of river valleys of the Cnidion dubii (6440)) grasslands, as well as marshes characterized by Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels (6430) and Calcareous fens with *Cladium mariscus* and species of the Caricion davallianae (7210). There are 10 amphibian species present in the region, the smooth newt (*Lissotriton vulgaris*), the Danube crested newt (*Triturus dobrogicus*), the common toad (*Bufo bufo*), the green toad (*Bufo viridis*), the common spadefoot toad (*Pelobates fuscus*), the common tree frog (*Hyla arborea*), the European fire-bellied toad (*Bombina orientalis*), the marsh frog (*Pelophylax ridibundus*), the agile frog (*Rana dalmatina*) and the moor frog (*Rana lessonae*). Of these amphibian species, the agile frog, the smooth newt, and the common toad tends to breed early in the spring (February – early March), the common spadefoot toad, the common tree frog, the Danube crested newt and the moor frog breed somewhat later (March - April), while the marsh frog, the green toad and the European fire-bellied toad breed later in the season (late April – early June). Two of those species, the European fire-bellied toad and the Danube crested newt are listed in the habitat directive of the EU as species of community interest whose conservation requires the designation of special areas of conservation, while the green toad, the agile frog, the European fire-bellied toad, the moor frog, the common tree frog and the common spadefoot toad are listed as species of community interest in need of strict protection (Council Directive 92/43/EEC, 2013).

While multiple natural ephemeral waterbodies are present in the area, in recent years hydroperiods in these are often too short for the development of amphibian larvae, especially for late-breeding species. Besides natural waterbodies, there are several drainage ditches and irrigation canals that amphibians use for breeding. These artificial waterbodies were created 50–80 years ago, in some parts resulting in near-natural plant communities, making them important habitat for wetland-dependent flora and fauna. Even though these artificial ditches support the breeding of most amphibian species, the majority of them can dry out completely before the metamorphosis of several species is completed in dry summers.

The wetland restorations took place between 2020 and 2022. Altogether 23 pools were created in 13 sites, in low-lying plots with

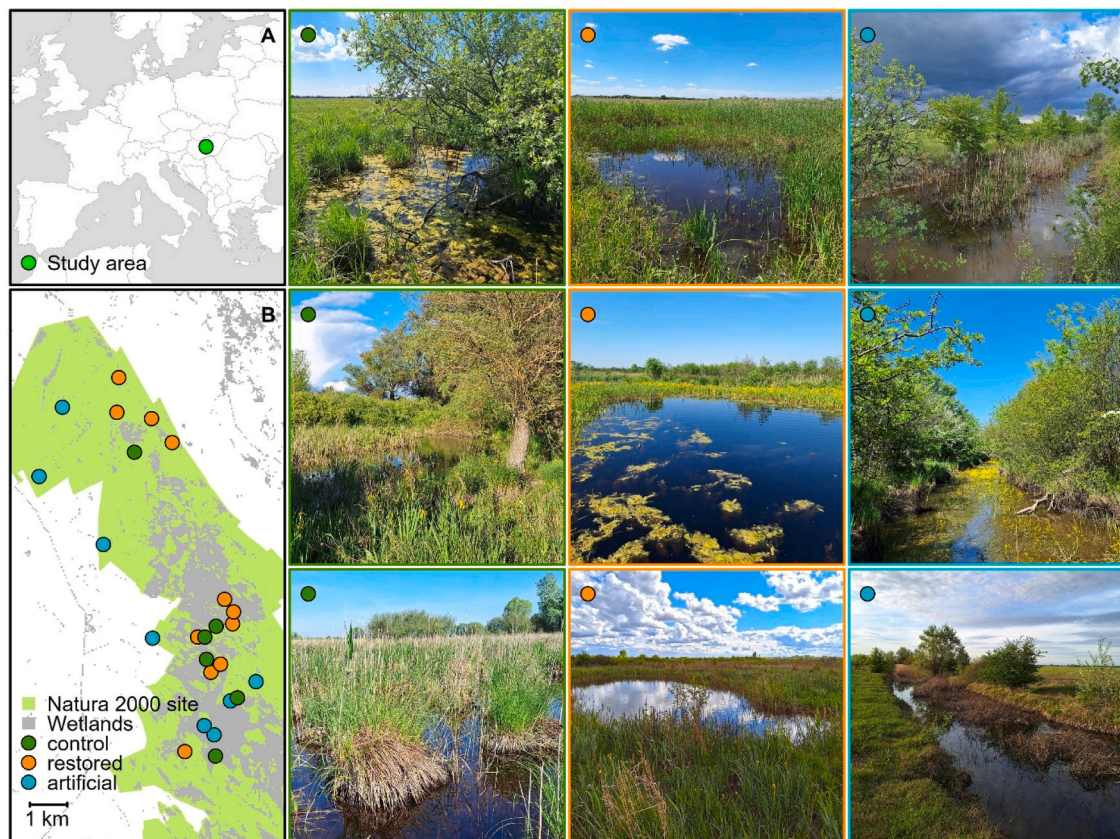


Fig. 1. A map of the study area (A) and the studied wetlands (B) with typical representations of the surveyed habitat types: nonrestored natural wetlands, restored wetlands and artificial ditches. Pictures were taken by Boldizsár Lestyán, all pictures were taken in April 2024.

higher groundwater levels. First the Grey Willow (*Salix cinerea*) shrubs were removed, which was followed by soil removal with excavating machinery. The majority of the restoration sites hold water at least until July even in dry years, so they are able to support amphibian breeding, even that of late-breeding species (larvae of early-breeding species tend to metamorphose in May and early June in the area, while late-breeding species metamorphose in late June and July). In 6 out of the 13 sites hay spreading, while in 4 sites mud transfer was applied to enhance the colonization by the native wetland-dwelling plant and invertebrate animal species characteristic of the region to improve habitat quality. In 2 of the 13 sites both hay and mud transfer were applied. Hay and mud were transferred from reference-state wetlands in the region. Hay was collected locally and it contained the following plant species: *Allium angulosum*, *Centaurea jacea*, *Deschampsia caespitosa*, *Filipendula vulgaris*, *Galium verum*, *Genista tinctoria*, *Gratiola officinalis*, *Inula britannica*, *Inula salicifolia*, *Iris sibirica*, *Linum catharticum*, *Lotus corniculatus*, *Lotus maritimus*, *Lysimachia vulgaris*, *Mentha aquatica*, *Molinia caerulea*, *Plantago altissima*, *Plantago vulgaris*, *Schoenus nigricans*, *Serratula tinctoria*, *Viola tinctoria*. Hay was spread evenly across the restoration sites; approximately 1 kg of hay was used for every m². For mud transfer, we used mud collected in a nearby canal with diverse native marsh vegetation. 2.5 m³ of mud were transferred to each restored pool. Amphibians were removed from the transferred mud before the transfer. Hay spreading was carried out in the first half of November in 2022, while mud transfer took place on 22. 03. 2023. We included all 13 restoration sites in the sampling, as well as 8 ditches (artificial waterbodies) and 6 nonrestored natural wetlands. Restored pools located within a few meters of each other were treated as one site as they form continuous waterbodies at least in the early spring. For artificial ditches, we included a 50–100 m long part in the sampling. A map of the study sites with typical representations of each wetland type are shown in Fig. 1.

2.2. Amphibian surveys

Amphibian surveys were conducted in the spring of 2024, between March and May to represent the breeding season of both early and late-breeding amphibians, and to allow for the detection of adults, spawn clutches and larvae. Visual, acoustic and dipnet surveys were conducted at least three times for each sampling site to ensure the detection of all species present at each waterbody. These surveys were conducted by 2 observers (BW, BBL) simultaneously, using a dipnet each. Duration of the surveys depended on the size and complexity of the waterbody and the number of observations, it varied between 15 min (a single smaller pool with little to no vegetation) and 3 h (large wetlands with multiple restored pools). Surveys were conducted during the day to avoid disturbing ground-nesting birds such as the great bustard (*Otis tarda*). During a single survey, all sampling methods (dipnetting, acoustic and visual surveys) were used. For each observation, we recorded the species, age, sex (when identifiable) and number of individuals encountered, as well as the method of detection (dipnetting/visual/acoustic surveys), the exact date and coordinates of the observation. In addition to these surveys we also conducted bottle trap surveys to ensure the detection of adult newts and amphibian larvae (Wilkinson, 2015). 15–50 bottle traps were used at each site, depending on the size of the waterbody. In cases of restoration sites with multiple restored pools, traps were set up in each pool (minimum 10). The traps were set up for 2 consecutive nights at each site, and checked each morning for amphibians. During each check we released the animals we found in the traps and set up the traps again in the same location after the first night or collected them after the second night. During both dipnet and bottle trap surveys we recorded all amphibians using the OpenBioMaps smartphone application (Bán et al., 2022).

2.3. Site covariates

Maximal water depth, underwater and emergent vegetation cover and species richness of aquatic vegetation were recorded between April 26 and April 29, 2024. These measurements were taken in the same period at all sites to avoid seasonal bias in precipitation and vegetation development. At restoration sites with multiple restored pools next to each other water depth was measured in each restored pool, and the maximum depth was selected. At these sites, vegetation cover and species richness were also measured separately for each pool and later averaged. Vegetation cover was measured in $n = 3$, randomly selected 1×1 m quadrats in each pool and later averaged for the waterbody. We measured underwater and emergent vegetation cover; surface (but not emergent) vegetation was treated as underwater vegetation. Ranges of the recorded wetland parameters are shown in Figures S1-S6.

2.4. Statistical analyses

Multi-species occupancy models (MSOM) allow for detailed insights into habitat relationships of rare species, while also providing valuable metrics on species richness and overall biodiversity (Dorazio and Royle, 2005; Kéry and Royle, 2007). A primary advantage of the hierarchical framework in MSOMs over single-species models is their capacity to capture individual species responses and the community's collective response to specific parameters. This community-level consideration enhances precision for rarely observed species by pooling information across the broader community (Sauer and Link, 2002; Kéry and Royle, 2007; Russell et al., 2009; Zipkin et al., 2009). In this study, we employed MSOM to identify spatial, biotic, and abiotic factors shaping community structure in an amphibian metacommunity. We also generated unbiased estimates of occupancy probabilities for each species within a wetland ecosystem.

Following the MSOM approach proposed by Rota et al. (2016), this hierarchical model connects species-specific detection and occupancy, representing a more robust extension of single-species hierarchical models typically used for occupancy estimation of species with imperfect detection (Dorazio et al., 2006; Dorazio and Royle, 2005; Kéry and Royle, 2007; Rota et al., 2016). By treating occupancy and detection parameters as random effects, rather than fixed or deterministic ones, MSOM enhances the accuracy of species-specific parameter estimates by contextualizing each within a set of related variables (Link et al., 2002; Link, 1999; Rota et al.,

2016). Ultimately, by separately estimating species-specific occupancy and detection probabilities and relating them to species richness, MSOM integrates both individual species and community-level data within a unified framework (Dorazio and Royle, 2005; Hunt et al., 2013; Rota et al., 2016; Zipkin et al., 2009).

To assess the influence of habitat properties and restoration methods, we used hierarchical modelling to estimate species-specific responses (probability of occupancy) to six habitat covariates: maximum water depth, the cover of underwater vegetation, the cover of emergent vegetation (only in case of restored sites, as there were correlations with underwater vegetation in case of control and artificial sites), total plant species richness, and the use of mud translocation and hay spreading as factor variables. In the models focusing on all wetlands, we also included wetland type (natural, restored or artificial) as a covariate, as well as the interactions of wetland type with underwater vegetation cover, plant species richness and depth. Before fitting the models all continuous variables were scaled to 0 mean and standard deviation of 1, and were checked for collinearity, which we did not find (Pearson's $r < 0.7$, Table S1).

We also included survey-specific (detection) covariates to jointly estimate the probability of detection: the number of days to capture detection since the start of the field surveys corresponding to the beginning of the activity season, and the survey method (visual, acoustic, dip netting, trapping) to account for variation of detection probability of the different sampling methods. Observations made during a site visit were separated by survey method and treated as distinct survey replicates. Records from the two observers were pooled, as both conducted visual, acoustic and dipnetting surveys during each survey session. The day of the year strongly influences the detection of amphibians, as there are species that breed as soon as temperatures are permanently above freezing, while other species have a breeding period that extends into early summer (Hamer and Horányi, 2024; Paton and Crouch III, 2002). Sampling method also influences detection, as trapping is most effective for detecting newts, while visual and acoustic surveys are more efficient methods for the detection of frogs (Baker, 2013).

As we were able to survey a limited number of sites, we fitted univariate MSOMs instead of complex models including several explanatory variables. This means we included only one habitat covariable in each model (occupancy submodel), we included the year and survey method as detection covariables (detection submodel), and we did not include any species interactions among the surveyed amphibians. The separate models were ranked by AIC and the effect of habitat covariables was assessed by the significance of coefficient estimates. We prepared and formatted the data of the surveys using the occupancy pipeline of the 'hunviphab' package (Mizsei 2022), and fitted the models applying the 'unmarked' package (Fiske and Chandler, 2011). All analyses were conducted in R in a fully reproducible way. The data and the code can be accessed via the Zenodo repository (doi: 10.5281/zenodo.15044114).

3. Results

At the 27 studied sites, we detected 9 amphibian species, *L. vulgaris*, *T. dobrogicus*, *B. bufo*, *B. viridis*, *H. arborea*, *P. fuscus*, *B. bombina*, *R. dalmatina* and *P. ridibundus*. We did not detect any individuals of *R. arvalis* at any of the studied wetlands. Naive occupancy (percentage of sites with at least one detection) for each wetland type and detection data are summarized in Table 1.

Based on the MSOM analyses focusing on all wetland types, occupancy of *B. bombina* was significantly lower in control (natural, nonrestored) wetlands ($\beta = -2.9404 \pm 0.3421$, $p < 0.0001$), while occupancies of *H. arborea* ($\beta = 3.1834 \pm 0.2178$, $p < 0.0001$) and *L. vulgaris* ($\beta = 1.7608 \pm 0.8687$, $p = 0.0427$) were significantly higher in artificial wetlands (ditches and canals) and occupancy of the *B. bombina* ($\beta = 2.2656 \pm 0.8032$, $p = 0.0048$) and that of *H. arborea* ($\beta = 2.262 \pm 0.8056$, $p = 0.005$) were significantly higher in

Table 1

Naive occupancy (proportion of sites with at least one detection) for each wetland type and proportion of surveys with at least one detection for each species.

	Naive occupancy			Proportion of surveys detected in:
	Artificial (n = 8)	Natural (n = 6)	Restoration (n = 13)	
<i>Lissotriton vulgaris</i>		0.8333	0.6923	0.1944
<i>Triturus dobrogicus</i>	1	0	0.3077	0.0259
<i>Bufo bufo</i>	0.25	0.6667	0.5385	0.1944
<i>Bufo viridis</i>	0.375	0.1667	0.5385	0.0463
<i>Pelobates fuscus</i>	0.25	0.3333	0.6154	0.1093
<i>Hyla arborea</i>	0.5	0.6667	0.9231	0.3852
<i>Bombina bombina</i>	1	0	0.9231	0.1277
<i>Rana dalmatina</i>	0.75	0.5	0.6154	0.1815
<i>Pelophylax ridibundus</i>	0.75	0.5	0.7692	0.1241
	0.625			

restored wetlands. Occupancies in each wetland type are shown in Fig. 2a.

Water depth positively influenced occupancy in case of most species, with a significant positive effect on the occupancy of *B. bombina* ($\beta=1.137 \pm 0.5765$, $p = 0.0486$), which was even stronger in natural wetlands ($\beta=2.828 \pm 1.2969$, $p = 0.0292$). Water depth significantly negatively influenced the occupancy of *H. arborea*, but only in artificial waterbodies ($\beta=-1.4815 \pm 0.6097$, $p = 0.0151$).

The cover of underwater vegetation influenced amphibian occupancies only slightly, we detected a significant negative effect of underwater vegetation cover on *P. ridibundus* in natural wetlands ($\beta=-2.0796 \pm 1.0059$, $p = 0.0387$), and a significant positive effect on *L. vulgaris* in artificial waterbodies ($\beta=1.6934 \pm 0.7939$, $p = 0.0329$). Plant species richness had both positive and negative effects on the occupancy of the studied species, with a significant positive effect on the occupancy of *H. arborea* ($\beta=1.3681 \pm 0.602$, $p = 0.023$). In control wetlands, the occupancy of *H. arborea* was significantly positively affected by plant species richness ($\beta=3.1388 \pm 1.3671$, $p = 0.0217$), while the occupancy of *R. dalmatina* was significantly negatively influenced by it ($\beta=-2.9604 \pm 0.6215$, $p < 0.0001$). In artificial waterbodies, the occupancies of *B. bufo* ($\beta=2.1629 \pm 0.508$, $p < 0.0001$) and *B. viridis* ($\beta=1.8896 \pm 0.481$, $p < 0.0001$) were significantly positively influenced by plant species richness, while occupancies of *H. arborea* ($\beta=-0.6371 \pm 0.2035$, $p = 0.0017$), *P. ridibundus* ($\beta=-2.0265 \pm 0.6512$, $p = 0.0019$), *P. fuscus* ($\beta=-2.4535 \pm 0.6533$, $p < 0.0001$) and *R. dalmatina* ($\beta=-1.8187 \pm 0.537$, $p < 0.0001$) were negatively influenced by it. The occupancy of *H. arborea* was positively affected by plants species richness in restored wetlands ($\beta=2.306 \pm 1.0463$, $p = 0.0275$). The effects of plant species richness, water depth and underwater vegetation cover are shown in Fig. 3a and in Figures S7-S10.

In the analyses only focusing on the restored wetlands, among additional restoration methods we detected a positive effect of hay spreading on most amphibian species (Fig. 2c), with a significant positive effect on the occupancies of *B. bombina* ($\beta=1.8158 \pm 0.8139$, $p = 0.0257$), *H. arborea* ($\beta=3.1832 \pm 0.1835$, $p < 0.0001$) and *P. ridibundus* ($\beta=2.0833 \pm 0.6133$, $p < 0.0001$). Mud transfer from other wetlands had positive effects on the occupancies of all amphibians (Fig. 2b), with a significant positive effect on the occupancies of *H. arborea* ($\beta=2.6459 \pm 0.3067$, $p < 0.0001$) and *P. ridibundus* ($\beta=2.6459 \pm 0.3067$, $p < 0.0001$). Cover of emergent vegetation had positive effects on the occupancy of most species, including a significant positive effect on the occupancy of *B. bombina* ($\beta=2.8205 \pm 0.6797$, $p < 0.0001$) and that of *P. fuscus* ($\beta=2.9942 \pm 0.5709$, $p < 0.0001$). Cover of underwater vegetation positively affected most species, with a significant positive effect on the occupancies of *B. bombina* ($\beta=2.5466 \pm 0.8944$, $p = 0.0044$) and *P. fuscus* ($\beta=1.8043 \pm 0.7247$, $p = 0.0128$). Water depth and plant species richness had mostly positive, but not significant effects on the occupancies of amphibians in the restored wetlands. Effects of hay and mud transfer, water depth, vegetation cover and plant species richness on each amphibian species in the restored wetlands are displayed in Fig. 3b and Figure S11.

4. Discussion

Our findings suggest that restored wetlands are suitable breeding sites for most amphibian species in the area. Estimated occupancy was in almost all cases higher in intervention sites than in control sites, and some species, like the Fire-bellied Toad also had a higher

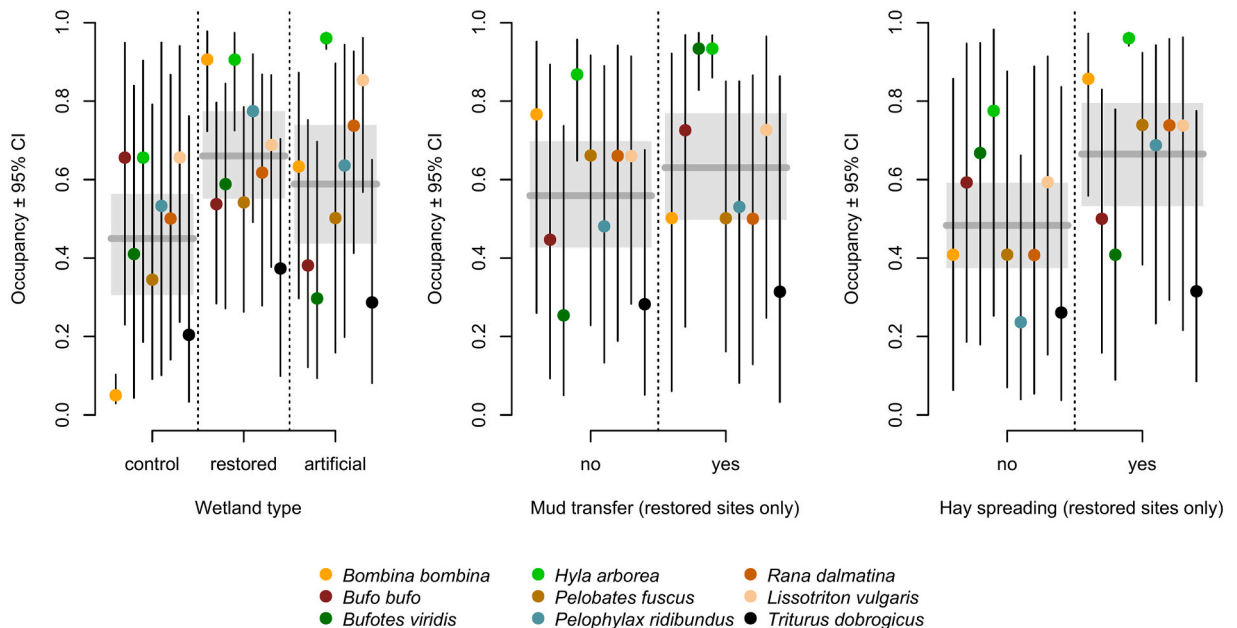


Fig. 2. Amphibian occupancy in response to wetland type (a), mud transfer in restored wetlands (b), hay spreading in restored wetlands (c). For each species mean occupancy probability and 95 % confidence intervals are shown, the grey horizontal line and area represent an averaged response and CI for all species.

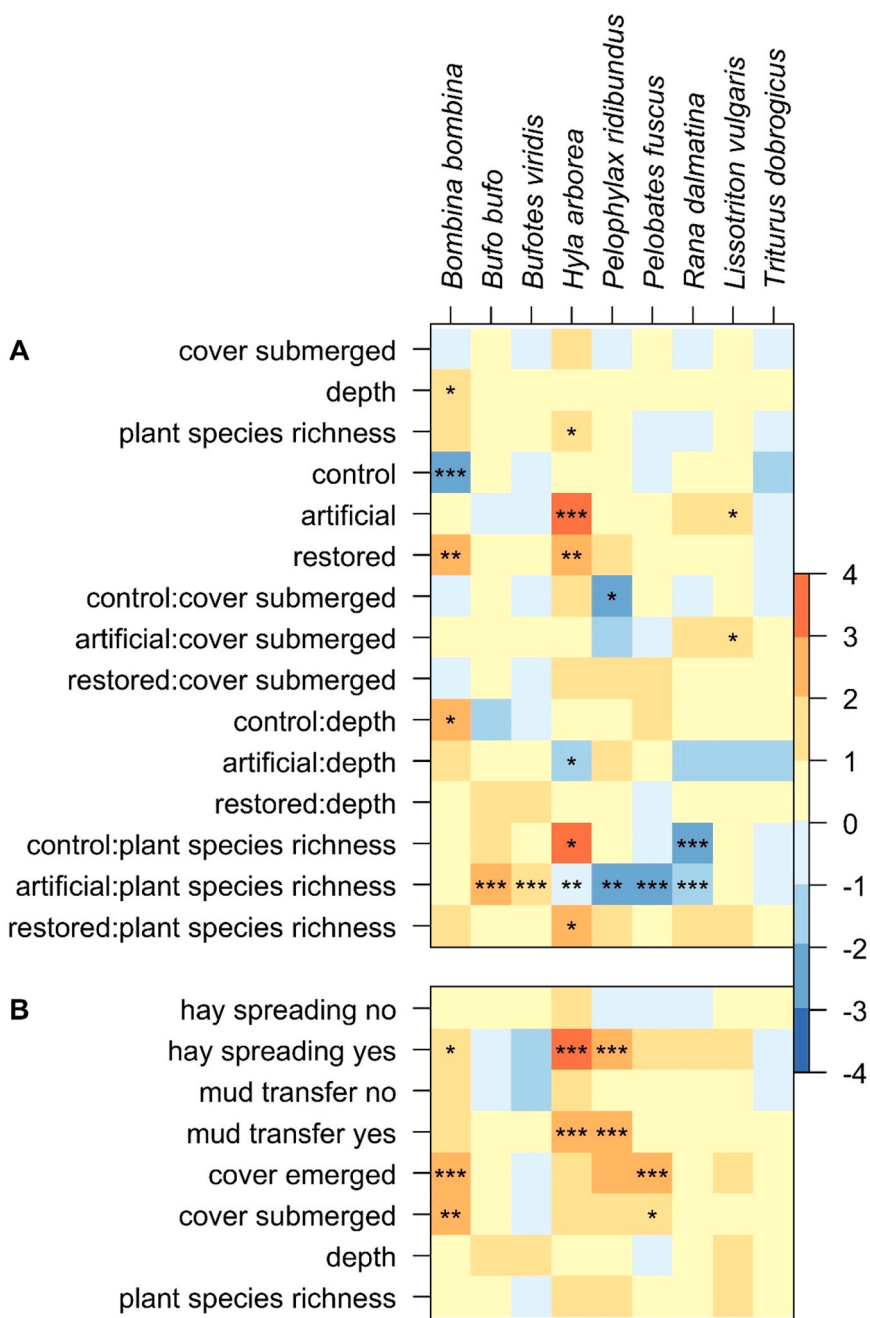


Fig. 3. Influence (coefficient estimates) of different wetland parameters on amphibian occupancy in all wetland types (a); and in restored wetlands (b). Asterisks indicate significant effects (** - $p < 0.01$, *** - $p < 0.001$).

occupancy probability in intervention sites compared to artificial ditches. We detected contrasting effects of the measured wetland parameters on the different species, however, generally water depth positively influenced amphibian occupancy. Our findings confirm our predictions that mud and hay transfer from other wetlands are favourable for amphibians, as mud transfer had a positive effect on the occupancy of all species while hay transfer had mostly positive effects. All significant effects of hay and mud transfer on amphibian occupancies were positive.

Based on our results, artificial ditches and restored wetlands are more suitable breeding sites for amphibians than natural wetlands in the study area. Natural, nonrestored wetlands are experiencing much shorter hydroperiods in the last few decades compared to historical trends, often drying out before the development of amphibian larvae is completed. Of the 6 natural wetlands, 2 dried out completely before the end of the amphibian surveys, and the remaining 4 dried out in the first half of the summer. Artificial ditches

tend to have a longer hydroperiod compared to natural wetlands, drying out only during the summer months, while most of the restored wetlands hold water throughout the majority of the year. Those restored wetlands that dry out, do so in the late summer droughts, after the metamorphosis of most amphibian larvae has already occurred, and the larvae have left the water. Our results also confirm our predictions that mud and hay transfer are efficient methods of wetland restoration and can be beneficial for amphibian communities. Mud and hay transfer can be effective tools in overcoming the dispersal limitations for numerous plant species, thus accelerating wetland regeneration (Pfadenhauer and Grootjans, 1999); and the presence of certain plant species can be important for amphibians (Magnus and Rannap, 2019).

We found that there are contrasting needs of the different amphibian species, however, there are attributes of wetlands that most species prefer. Considering all wetland types, water depth had positive effects on all amphibian species, including a significant positive effect on the occupancy of *B. bombina*, which was even stronger in natural wetlands used as controls. Until recently, this species was rather common in the area, however, its population sizes are declining due to habitat loss and shorter hydroperiods of wetlands because of droughts, similarly to other areas in Europe (Stravinskaitė et al., 2024). As this species breeds rather late in the season, a longer inundated period of the wetlands is crucial for it (Stravinskaitė et al., 2024), and water depth is correlated with the length of the hydroperiod. In artificial ditches, water depth had a significant negative effect on the occupancy of *H. arborea*. This species is one of the earliest breeding amphibian species in the area, so it most likely tolerates droughts better than other species, and it is likely that deeper canals host a higher density and diversity of predators, which may lead to reduced breeding success (Pearman, 1995). The majority of the studied wetlands are not inhabited by fish (in earlier years fish were detected in one of the artificial ditches, however, no fish were found during amphibian surveys), however, larger wetlands in the area host higher densities of known amphibian predators like the European pond turtle (*Emys orbicularis*) and the grass snake (*Natrix natrix*) as well as several arthropods.

The cover of underwater vegetation had a significant negative effect on the occupancy of *P. ridibundus* in natural wetlands. *P. ridibundus* is usually absent from the studied natural wetlands, we only detected it in one of the 6 sites, where underwater vegetation cover was low. Other studies also found that this species prefers ponds with lower vegetation cover (Pille et al., 2024). We found a significant positive effect of underwater vegetation cover on the occupancy of *L. vulgaris* in artificial ditches. As newts lay their eggs on submerged aquatic plants and use aquatic vegetation as shelter and hunting grounds, the presence of their preferred species is an important factor in breeding site selection (Magnus and Rannap, 2019; O'Brien et al., 2021). It is possible that in artificial ditches these preferred aquatic plants are present in a smaller number of the sites or in lower abundance only. Plant species richness had contrasting effects on the amphibian community. In natural wetlands, plant species richness had a significant positive effect on the occupancy of *H. arborea* and a significant negative effect on that of *R. dalmatina*, while in artificial ditches it had significant positive effects on the occupancies of *B. bufo* and *B. viridis*, and significant negative effects on the occupancies of *H. arborea*, *P. ridibundus*, *P. fuscus* and *R. dalmatina*. Plant species richness might be related to the hydroperiod length, as in wetlands that dry out more quickly, the number of plant species could be higher due to the presence of inundation-tolerant, but non-aquatic plant species (Boers et al., 2007; Little and Church, 2018). Plant species richness could also be correlated to other attributes of the wetlands, such as the species richness of several invertebrate taxa, that can serve as prey or predators of amphibian larvae (Baattrup-Pedersen et al., 2025; Hassall et al., 2011). In restored wetlands we only found positive effects of plant species richness, with a significant effect on the occupancy of *H. arborea*. Hydroperiod length is less variable in these sites, plant species richness is mainly dependent on fully aquatic plants, the presence of which is beneficial for most amphibian species. It is also important to mention that plant species richness might be a limiting factor in some of the restored wetlands as among these, the variability of plant species richness is greater (Figure S18); some of these wetlands, especially those without hay spreading or mud transfer are in the early stages of succession, and certain plant species important for amphibians could be absent from them.

In the analyses only focusing on restored sites, we found that both hay and mud transfer have positive effects on amphibian occupancies, with hay spreading having a net positive effect across all amphibian species (Fig. 2C) and mud transfer having a positive effect on all species (Fig. 3B). Hay spreading had a significant positive effect on the occupancies of *B. bombina*, *H. arborea* and *P. ridibundus*, and mud transfer having a significant positive effect on the occupancies of *H. arborea* and *P. ridibundus*. Mud and hay transfer can be efficient restoration tools to ensure the colonization of plant species with low dispersal capabilities, including that of the preferred plant species of amphibians (Kaplan et al., 2014). In the studied restoration sites, sites where plant introduction methods were implemented showed a higher number of plant species (Figures S12-S13). Underwater and emerged vegetation cover were higher at restoration sites with hay transfer, however, these were similar between sites with and without mud transfer (Figures S14-S17). In restored wetlands, both emerged and underwater vegetation cover had positive effects on most amphibian species, including significant positive effects on the occupancies of *P. fuscus* and the *B. bombina*. Aquatic vegetation can be crucial for amphibians as these plants not only provide shelter but also surface for egg placement and food for the tadpoles (Burrow and Maerz, 2022). We found no significant effect of plant species richness or depth on amphibian occupancy in restored wetlands, it is most likely that almost all restored wetlands provide a sufficient hydroperiod for amphibian development. We note that both predicted occupancies (Fig. 2) should be interpreted with caution as predicted values reflect marginal treatment effects and may be influenced by unmeasured variability.

While our study provides valuable insights, limitations are acknowledged. We did not consider habitat connectivity in the analyses, even though it is known that distance from a possible source for colonization can have a strong influence on amphibian occurrence in restoration sites (Clauzel et al., 2015; Moor et al., 2024; Rannap et al., 2009). For example, *T. dobrogicus* was not found at any sites in the Northern part of the area, therefore it is possible that the species was absent from the restored wetlands due to a lack of a source for colonization. We also did not consider the surrounding terrestrial habitat in the analyses, which is known to influence the breeding site selection of amphibians as well (Magnus and Rannap, 2019; O'Brien et al., 2021), however, almost all studied wetlands are surrounded by a mixture of dry and wet grasslands, so the surrounding terrestrial habitat is rather similar for all studied sites. We also neglected

chemical parameters of the waterbodies, even though it is known to influence amphibian breeding site selection (O'Brien et al., 2021), however, as all of the waterbodies are supplied by groundwater and are located in the same area, it can be assumed that water chemistry is similar among the sites. We only considered the presence of each species at the studied sites and did not measure breeding success. It is possible that there are sites where even though amphibians lay their eggs, the larvae are unable to complete metamorphosis due to the shorter hydroperiod (Stravinskaitė et al., 2024). There are also cases, where even though there is a higher number of adults or even spawn clumps at a site, the difference is insignificant in the number of larvae (Soomets et al., 2023). It is also possible to find adults of a species at a site, that are not breeding there (Clauzel et al., 2015), however, apart from a few exceptions (mainly in the case of *T. dobrogicus*), when we detected a species at a certain site, we also detected breeding activity (larvae, spawn clumps, calling males). Since our study was conducted in a single year, we were unable to control for the effects of study year in our analyses. Even though our study yields promising results on the short-term, further monitoring of these wetlands is necessary to assess the long-term effects of these interventions (Adam et al., 2024).

Despite the intensive surveys, we failed to detect *R. arvalis* at any of the studied waterbodies. While this species is known from a few of the studied sites historically, it is rare regionally and is possibly extinct in the studied sites. We found no significant effects on the occupancy of *T. dobrogicus*, possibly due to the limited number of sites where we detected the species. It is likely that population sizes of this species decreased significantly due to the loss of suitable habitat and climate change in the Hungarian lowlands, including in the study area. It will be crucial to assess the habitat preferences of this species thoroughly in the future, as future habitat loss can push this species to the brink of extinction in the region. It would also be important to expand the study spatially and temporally, as regular, repeated monitoring could reveal the long-term impacts of wetland restorations on amphibian communities and allow for the study of the succession of wetland communities (Adam et al., 2024; Clauzel et al., 2015). While all restoration sites were included in the study, we could also include other artificial and natural wetlands in the region, including reference-state wetlands outside the study area.

Our study highlights the importance of restoring wetlands in amphibian conservation in areas where the loss of suitable breeding sites threatens amphibian populations. At our study site, in Central Hungary amphibian occupancy was higher in restored wetlands compared to nonrestored controls. Restored wetlands have a longer hydroperiod, allowing amphibians to complete their metamorphosis. While some attributes of wetlands have contrasting effects on the different species, however, it can be said that water depth has a positive effect on amphibian occupancy. In restoration sites, vegetation cover also had a positive influence on most species. Based on our results, wetlands restored to provide breeding sites for amphibians should be deep enough to provide a sufficient hydroperiod for the development of amphibian larvae, including late-breeding species such as *B. bombina*. However, it is important that these wetlands remain temporary and ideally dry out (or have low water levels) in some years, after the completion of amphibian metamorphoses, in order to avoid colonisation by predators connected to permanent waterbodies such as predatory fish. In practice, maximal water depth should ideally range between 150 and 300 cm in our study area, to support a sufficient hydroperiod without shifting to permanence. At the same time, we note that amphibians in the region coexist with several native, wetland-dwelling fish species (e. g. *Umbra krameri*, *Misgurnus fossilis*, *Carassius carassius*), which have themselves become endangered due to the widespread loss of their aquatic habitats. Ideally, some of the reconstruction sites could also support some of these fish species, enhancing their conservation status and decreasing the risk of local extinction. Hay and mud transfer from reference-state wetlands have also proved to increase amphibian occupancy, most likely by accelerating the regeneration of aquatic plant communities that are important for amphibians. While we were able to assess the habitat preferences of most species, further research is needed to better understand the habitat requirements of rarer species such as *T. dobrogicus* and *R. arvalis*.

Ethics statement

Not applicable: This manuscript does not include human or animal research. If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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CRedit authorship contribution statement

András Kelemen: Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Csaba Vadász:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Attila Mór:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Boldizsár Botond Lestyán:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Bálint Wenner:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Data curation, Conceptualization. **Edvárd Mizsei:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03837](https://doi.org/10.1016/j.gecco.2025.e03837).

Data availability

I have shared the link to my data in the attach file step

[Effectiveness of wetland restoration on amphibians in a drying grassland habitat losing its breeding sites \(Zenodo\)](#)

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Further reading

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