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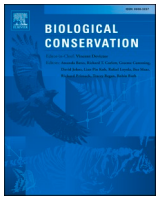

Grassland restoration benefits declining farmland birds: A landscape-scale before-after-control-impact experiment

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ABSTRACT

The decline of farmland bird populations starting in the 1980s has induced intense research on farmland biodiversity conservation in Europe. Although many studies assessing the effectiveness of agri-environmental schemes have concentrated on birds, farmland birds, surprisingly, have not yet been targeted directly by permanent, landscape-scale restoration of grassland ecosystems on former croplands in Europe. We compared farmland bird responses to grassland restoration by grass sowing, alfalfa sowing followed by spontaneous grassland recovery, and hay transfer (impact sites) with responses to extensive, low-intensity cropland cultivation (controls) in a Before-After-Control-Impact design, and also compared extensive croplands against a baseline reference of intensive croplands. Point counts in 69 sites on 910 ha in at least two years before and three years after the interventions showed that farmland bird species richness increased in both restored grasslands and in extensive croplands, whereas abundance and Shannon diversity increased only in restored grasslands but not in extensive croplands. Abundance increased in restored grasslands for five farmland species and two species of conservation importance, and in extensive croplands for one farmland and one species of conservation importance. Active restoration by grass sowing increased both species richness and diversity and active restoration by hay transfer increased abundance, while passive restoration targeting spontaneous grassland recovery after alfalfa sowing increased richness and abundance. Extensive croplands had four-five times more species and individuals than intensive croplands. Our results suggest that landscape-scale grassland restoration can locally reverse regional farmland bird declines and can thus be a promising tool in farmland biodiversity conservation.

1. Introduction

The United Nations General Assembly has declared 2021–2030 the Decade on Ecosystem Restoration (https://www.decadeonrestoration.org). In the European Union (EU), ecosystem restoration is the fundamental focus of the Nature Restoration Law, a centerpiece of the EU Biodiversity Strategy for 2030. The term "ecosystem restoration" requires that whole functioning ecosystems that include both plants and animals are restored permanently to recover ecosystem health, integrity and services. Animals represent fundamental ecosystem functions and services, thus, ecosystem restoration should include higher trophic levels such as consumers, predators and decomposers beyond producers (Kollmann et al., 2016; Vander Zanden et al., 2016). Birds, for example, are important in ecosystem functioning and services such as seed dispersal, pollination, pest control, waste decomposition, nutrient deposition and ecosystem engineering (Sekercioglu, 2006). Despite previous calls to focus more on animals in restoration (Brudvig, 2011; Majer, 2009; Young, 2000), animals are still mostly overlooked in restoration science and practice (Cross et al., 2020; Hale et al., 2019; Lengyel et al., 2020). This is unfortunate also because many other conservation interventions such as species protection/listing, ecosystem/habitat management and agri-environmental schemes target

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vertebrate species, yet we know little on whether and how their populations and communities can be restored.

Farmland birds include bird species dependent on open agro-ecosystems for feeding and/or breeding. Since 1990, farmland bird populations have declined by 32 % in Europe (European Environment Agency, 2019) and populations of 74 % of farmland birds have declined between 1966 and 2013 in North America (Stanton et al., 2018). Farmland birds make up 55 % of the bird species listed in the IUCN Red List in Europe (Traba and Morales, 2019). The major causes of the decline are the loss, degradation and fragmentation of semi-natural farmland habitats mainly due to agricultural intensification (Donald et al., 2001; Jeliazkov et al., 2016; Newton, 2004). Intensification involves the increasing use of fertilizers resulting in soil and water pollution, increasing use of insecticides resulting in population declines of arthropods that are important food for farmland birds (Musitelli et al., 2016; Vickery et al., 2009), disappearance of treelines, windbreaks, hedgerows and field edges resulting in landscape simplification/homogenization and increasing field sizes (Guerrero et al., 2012). The abandonment of semi-natural grasslands managed by traditional low-intensity agriculture (grazing, mowing etc.) also threatens farmland biodiversity (Henle et al., 2008; Tartally et al., 2019; Terres et al., 2015). Despite ambitious biodiversity targets and large-scale efforts, farmland biodiversity continues to decline in Europe (Elbakidze et al., 2018). Measures such as agri-environmental support systems run under the Common Agricultural Policy of the EU have largely proved ineffective in halting the decline of farmland biodiversity (European Court of Auditors, 2020). For example, the farmland bird index, that represents population trends of selected bird species, continues to decline, at a rate of 5 % between 2013 and 2018, in the UK despite wide-scale uptake of agri-environmental subsidy programs (Burns et al., 2020). In countries

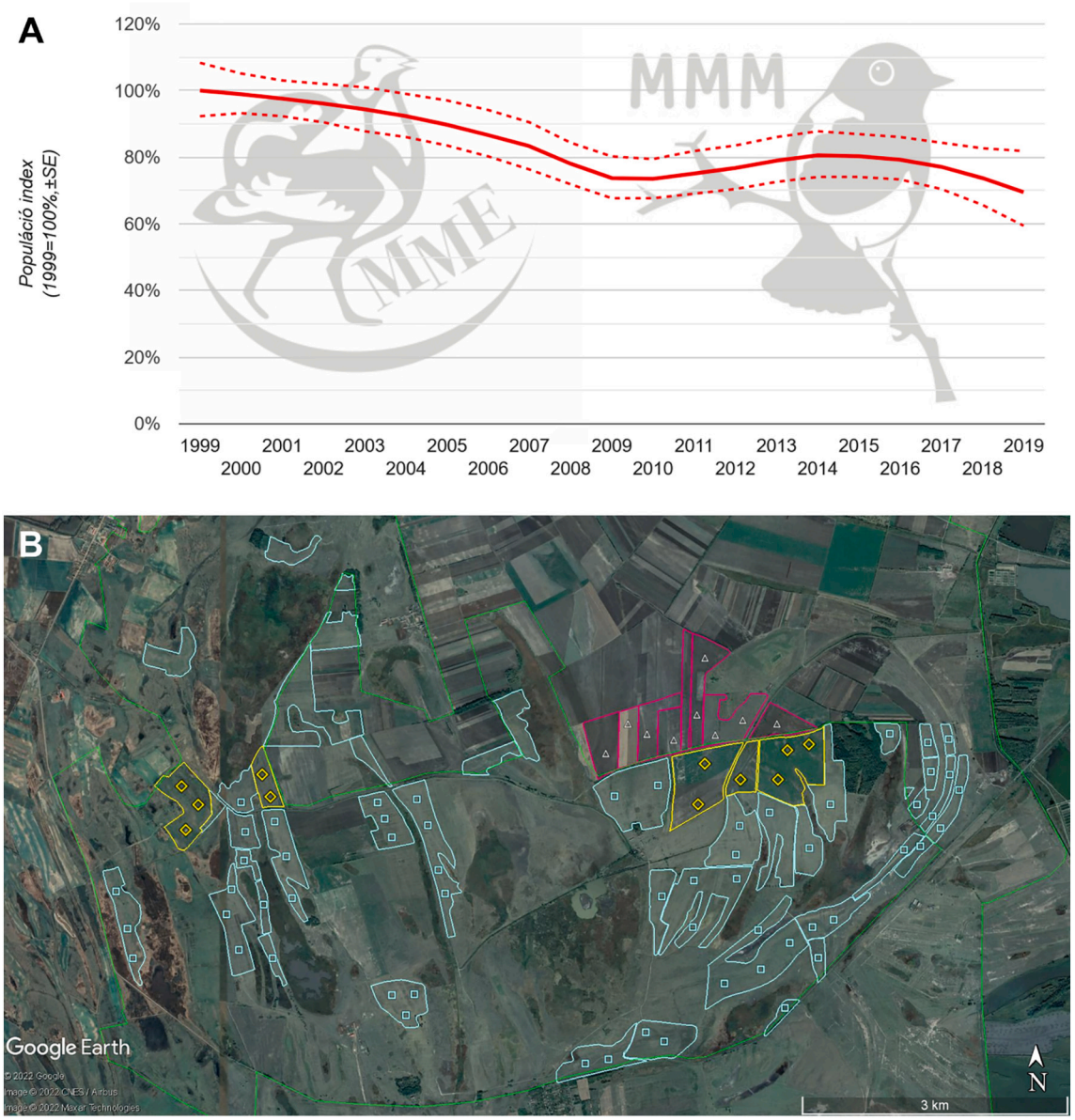

Fig. 1. (A) Changes in the farmland bird indicator (FBI) of Hungary in 20 years (1999 = 100 %). The trend is significant negative ($b = -1.50 \pm$ S.E. 0.30, $p < 0.01$). Source: Hungarian Common Bird Monitoring program, data visualization page (https://mmm.mme.hu/charts/trends, accessed: March 20, 2022). (B) Map of the study area with restored grasslands (impact sites, light blue), extensive croplands (control sites, yellow) and intensive croplands (reference sites, red) in the Egyek-Pusztakócs marshes of Hortobágy National Park, NE Hungary (green line: protected area) (B). Bird counting points are indicated by light blue squares in restored grasslands, yellow rhombuses in extensive croplands and white triangles in intensive croplands. Source of imagery: Google Earth, year 2004 (before restoration). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

that joined the EU later, the decline started later (Báldi and Batáry, 2011). For example, in Hungary, farmland bird decline has accelerated due to the intensification of agriculture, especially after the accession of Hungary to the EU in 2004, leading to a 30 % total decrease in the national farmland bird index between 1999 and 2019 (Fig. 1A).

Experience from studies conducted in North America suggests that the permanent restoration of grassland ecosystems on former croplands can benefit grassland birds. In the USA, >14 million hectares (ha) of cropland were restored to grassland in the Conservation Reserve Program (Vickery et al., 1999), whereas in Canada, 445,000 ha of cropland were restored in the Permanent Cover Program (McMaster and Davis, 2001). Several studies on the impacts of these programs found that grassland restoration can benefit grassland birds by re-establishing habitat and/or improving habitat quality (Johnson, 2005; McCoy et al., 1999; Vander Haegen et al., 2015), which can lead to increased breeding success and larger populations (Johnson and Igl, 1995; Wakeham-Dawson et al., 1998). Restored grasslands can also host more species than croplands (McMaster and Davis, 2001) or as many species (Fletcher and Koford, 2002) or more species than native grasslands (da Silva and Fontana, 2020), although the increase in bird diversity may be temporal (Millenbah et al., 1996), or may not reach the diversity of natural prairies (Rahmig et al., 2009). While these studies demonstrate the benefits of restoration of seminatural grasslands on former croplands to grassland birds, we know little on whether and how grassland restoration influences farmland birds in Europe. Importantly, farmland birds in Europe include species of open agroecosystems, that are often different from species of North American grasslands and prairies, which include many songbirds, several species of raptors and owls, prairie-chickens and grouse, and shorebirds not found in Europe, which can make experience from North American grassland studies difficult to interpret for agroecosystems of Europe. Except for one study in the U.K. (Wakeham-Dawson et al., 1998) and one in Brazil (da Silva and Fontana, 2020), all studies of grassland restoration listed in the Conservation Evidence website ("Restore or create grasslands" action, n = 23 studies, https://www.conservationevidence.com/actions/361) are from North America. The shortage of restoration studies in Europe is particularly alarming, where farmland bird populations have been declining since the 1980s (Gregory et al., 2004). While the benefits of agri-environmental schemes and low-intensity agriculture on farmland bird species and communities are intensively studied (e.g. Zellweger-Fischer et al., 2018; Zingg et al., 2019), many of these studies focus on one species (e.g. Bretagnolle et al., 2011), on temporary, short-term (e.g. 1 to 5-year) and/or small-scale (few 10s ha) restorations such as field margins, fallows, set-asides or abandoned old fields (e.g. Schlaich et al., 2015), or on habitat management e.g. in High Nature Value farmlands (e.g. Doxa et al., 2010). It is thus surprising that the impact of permanent, as opposed to temporary fallows or set-asides, restoration of grasslands on former croplands on farmland birds has not yet been assessed in Europe. The lack of such studies may be related to the limited spatial extent of restoration projects in Europe (Lengyel et al., 2012), which does not allow a spatially replicated assessment of restoration impacts on birds, a group with high mobility and large area requirements. The lack of studies also explains why there is only anecdotal information on which method of grassland restoration (e.g., spontaneous succession on old fields or after alfalfa sowing, introduction of seeds or other propagula, e.g., hay, of target plant species) benefits birds the most. Such knowledge is urgently needed as it will be essential in meeting the targets of the EU's recently proposed Nature Restoration Law, which will likely require member states to restore at least 30 % of the habitat types that are in not good condition until 2030.

Here we assess whether and how grassland restoration affects farmland bird communities and species of conservation importance. We address three questions: (i) How does grassland restoration influence farmland birds? (ii) Does grassland restoration provide greater benefits to farmland birds than extensive cropland cultivation does? (iii) Which method of grassland restoration (grass seed sowing, alfalfa sowing, hay transfer) benefits farmland birds the most? We hypothesized (i) that grassland restoration will positively affect farmland birds, (ii) that grassland restoration will lead to increased abundance, species richness and diversity of farmland birds compared to extensive croplands and (iii) that grass seed sowing as an active restoration method will provide more benefits to farmland birds compared to more passive methods such as hay transfer or alfalfa sowing followed by spontaneous grassland recovery. We conducted a landscape-scale field experiment based on a Before-After-Control-Impact (BACI) study design over eight years to compare the responses of farmland birds to three methods of grassland restoration (Impact sites) with responses to extensive cropland cultivation (Control sites), and also compared extensive croplands against a baseline reference of intensive croplands. The novelty of our approach is that the BACI design allowed us to compare farmland bird responses to both restoration and extensive cropland cultivation, and against the baseline reference intensive croplands, at spatial and temporal scales rarely available for field study in Europe, and to compare the impact of different restoration methods, which is rarely done in restoration studies on birds.

2. Materials and methods

2.1. Study area

We surveyed birds in the Egyek-Pusztakócs unit (4073 ha) of Hortobágy National Park (E Hungary), a World Heritage cultural landscape, which is a lowland (88 to 94 m a.s.l.) mosaic of former active floodplains, extensive alkali marshes in lower-lying depressions, surrounded by alkali meadows and salt steppes and separated by higher-lying loess plateaus (Fig. 1B). Loess plateaus had been croplands since the 1800s, and many steppes have been converted to croplands after floods no longer reached the area after nearby river Tisza had been regulated (1860s). The unit has been protected since 1973, and the water supply to the marshes has been reconstructed between 1976 and 1997.

2.2. Grassland restoration

Phase 2 (2005–2008) of the landscape rehabilitation decreased the proportion of croplands from 33 % to 14 % by the restoration of grasslands on 760 ha cropland (Lengyel et al., 2012). Grasslands were restored on extensively cultivated alfalfa, cereal, and sunflower fields in the order in which they became available for restoration upon the expiration of rental contracts between farmers and the land manager National Park. Restoration was designed and implemented exclusively for biodiversity/nature conservation purposes and targeted alkali steppes (EU Natura 2000 priority habitat type "Pannonic salt steppes and marshes") in lower-lying areas and loess grasslands ("Pannonic loess steppic grasslands") on higher loess plateaus. Three restoration methods were used: grass seed sowing, alfalfa seed sowing followed by spontaneous grassland recovery, and hay transfer. In active restoration of grass seed sowing, we used four foundation grass species that dominate the desired, target-state natural grasslands. After field preparation by ploughing, seeds of two grasses (67 % *Festuca pseudovina* and 33 % *Poa angustifolia*) were sown in alkali restorations and seeds of three grasses (40 % *Festuca rupicola*, 30 % *Poa angustifolia*, 30 % *Bromus inermis*) were sown in loess restorations (20 kg/ha each). Most of the grass seeds used in the restoration were harvested in nearby natural grasslands (18.5 t), whereas some grass seeds and alfalfa seeds were purchased from commercial sources (7.9 t). In passive restoration, we targeted spontaneous grassland recovery after sowing the fields with seeds of alfalfa *Medicago sativa* (20 kg/ha) after ploughing. In hay transfer, we mowed hay in target-state natural grasslands and spread it on the fields to be restored to facilitate the establishment of desired grasses and forbs.

Restoration actions were implemented in July (hay transfer) or September (grass and alfalfa sowing) each year. As a rule, the restored

fields were managed only by mowing once (after 15 June, grass-sown and hay-transfer fields) or 2–3 times a year (alfalfa-sown fields) for two full years after restoration. Other types of management (grazing by cattle) were introduced in a few restored grasslands in the third year after restoration. Because all fields were managed by mowing for at least two years and most of the counts were conducted in Years 1–3 after restoration, we did not test the effect of management in this study.

In the first year after restoration, the grass-sown and hay-transfer fields were dominated by weedy forbs, and grasses became dominant in Year 2 and 3. By Year 4, plant species composition approached that in target natural grasslands in alkali restorations, but not in loess restorations (Lengyel et al., 2012). In alfalfa restorations, no tillage, harrowing or oversowing was applied after alfalfa sowing, which allowed the spontaneous recovery of grasslands, during which alfalfa grew intensively in Years 1–2 and thinned out in later years, allowing the colonization and establishment of native grasses and forbs (Török et al., 2011). More details are given on the restoration in Lengyel et al. (2012, 2020), on vegetation development in Török et al. (2010) and Vida et al. (2010), and on animals' responses elsewhere (arthropods: Déri et al., 2011; small mammals: Mérő et al., 2015; amphibians: Mester et al., 2020; grasshoppers, locusts and crickets: Rácz et al., 2013).

2.3. Extensive cropland cultivation

Croplands within the National Park have been cultivated in a low-intensity ("extensive") cropping system since 2000, with restrictions on crop type and agrochemical use. We selected extensive alfalfa, cereal and sunflower croplands for this study on five fields totalling 150 ha in 2004 (Fig. 1B). From autumn 2006, corn, millet, sorghum and winter pea were also grown besides alfalfa and cereals in 100-m-wide strips on three of these croplands. In extensive alfalfa croplands that were part of 'control' fields, alfalfa was regularly rejuvenated by tillage, harrowing or oversowing as necessary, resulting in homogeneous alfalfa fields throughout the study period.

2.4. Study design

We applied a Before-After Control-Impact (BACI) design in which fields restored to grasslands were "Impact" sites (n = 35 fields, n = 58 counting points), whereas croplands with continued extensive cultivation were "Control" sites (n = 5 fields, n = 11 points) (Table 1, Fig. 1B). While the BACI design has been subject to debate (Underwood, 1994), well-designed BACI designs, with adequate number of replicates in both control and impact sites, remain one of the best designs at detecting and monitoring environmental effects (Smokorowski and Randall, 2017). Each counting point was surveyed in 2 to 4 years before and in 3 to 6 years after the interventions, or at least a total of 5 years over a period of eight years (2004–2011). The mean number of annual counts per counting point was 7.0 for restorations and 6.5 for extensive croplands (Table 1). As a baseline reference, we also surveyed intensive, conventional croplands <2 km from experimental fields in one year (2009) only as their bird fauna was less likely to change across years (n = 7 fields, 9 points; Table 1, Fig. 1B). We used these data only to compare response variables between extensive and intensive croplands as reference in 2009.

2.5. Field methods

We surveyed farmland bird communities and species using point counts (Gregory et al., 2005). The point count method is frequently used to survey and monitor the breeding bird community and is the basis of the integrated, continental-scale Pan-European Common Bird Monitoring Scheme (Gregory et al., 2005). We implemented point counts based on the protocol of the Hungarian Common Bird Monitoring scheme (Szép et al., 2012), a constituent scheme of the PECBMS. Counting points were at least 100 m from the field edge and at least 250 m from each other to avoid overlap. During counting, we recorded every bird seen or heard in 5 min within 100 m from the counting point. We recorded every bird that used the survey area for any activity (feeding, hunting, interacting with others, resting, singing, etc.) but excluded birds flying over. We also recorded ancillary information on bird behavior (territorial behavior, defense, singing, carrying nest material or food) that could be used to infer whether the bird species observed was breeding in the study area. Counts were made by experienced birders (GN, SL, TOM) between sunrise and 10 a.m. once in early spring (April 20 to May 5) and once in late spring (May 20 to June 15) at each counting point. We pooled data from the two occasions and our primary data were relative abundances (counts) per species per counting point per year.

2.6. Data analysis

We analyzed the farmland bird community by using only the observations of species included in the official Farmland Bird Index (FBI) of Hungary (https://mmm.mme.hu/charts/trends) to calculate species richness (number of species), Chao richness (Chao, 1984), abundance (number of individuals), and Shannon species diversity (Magurran, 2004). In species-level analyses, the response variable was the relative abundance (counts) of species. In species analyses, we analyzed eight FBI species with >10 recorded individuals, and we also analyzed five other species of conservation importance (Table 2).

First, we evaluated the Before/After and Control/Impact effects and their interaction as fixed effects on the community and species-level response variables. Two random factors accounted for annual variation in bird numbers (survey year), and spatial non-independence of counting points in the same field (field identity). For count-based variables (species richness, abundance), we built Generalized Linear Mixed Models (GLMM) specifying Poisson error distribution and log link by using the 'glmer' function, and for continuous variables (Chao richness, diversity), we built Linear Mixed Models (LMM) with Gaussian error distribution and identity link by using the 'lmer' function of the 'lme4' R package. Both functions use an iterative process based on maximum likelihood, allow unequal variances and are robust to unbalanced designs (Bates et al., 2015). We checked for overdispersion in count data, which may lead to spurious results in Poisson regressions, by the 'dispersiontest' function of the 'AER' package of R. Overdispersion was found in counts of three species (Greylag Goose *Anser anser*, Red-footed Falcon *Falco vespertinus*, Yellow Wagtail *Motacilla flava*), thus, for these species we fitted quasipoisson models. All statistics presented are based on the full models containing the two main effects, their interaction and the two random effects. We interpreted a significant interaction as the

Table 1
Study design and the number of fields, counting points and bird counts in each cell of the Before-After-Control-Impact (BACI) design used.

Intervention	Method	N fields	N points and counts		
			Before	After	Total
Restoration (impact)	Grass seed sowing	18	39, 90	39, 199	39, 289
	Alfalfa sowing	13	15, 46	15, 49	15, 95
	Hay transfer	4	4, 11	4, 12	4, 23
Extensive cropland (control)	Alfalfa, cereal, corn, millet	5	11, 22	11, 49	11, 71
Intensive cropland (reference)	Alfalfa, cereal, sunflower	7	–	–	9, 9

Table 2
The list and number of individuals of 12 farmland bird species (FB) and 5 species of conservation importance (CI) recorded in point counts in impact, control and reference sites of the study.

Rank	English name	Scientific name	Status	Impact			Control	Reference	Total
				Grass sowing	Alfalfa sowing	Hay transfer	(extensive cropland)	(intensive cropland)	
1	Skylark	*Alauda arvensis*	FB	392	108	56	57	4	617
2	Yellow Wagtail	*Motacilla flava*	FB	249	81	70	51	0	451
3	Greylag Goose	*Anser anser*	CI	197	81	2	50	0	330
4	Barn Swallow	*Hirundo rustica*	CI	105	74	11	27	0	217
5	Tree Sparrow	*Passer montanus*	CI	63	56	6	52	7	184
6	Corn Bunting	*Emberiza calandra*	FB	112	40	10	18	1	181
7	Northern Lapwing	*Vanellus vanellus*	FB	72	63	9	18	0	162
8	Common Quail	*Coturnix coturnix*	FB	59	20	4	14	0	97
9	Red-footed Falcon	*Falco vespertinus*	CI	67	22	6	0	0	95
10	Common Starling	*Sturnus vulgaris*	FB	27	31	0	35	0	93
11	Western Marsh Harrier	*Circus aeruginosus*	CI	52	14	6	7	3	82
12	Common Kestrel	*Falco tinnunculus*	FB	22	7	3	0	0	32
13	Lesser Grey Shrike	*Lanius minor*	FB	9	6	0	2	0	17
14	Red-backed Shrike	*Lanius collurio*	FB	2	3	0	1	0	6
15	Grey Partridge	*Coturnix coturnix*	FB	1	0	0	4	0	5
16	Tawny Pipit	*Anthus campestris*	FB	1	0	0	2	0	3
17	European Bee-eater	*Merops apiaster*	FB	0	1	0	0	0	1
		Total:		1430	607	183	338	15	2573

two main effects were not independent, e.g. the relative abundance of one species increased in restorations but decreased in croplands from before to after the interventions. In contrast, when the interaction term was not significant, we concluded that the two effects were independent. Adjusted means ± S.E.s were calculated by the 'emmeans' function of R.

Second, using data from restored fields only, we evaluated the effects of restoration methods and the Before/After factor, and the Method * Before/After interaction as fixed effects and the same two random factors (survey year, field identity) on community and species variables using GLMMs, LMMs and calculations as described above. A significant interaction term would indicate that the three restoration methods cause different changes, e.g. increases vs. decreases, in the response variable from before to after restoration, whereas a lack of interaction was interpreted as the three methods cause similar changes in the response variable. Finally, we compared community variables in extensive croplands (11 counting points on 5 fields, Table 1) vs. intensive croplands (9

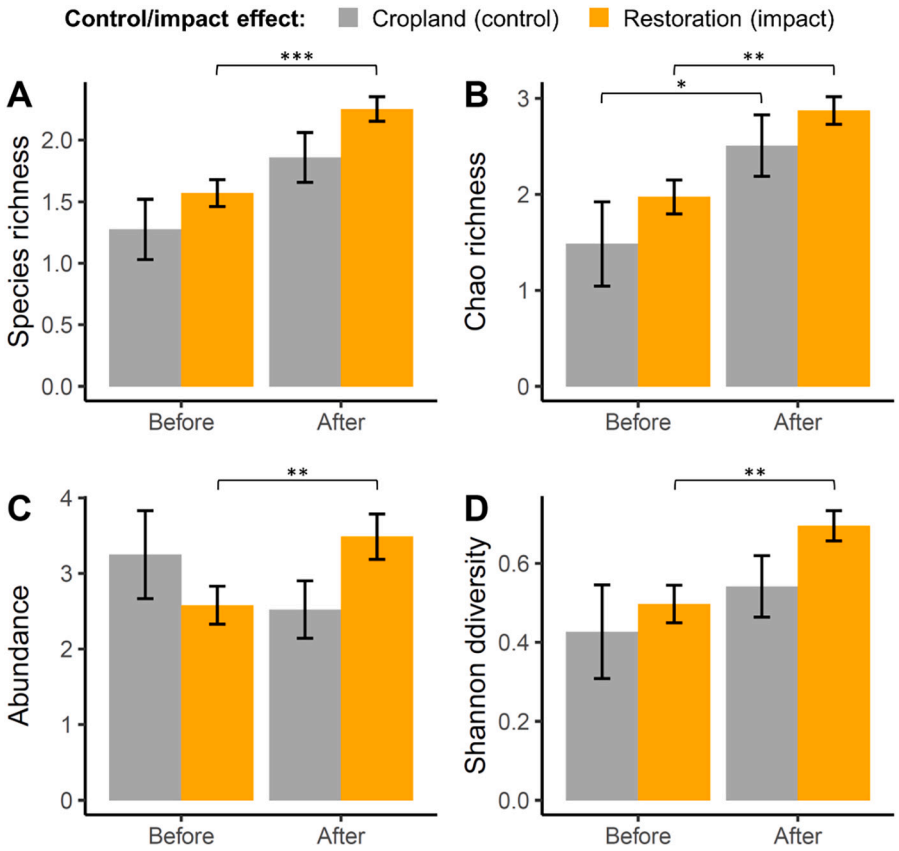

Fig. 2. Farmland bird community variables on extensive cropland fields before intervention ("Before") and on fields remaining extensive croplands (grey) and on fields restored to grasslands (orange) after intervention ("After"). Statistics are reported in the text, adjusted means ± S.E. are shown. *** $p < 0.0001$, ** $p < 0.005$, * $p < 0.05$.

points on 7 fields) by Kruskal-Wallis tests.

Because imperfect detection of some species can bias estimates of species richness, we adjusted for differences in detection probability by calculating extrapolated richness based on the bias-corrected Chao and the Abundance Coverage Estimator measures (Chiu et al., 2014; O'Hara, 2005) as implemented in the function 'estimateR' in package 'vegan' (Oksanen et al., 2011) and by repeating all analyses of species richness. The results were qualitatively identical to those obtained based on the number of species and Chao richness, thus we present results using the latter two variables.

3. Results

3.1. Farmland bird community

We recorded 1665 individuals of 12 of the 16 species considered in the calculation of the Farmland Bird Index of Hungary and 908 individuals of five other species of conservation importance (Table 2). All 12 farmland species recorded and analyzed in the study (Table 2), and all four other farmland bird species not recorded in point counts (Barred Warbler *Curruca nisoria*, Common Whitethroat *Curruca communis*, Crested Lark *Alauda cristata*, Grey Partridge *Perdix perdix*) are known to breed in the study area.

Each of the four community response variables changed significantly from Before to After the interventions (species richness, GLMM: R^2 = 0.086, estimate 0.4 ± S.E. 0.22, $\chi^2 = 24.212$, $p < 0.0001$; Chao richness, LMM: $R^2 = 0.102$, 1.0 ± 0.46, $\chi^2 = 27.170$, $p < 0.0001$; total abundance, GLMM: $R^2 = 0.277$, −0.3 ± 0.17, $\chi^2 = 6.247$, $p = 0.012$; Shannon diversity, LMM: $R^2 = 0.106$, 0.1 ± 0.13, $\chi^2 = 14.487$, $p = 0.0001$). Species richness increased significantly by 44 % in restorations ($z = 4.597$, $p < 0.0001$) but not in extensive croplands, where a 49 % increase was marginally non-significant ($z = 1.752$, $p = 0.080$; Fig. 2A). Chao richness increased in both restorations (+46 %, $t = 4.478$, $p = 0.0002$) and in extensive croplands (+70 %, $t = 2.136$, $p = 0.034$; Fig. 2B). Abundance increased by 35 % in restorations ($z = 3.229$, $p = 0.001$) and decreased non-significantly in extensive croplands ($z = -1.498$, $p = 0.134$; Fig. 2C), resulting in a significant interaction between the Before/After and Cropland/Restoration effects (0.6 ± 0.17, $\chi^2 = 11.320$, $p = 0.0008$). Finally, Shannon diversity increased by 40 % in restorations ($t = 3.585$, $p = 0.002$) but did not change in extensive croplands ($t = 0.895$, $p = 0.372$; Fig. 2D).

3.2. Farmland birds and species of conservation importance

Abundance increased in restorations but not in extensive croplands for five farmland bird species: Yellow Wagtail (+59 %, GLMM, $R^2 = 0.055$, $z = 2.881$, $p = 0.004$), Corn Bunting *Emberiza calandra* (+183 %, GLMM, $R^2 = 0.225$, $z = 3.775$, $p = 0.0002$), Common Quail *Coturnix coturnix* (three-fold increase, GLMM, $R^2 = 0.200$, $z = 3.163$, $p = 0.002$), Common Starling *Sturnus vulgaris* (five-fold increase, GLMM, $R^2 = 0.613$, $z = 2.035$, $p = 0.042$), and Common Kestrel *Falco tinnunculus* (three-fold increase, GLMM, $R^2 = 0.939$, $z = 2.140$, $p = 0.032$) (Fig. 3), and two species of conservation importance (Barn Swallow *Hirundo rustica*: two-fold increase, GLMM, $R^2 = 0.564$, $z = 3.466$, $p = 0.0005$; Red-footed Falcon: two-fold increase, GLMM, $R^2 = 0.954$, $z = 2.165$, $p = 0.030$) (Fig. 3). In contrast, abundance increased in extensive croplands but not in restorations for Northern Lapwings *Vanellus vanellus* (nine-fold increase, GLMM, $R^2 = 0.815$, $z = 2.805$, $p = 0.005$) and decreased in restorations but not in extensive croplands for Greylag Geese (GLMM, $R^2 = 0.987$, $z = -2.304$, $p = 0.021$) (Fig. 3). In the Skylark *Alauda arvensis*, abundance was higher in restorations than in extensive croplands both before and after the interventions (GLMM, $R^2 = 0.136$,

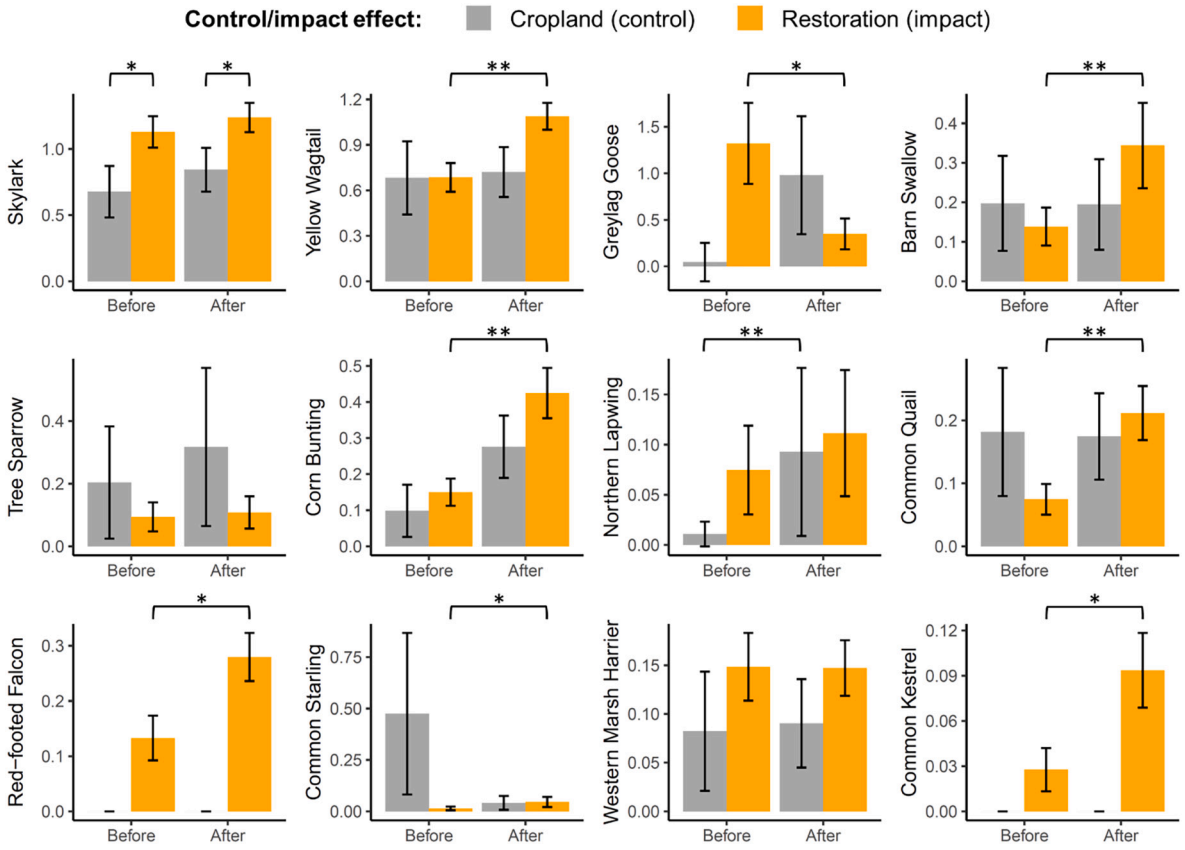

Fig. 3. Relative abundances of the 12 most abundant bird species (in order of decreasing total abundance from left to right and top to bottom) on extensive cropland fields before intervention ("Before") and on fields remaining extensive croplands (grey) and on fields restored to grasslands (orange) after intervention ("After"). Adjusted means ± S.E.s are shown. ** $p < 0.005$, * $p < 0.05$.

Cropland/Restoration effect $\chi^2 = 4.981$, df = 1, p = 0.026) (Fig. 3). Finally, abundance did not vary in the reedbed-nesting Western Marsh Harrier *Circus aeruginosus* (Fig. 3) and two tree-nesting species (Tree Sparrow *Passer montanus*, Lesser Grey Shrike *Lanius minor*) (results not shown).

3.3. Restoration methods

Lack of interactions between the Before/After factor and restoration method suggested generally similar positive effects of restoration on the farmland bird community (GLMMs or LMMs, interaction $\chi^2 < 1.800$, p > 0.4 for all four community variables, Fig. 4), while the Before/After factor was significant for all community variables (species richness: GLMM, $R^2 = 0.076$, $\chi^2 = 20.795$, p < 0.0001; Chao richness: LMM, $R^2 = 0.092$, $\chi^2 = 21.774$, p < 0.0001; abundance: GLMM, $R^2 = 0.275$, $\chi^2 = 9.108$, p < 0.003; Shannon diversity: LMM, $R^2 = 0.099$, $\chi^2 = 23.954$, p < 0.0001). Grass seed sowing led to significant increases in species richness (+44 %, z = 3.783, p < 0.001), Chao richness (+43 %, t = 3.445, p = 0.003), Shannon diversity (+56 %, t = 4.337, p < 0.001) and a marginally non-significant increase in abundance (+26 %, z = 1.958, p = 0.050) (Fig. 4). Alfalfa sowing increased species richness (+49 %, z = 2.547, p = 0.011), Chao richness (+62 %, t = 3.019, p = 0.003), abundance (+42 %, z = 2.581, p = 0.010), while hay transfer increased abundance (+64 %, z = 2.297, p = 0.022) (Fig. 4).

Grass sowing led to increased abundance of Barn Swallows (four-fold increase, GLMM, $R^2 = 0.658$, z = 4.287, p < 0.0001), Corn Buntings (four-fold increase, GLMM, $R^2 = 0.856$, z = 4.036, p = 0.0001), Common Quail (three-fold increase, GLMM, $R^2 = 0.899$, z = 3.038, p = 0.002), and decreased abundance of Greylag Geese (GLMM, $R^2 = 0.992$, z = −2.114, p = 0.035) and Tree Sparrows (GLMM, $R^2 = 0.755$, z = −2.004, p = 0.045) (Fig. 5). Alfalfa sowing resulted in increased abundance of Northern Lapwings (three-fold increase, GLMM, $R^2 = 0.835$, z = 3.289, p = 0.001) and Barn Swallows (two-fold increase, GLMM, $R^2 = 0.658$, z = 2.175, p = 0.030) (Fig. 5). Finally, hay transfer led to increased abundance in Barn Swallows (two-fold increase, GLMM, $R^2 = 0.658$, z = 2.952, p = 0.003) and Yellow Wagtails (two-fold increase, GLMM, $R^2 = 0.280$, z = 2.485, p = 0.013) (Fig. 5). The changes in the abundance of the Skylark and the Red-footed Falcon could not be explained by either restoration method (Fig. 5) and models did not converge in four studied species (Common Starling, Western Marsh Harrier, Common Kestrel, Lesser Grey Shrike).

3.4. Intensive vs. extensive croplands

In 2009, we recorded 15 individuals of 4 species (Corn Bunting, Skylark, Tree Sparrow, Western Marsh Harrier) in 9 point counts in intensive croplands, whereas in extensive croplands, we recorded 49 individuals of 8 species in 11 point counts. Farmland bird richness, abundance and diversity were significantly lower in intensive croplands than in extensive croplands (species richness, intensive: mean 0.4 ± S.D. 0.53 species (median: 0), extensive: 2.1 ± 1.04 (2), Kruskal-Wallis-test, H = 9.447, p = 0.002; Chao richness, intensive: 0.4 ± 0.53 (0), extensive: 3.3 ± 2.10 (3), H = 9.326, p = 0.002; abundance, intensive: 0.6 ± 0.73 (0), extensive: 2.4 ± 1.43 (2), H = 8.111, p = 0.004; Shannon diversity, intensive: 0 ± 0 (0), extensive: 0.7 ± 0.43 (0.8), H = 5.654, p = 0.017).

4. Discussion

Compared to the baseline reference in one year, extensive croplands had a farmland bird community an order of magnitude more diverse than that on intensive croplands. Our most interesting finding is that restored grasslands provided even greater benefits to farmland birds than extensive croplands did, which is supported by two results. First, both abundance and diversity increased after grassland restoration (by 35 % and 40 %, respectively) but not after extensive cultivation. Second, five farmland bird species and two species of conservation importance showed increases after grassland restoration but not after extensive

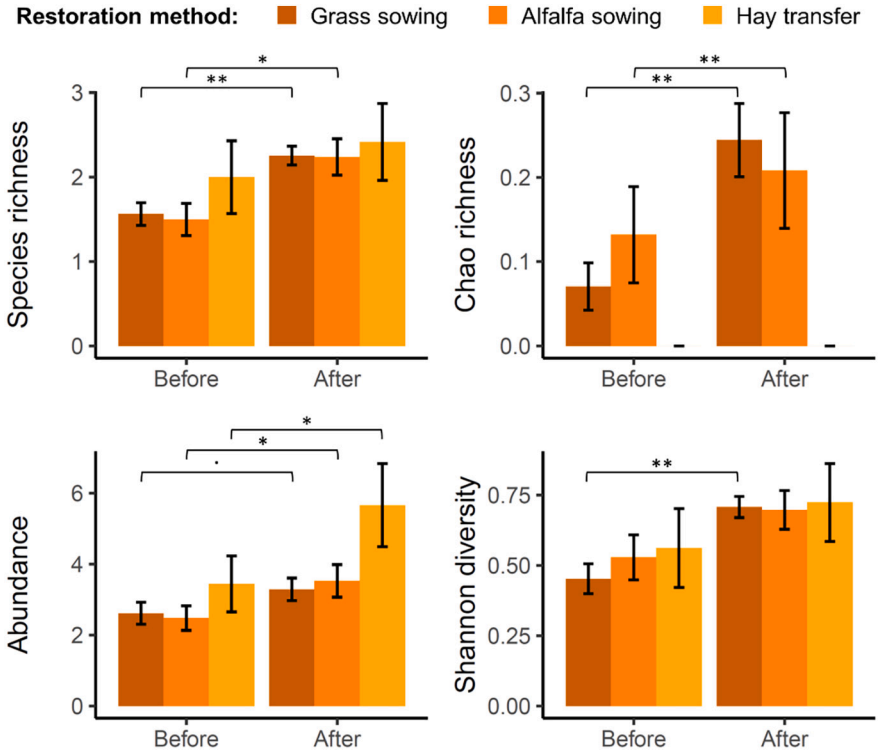

Fig. 4. Farmland bird community variables before and after grassland restoration by three methods: grass sowing (dark orange), alfalfa sowing followed by spontaneous grassland recovery (orange), and hay transfer (light orange). Adjusted means ± S.E. are shown. ** p < 0.005, * p < 0.05, • p = 0.05. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

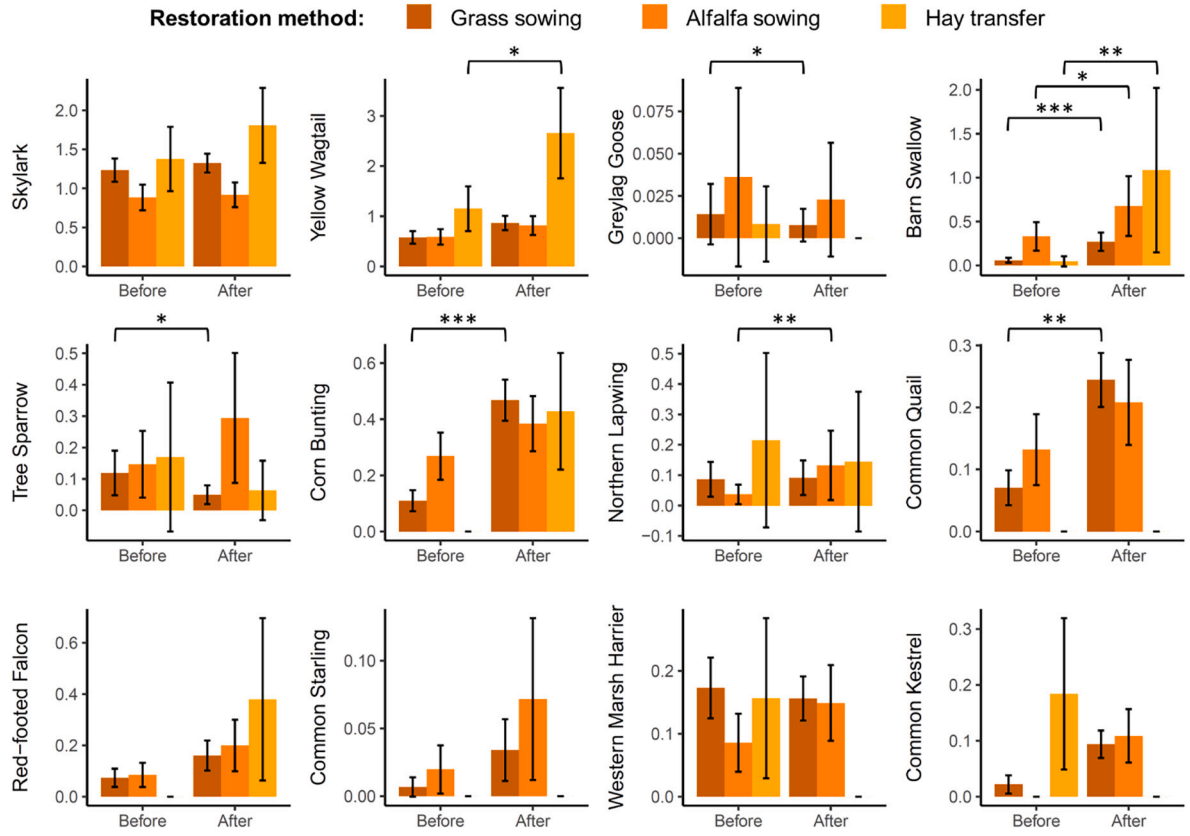

Fig. 5. Relative abundances of bird species before and after grassland restoration by three methods: grass sowing (dark orange), alfalfa sowing followed by spontaneous grassland recovery (orange), and hay transfer (light orange). Adjusted means ± S.E. are shown. *** $p < 0.0001$, ** $p < 0.005$, * $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cultivation, whereas only two wetland species showed increases after extensive cropland cultivation.

The benefits of extensive croplands over the reference intensive croplands found here are in line with findings from previous studies. Depending on crop type, extensive croplands received no herbicides or fertilizers and limited amounts of pesticides, leading to more weeds/forbs that provided enhanced food availability to farmland birds (Newton, 2004; Traba and Morales, 2019). Moreover, extensive croplands were cultivated in 100-m-wide strips, resulting in a higher diversity of crops and habitats due to smaller field sizes (Zellweger-Fischer et al., 2018).

The extra benefits of restored grasslands relative to extensive croplands likely involved permanent vegetation cover, more stable resources, less disturbance by human activity and increased habitat diversity. The termination of ploughing allows continuous plant cover and permanent availability of food (seeds and arthropods) and other resources (e.g. nesting, hiding places), which can lead to increased food availability, lower predation rates and higher breeding success for farmland birds (Whittingham and Evans, 2004). The absence of ploughing, spraying, weeding also meant that restored grasslands were less disturbed by agricultural activity than extensive croplands. Finally, until Year 2, restored fields often resembled set-aside fields with tall weeds and increased structural vegetation diversity, providing habitat for several farmland birds (Vickery et al., 2008). In later phases of restoration, higher habitat diversity arose from our near-natural, low-input restoration method of sowing seeds of two or three grasses on three cropland types, which initiated locally divergent pathways of secondary vegetation succession (Lengyel et al., 2020; Lengyel et al., 2012).

While each restoration method generally led to positive changes for farmland birds, grass seed sowing increased both species richness (+43–44 %) and diversity (+56 %), whereas alfalfa sowing increased richness (+49–62 %) and abundance (+42 %) but not diversity, and hay transfer increased abundance (+65 %). These results suggest that grass seed sowing is related to increases in species richness and diversity, whereas alfalfa sowing followed by spontaneous grassland recovery is related to increases in richness and abundance, rather than diversity. Alfalfa-sown fields initially had low habitat diversity and more frequent disturbance (mowing 2–3 times per year), and grasses became dominant only after 4–5 years of secondary vegetation succession (Török et al., 2011), whereas grass seed sowing was associated with higher habitat diversity, less disturbance (mowing once) and earlier dominance of grasses (from Year 2–3) (Lengyel et al., 2012). These results suggest that active restoration by grass seed sowing can provide benefits to farmland birds faster than more passive restoration by spontaneous grassland recovery after alfalfa sowing. These results agree with the expectation that restoration method matters. For example, grasslands restored by sowing cool-season grasses and legumes had higher abundances of four bird species (and were population sources for two of these species) than grasslands restored by sowing warm-season grasses, which benefitted only one species (McCoy et al., 2001). These and our results suggest that if the goal of restoration is to increase the landscape-scale diversity of the bird community, a mosaic of fields restored with different methods is desirable.

The responses of individual species to restoration can be explained by matches between the habitat requirements of different species and the properties of the grassland habitats established by the restoration. It is not surprising that the largest increases were found for grassland specialists that depend on grasslands both for nesting and feeding: Yellow Wagtail (+59 %), Corn Bunting (+183 %), Common Quail (three-fold increase). Although the most abundant grassland specialist, the Skylark had rather high numbers on extensive croplands even before

the interventions, its abundance remained higher in restorations than in extensive croplands. One species nesting on buildings in farms and nearby villages (Barn Swallow) hunted flying insects above the restored grasslands, whereas another species nesting in cavities in tree-rows (Common Starling) used the soil surface of the restored grasslands for feeding in high numbers. Restored grasslands had higher abundance of Orthoptera (up to ten times more than on starting croplands, Rácz et al., 2013), and thus provided feeding opportunities for small raptors (Red-footed Falcon, Common Kestrel). Finally, restored grasslands appeared to be indifferent for two wetland species (Northern Lapwing, Western Marsh Harrier) and two cavity-nesting species (Tree Sparrow, Lesser Grey Shrike), or even avoided by one other wetland species (Greylag Goose). We note that two wetland species had higher abundance in extensive croplands, which they used mostly for feeding (Greylag Goose) or nesting (Northern Lapwing).

We found fewer differences in species responses to restoration method. The abundance of Barn Swallows increased in each restoration method, all of which led to high structural diversity in early phases of restoration, which likely enhanced the abundance of flying insects. Restored fields also attracted large groups of other bird species feeding on flying insects (e.g., European Bee-eaters, Whiskered Terns *Chlidonias hybrida* and White-winged Terns *Chlidonias leucoptera*). High structural diversity also likely enhanced nest concealment in Common Quail, and also in Corn Buntings, in which males use tall weeds or dry stems as singing post. Tall weeds, however, were avoided by Northern Lapwings, which often used the bare ground or short vegetation on extensive croplands for nesting. Finally, the positive effect of hay transfer on Yellow Wagtail abundance can be related to the higher availability of nesting materials on hay-transfer fields in addition to the benefits of nest concealment in the structurally diverse habitat.

To our knowledge, this is the first landscape-scale BACI experiment for birds in the context of grassland restoration in Europe. The Conservation Evidence knowledge hub ("Restore or create grasslands" action, https://www.conservationevidence.com/actions/361), lists one BACI study on five duck species in Conservation Reserve Program fields and croplands in the U.S.A. (Reynolds et al., 2001) and another on eight bird species in revegetated plots and sand barrens in Iceland (Gunnarsson and Indridadottir, 2009). Nevertheless, our study has some limitations that are relevant in the interpretation of the results. Most importantly, we did not quantify breeding success, even though several earlier studies detected differences in bird breeding success between restored grasslands and non-restored croplands (McMaster and Davis, 2001; Vander Haegen et al., 2015; Wakeham-Dawson et al., 1998). In addition, our study did not include post-restoration management effects. In the first two years after restoration, all the restored grasslands were managed by mowing, thus, it was not possible to test the effect of different management regimes. Finally, it also requires further study to assess whether or not restoration occurs at a scale sufficient to have population-level impacts for species of conservation importance to offset declines in surrounding areas under intensive agriculture.

We conclude that the richness, abundance and diversity of farmland birds increased after grassland restoration, which can thus be a promising conservation strategy to address farmland bird decline at the landscape scale. Active restoration by grass seed sowing emerged as the method most beneficial to farmland birds, followed by hay transfer and by alfalfa sowing, which led to fewer and slower positive changes. The most important conservation implication of our results is that large-scale restoration of grasslands can counter the decline of farmland birds even if the general regional trend is negative, as was the case in Hungary between 2004 and 2011 (Fig. 1A). Our results are relevant for conservation policy as they reinforce the role of ecosystem restoration and extend its applicability and potential benefits to farmland biodiversity conservation. Our study shows that several species of farmland birds and other birds of conservation importance can simultaneously benefit from restoration but also that this requires large-scale, multi-year approaches, and, in particular, landscape-scale planning and implementation. The results will thus be useful to conservation professionals, researchers, and citizen scientists as well as agricultural policy makers and farmers, and will contribute to the fulfillment of recent international commitments to nature and ecosystem restoration.

CRediT authorship contribution statement

Szabolcs Lengyel: Conceptualization, Data curation, Formal analysis, Funding acquisition, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Gergő Nagy:** Conceptualization, Data curation, Investigation, Methodology, Project administration. **Máté Tóth:** Investigation, Methodology. **Gábor Mészáros:** Data curation, Methodology, Project administration, Resources. **Csaba P. Nagy:** Data curation, Investigation, Methodology, Validation. **Edvárd Mizsei:** Formal analysis, Software, Visualization. **Márton Szabolcs:** Methodology, Project administration, Resources, Writing – original draft. **Béla Mester:** Methodology, Project administration, Validation. **Thomas O. Mérő:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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