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SPECIAL FEATURE: VEGETATION RESTORATION

Grassland restoration to conserve landscape-level biodiversity: a synthesis of early results from a large-scale project

Szabolcs Lengyel, Katalin Varga, Beatrix Kosztyi, László Lontay, Eszter Déri, Péter Török & Béla Tóthmérész

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Nomenclature
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Lengyel, S. (corresponding author, szabolcslengyel@yahoo.com), **Varga, K.** (varg.kata@gmail.com), **Kosztyi, B.** (cleo.deb@gmail.com), **Déri, E.** (d_eszter@yahoo.com), **Török, P.** (molinia@gmail.com) & **Tóthmérész, B.** (tothmerb@delfin.unideb.hu) Department of Ecology, University of Debrecen, 4032, Debrecen, Egyetem tér 1., Hungary
Lontay, L. (lungocska@freemail.hu) Aggtelek National Park Directorate, 3758, Jósvafő, Tengerszem oldal 1., Hungary

Abstract

Question: European landscapes have long been influenced by intensifying use by humans. Although habitat restoration can reverse this process, it is often limited in scope by socioeconomic constraints. Here we present a grassland restoration project that is exceptional in spatial scale in Europe.

Location: A total area of 760 ha of arable land was restored in the Egyek-Pusztakócs unit (50 km^2) of Hortobágy National Park, east Hungary, between 2005 and 2008.

Methods: Restoration targeted alkali steppes and loess grasslands by sowing seeds of either two (alkali) or three (loess) foundation grass species. In 2009, we surveyed the vegetation in restored and target grasslands and quantified the factors influencing restoration success in a space-for-time substitution design.

Results: We recorded 100 species of flowering plants, of which 37 species were non-weed, 'target' species. Annual weeds dominated 1-yr-old fields but had decreased dramatically by the third year due to a developing perennial grass cover. Former alfalfa fields had proportionally fewer weeds than former cereal and sunflower fields. The diversity of common species and the cover of target species increased from 1- to 4-yr-old restored fields. Alkali-restored fields had more heterogeneous vegetation and more species than loess-restored fields. Distance to the target vegetation did not directly affect vegetation variables. There was significant spatial variability in vegetation development, possibly suggesting several local pathways of succession.

Conclusions: Grassland restoration was generally successful in accelerating secondary succession towards alkali steppes and loess grasslands. However, further management is necessary to counter the homogenizing effects of litter accumulation, to reduce perennial weeds and to enhance the colonization of target species. Our project provides useful practical insights into grassland restoration and in applying restoration at a number of sites within a larger area to conserve biodiversity at the landscape scale.

Introduction

European landscapes and their vegetation have been affected by centuries of human use. Although habitat restoration has long been available as a key policy option and conservation tool to reverse negative impacts on biodiversity, it is usually limited in scope by socioeconomic constraints. Most wetland restoration projects, for example, are highly local and are under 1 ha in extent (Wagner et al. 2008). Large-scale restoration can initiate multiple, locally dependent pathways of secondary succession, which can in turn lead to an increased diversity of habitats within the landscape. Such restoration can be carried out if the habitat patches to be restored differ in either their previous history or the starting conditions at the beginning of restoration (Drake et al. 1999). Alternatively, different

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disturbance regimes or post-restoration management allocated to similar habitats restored in similar ways may also lead to multiple pathways of secondary succession (Walker et al. 2004). Multiple pathways can lead not only to the recovery of previously existing natural habitats, but also to the emergence of novel communities or ecosystems (Hobbs et al. 2006).

Despite these benefits of large-scale restoration, there is a serious lack of large-scale projects in practice and in the literature (Henry et al. 2008; Wagner et al. 2008; Déri et al. 2011). Moreover, only a few of the existing large-scale restoration projects have been monitored (Lunt 1991; Bakker et al. 2003; Wagner et al. 2008), and monitoring of multiple taxa is also rare (Ruiz-Jaen & Aide 2005; Woodcock et al. 2008). These shortcomings impede our understanding of the processes generating and governing local biodiversity (Wagner et al. 2008). Large-scale restoration has thus become an urgent task in conservation. One reason why large-scale restoration is infrequently applied is that its success cannot be guaranteed, and costly post-restoration management is often required to manipulate ecological processes towards the high-diversity target state (Young 2000). Therefore, the manipulation of the ecological processes requires both the implementation of restoration and post-restoration management of habitats (Hobbs & Cramer 2007).

Grassland restoration on former croplands is one of the most frequent types of restoration in terrestrial ecosystems (Török et al. 2011b). Grasslands have been particularly prone to be incorporated into agricultural production because their fertile soils and lack of trees made them an easy target for cultivation. As a result, many former grasslands are now cultivated or have become fragmented (Bakker & Berendse 1999; Muller 2002; Pywell et al. 2002). In Eastern Europe, the collapse of socialist agriculture, privatization of land and the inability of new owners to properly cultivate lands due to lack of financing have resulted in large-scale abandonment of croplands since the early 1990s (Ramankutty & Foley 1999; Cramer et al. 2008; Török et al. 2010). For example, 10% of agricultural croplands have been abandoned in Hungary since 1990, and the rate is similar (10–20%) in at least four other countries in Eastern Europe (Hobbs & Crammer 2007). These changes create opportunities and favourable conditions for large-scale restoration of grassland habitats that existed before agricultural cultivation. Grassland restoration can deliver conservation benefits by the establishment of new grassland patches, by the enlargement of remaining natural or semi-natural patches or by the enhancement of connectivity between remaining patches in fragmented landscapes (Hobbs & Crammer 2007).

The aim of this paper is to present a grassland restoration programme that is exceptional in spatial scale in Europe. We first describe the rationale and implementation of restoration and then our observations on germination and early vegetation development. Second, we analyse vegetation structure by comparing patterns in diversity and cover in a space-for-time substitution design using data from 1- to 4-yr-old restored grasslands and natural target-state grasslands. We specifically study the role of last crop type, seed mixture and distance to target-state vegetation in determining vegetation diversity and cover. Finally, we describe longer-term general changes in vegetation and soil, which are likely to affect the restoration process in the future. We conclude that vegetation development was rapid and progressed mostly in favourable directions after restoration, but we also identify the need for further post-restoration management.

Methods

Location and site history

Grassland restoration was carried out in the Egyek-Pusztakócs marsh and grassland system (50 km^2, 47° 33′N, 20° 54′E), a spatially distinct unit of Hortobágy National Park (northeast Hungary), a World Heritage Site. The area has a continental climate with a mean annual temperature of 9.5 °C. The mean annual precipitation is 550 mm and large fluctuations both in mean temperature and annual rainfall are typical. The marshes are remnants of ancient waterways formed by floods that frequently reached the area before the regulation of the nearby River Tisza. Between marshes, higher (2–4 m) plateaus running mostly N to S and covered by alluvial loess were formed, resulting in small differences in microtopography (range 88–96 m a.s.l.). A map of potential habitats (Lengyel et al. 2005) suggested that the lower-lying (below 89 m a.s.l.) areas were mostly covered by extensive alkali marshes (*Bolboschoenatalia maritimi* and *Typhaetum latifoliae* and *angustifoliae*). The marshes were surrounded by wet alkali grasslands (*Alopecurion pratensis*). Higher elevations (90–92 m) were covered by dry short-grass alkali steppe (*Festucion pseudovinae*), and the highest plateaus by loess grasslands (*Festucion rupicolae*).

Maps from military surveys (1856–66) show that many of the plateaus were cultivated as croplands as early as the mid-19th century. After the regulation of River Tisza, floods no longer reached the area and it was gradually drained by canals. In parallel with drainage of the area, intensive agriculture was extended to former alkali steppes and even wet meadows, and has increasingly transformed the landscape, resulting in the loss, fragmentation and degradation of the natural habitats. Drainage was further accelerated after the construction of water-diverting canals in the 1960s. By the 1970s, several large marshes had dried up completely, which triggered the first active habitat

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restoration project in Hungary, started in 1976. The first phase of this long-term landscape rehabilitation programme ended in 1997, when a water supply system to each of the seven major marshes was completed. The water supply system has brought back the water of River Tisza to the marshes and this facilitated rapid revitalization. The areal extent of marshes approached that before the regulation of River Tisza and many of the marsh vegetation types, as well as bird species, have re-established in the marshes (Gőri et al. 2000, 2006).

Despite the positive changes to wetlands, significant threats remained for terrestrial habitat types. Croplands made up 33% of the area within the national park and caused the fragmentation of grasslands, which covered 26% of the protected area. Almost all loess plateaus were cultivated as croplands and only a handful of small fragments of native loess grassland survived. Chemicals used on croplands (pesticides, fertilizers) infiltrated the marshes that had already been rehabilitated and caused their eutrophication and degradation.

Project objectives and socioeconomic background

To address these threats, the second phase of the long-term rehabilitation programme, financed by a LIFE-Nature programme of the European Union, aimed to (i) decrease the areal proportion of croplands from 33% to 14% by converting them to grasslands; (ii) establish two ecological corridors to connect northern and southern grasslands; (iii) create buffer zones between marshes and remaining croplands; and (iv) restore grasslands on plateaus surrounded by marshes. We designated croplands to be restored at 26 fields (Fig. 1). The restoration targeted two habitat types listed as priority habitat types of Annex I of the Habitats Directive: Pannonic loess steppic grasslands (Natura 2000 code 6250) and Pannonic salt steppes and marshes (code 1530). Areal targets were determined flexibly (51–95 ha loess grassland on a potential of 156 ha loess plateaus, and alkali steppes on the remaining 585–629 ha), because the area to be restored each year depended on seed availability, particularly of *F. rupicola* (see below). Eighty-five per cent of the area designated for restoration was owned by the state of Hungary and managed by Hortobágy National Park Directorate, and 15% of the land was purchased from private owners before the actual restoration. Local farmers had rented state-owned lands through long-term (5 or 10 yr) contracts, and restoration was scheduled after these rental contracts expired (2004–2006). The order in which fields were restored was thus determined by the year when they became available for restoration. The main crops grown by farmers on the fields were alfalfa, sunflower and cereals (wheat or barley).

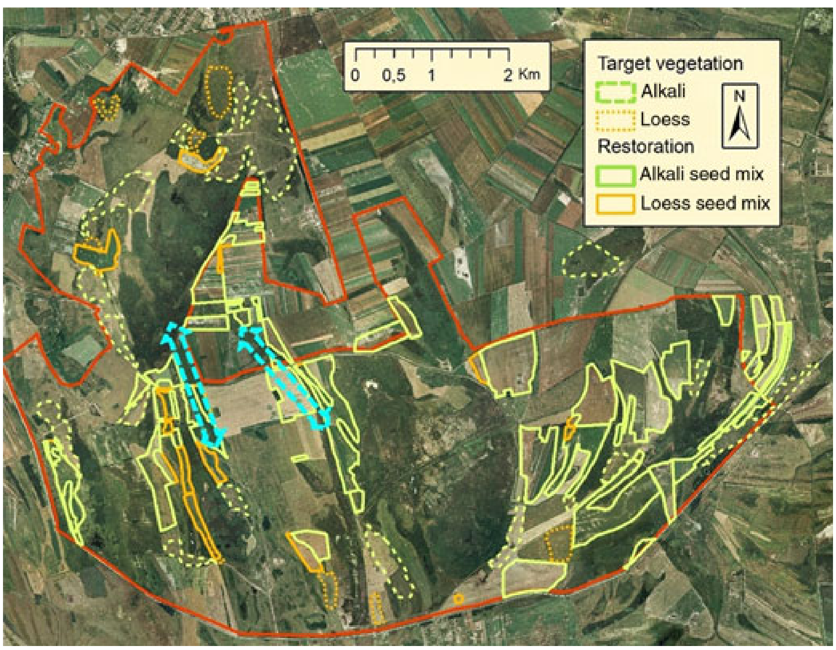

Fig. 1. Map of restored and target-state grasslands in the Egyek-Pusztakócs unit of Hortobágy National Park (dark orange line), east Hungary. The orthophotograph (2005) was obtained from the Institute of Geodesy, Cartography and Remote Sensing (FÖMI, Budapest, Hungary). Dark green areas show marshes, and light blue arrows indicate ecological corridors linking northern and southern marshes and grasslands.

The implementation of restoration

Grassland restoration on old fields is usually conducted either by spontaneous succession or through active restoration by sowing seeds (Török et al. 2011b). Most grassland restoration reported in the literature have used high-diversity seed mixtures consisting of up to 40 species (Pywell et al. 2002; Warren et al. 2002; Foster et al. 2007; Jongepierova et al. 2007). However, such seed mixtures are costly or very time-consuming to obtain, or cannot be obtained in quantities required for large areas. Thus, low-diversity seed mixtures (<10 species) have been used in several projects (Manchester et al. 1999; Lepš et al. 2007).

Here we used two low-diversity seed mixtures for restoration. The seed mixture for loess grasslands consisted of three species (40% *Festuca rupicola*, 30% *Poa angustifolia* and 30% *Bromus inermis* by weight), whereas the mixture for alkali steppes had seeds of two species (67% *Festuca pseudovina* and 33% *Poa angustifolia*). We selected these grass species because previous studies suggested that they are important foundation species of the target habitat types (Kelemen 1997). Seeds were obtained either from harvesting in nearby areas of good conservation status (*F. pseudovina*, *F. rupicola*) or purchased from commercial sources (*P. angustifolia*, *B. inermis*). Seeds of *F. rupicola* were not available commercially; therefore, the amount that could be harvested in early Jun of every year determined the amount of loess seed mixture available for restoration and thus the size of the area for loess restoration in that year. We harvested *F. rupicola* seeds in several small loess grassland fragments in the Hortobágy area and *F. pseudovina* seeds in nearby alkali steppes. We harvested a total of 18 500 kg grass seeds. Harvested plant material was thoroughly cleaned by threshing and seeds of targeted grass species were separated from the others by mechanical sieving (Agrohungária Llc., Karcag, Hungary). A total of 7900 kg seed of *P. angustifolia*, *B. inermis* and *F. pseudovina* were purchased from a commercial source (Agricultural Research and Development Institute, Szarvas, Hungary) in years of low seed productivity (2006, 2007). The stock of this company originated from the same region (greater Hortobágy area) for each of the three species. The loess seed mixture was sown on higher loess plateaus (above 91 m a.s.l.), whereas the alkali mixture was sown in lower-lying areas closer to the water table and more alkaline in character.

We sowed 20–25 kg seed mixture per hectare, which density is lower than in most grassland restoration projects (20–45 kg·ha^{-1}, mean in 11 projects: 31 kg·ha^{-1}) and is much lower than that used in agricultural pasture management (up to 80–500 kg·ha^{-1}) (Török et al. 2011b). The aims of sowing low-diversity seed mixtures in low densities were to (i) accelerate spontaneous secondary succession, i.e. to jump-start but not exclusively determine the pathways of succession; (ii) establish grasslands that become similar to the target grasslands with time; and (iii) allow ecological processes (secondary succession, colonization and establishment of non-sown target species) to operate more freely, similarly to spontaneous regeneration of vegetation on old-fields. Such low human control over the restoration process was warranted because the targeted grasslands are not extremely species-rich. Loess grassland fragments in the study site hold on average 14 ± 3.6 (SD) (range: 8–22) species of flowering plants per 4 m^2 (n = 21 plots), whereas alkali steppes have 7 ± 2.3 (range: 2–14) species per 4 m^2 (n = 33 plots) (B. Deák and S. Lengyel, unpublished data). Furthermore, target grasslands of good conservation status (with sources of propagules) were available relatively close (<2 km) to all fields restored (Fig. 1) and this method was expected to leave room for natural colonization processes.

Soil on the fields to be restored was thoroughly prepared for sowing. Because most fields had been cultivated as croplands for a long time, we first applied deep ploughing to reduce the amount of nutrients and bury seeds of weedy species deeper in the soil. This was followed by disc harrowing and surface rolling using field rollers. A modified fertilizer-spreader machine was used for sowing. After sowing, the soil was rolled again to cover the seeds.

The restoration was carried out each year between 2005 and 2008. The last crops on the fields to be restored were harvested by the farmers in Jul or Aug. Soil was prepared for sowing in late Aug and early Sep, followed by sowing in late Sep. The process was scheduled to end by early Oct, the usual time for germination of the sown grasses and when a rainy period starts in most years in eastern Hungary.

Post-restoration management involved mowing in the first and second year after restoration. Mowing was conducted once a year, before the seeds of weedy species ripened (early Jun) and hay was carried away from the fields. Mowing once (or twice in rare wet years) is a traditional land use in this region. In the third year, we designated either mowing or grazing for all restored fields as these are the most frequent types of land use. Fields that were close to livestock farms were grazed by cattle or sheep, whereas those farther away from farms continued to be mowed from the third year following restoration.

Monitoring

The principal aim of monitoring was to follow the development of the vegetation (vascular plants) by quantifying the establishment of the sown grasses and the colonization of the newly restored habitats by the species characteristic to the target habitat types. We started monitoring in the year following restoration by designating one sampling site per ca. 25 ha restored land. The last crop and seed mixture used were recorded for each sampling site. At each site, we established two (grazing management) or three (mowing management) 5-m × 5-m permanent plots marked by wood exclosures to keep out grazing animals (livestock, deer). Within each permanent plot, four 1-m × 1-m subplots were laid out systematically to facilitate monitoring of the small-scale mosaic structure characteristic of the target loess grasslands and alkali steppes. In total, we established 300 subplots in 75 permanent plots at 33 sampling sites on 23 fields between 2005 and 2009. For this study, we used data from those permanent plots (n = 45 plots on 23 sampling sites on 17 fields) that were not part of the grazing, mowing and hay transfer experiments initiated in 2008–2009 (Supporting Information Table S1).

Vegetation surveys of the permanent plots were carried out in early Jun, at the flowering peak of most species. In these surveys, we recorded plant species composition and cover by each species identified. To obtain reference data to relate species composition of the restored fields to natural, target-state grasslands, we used data from a baseline survey carried out in 2007 in the north-western part of the Egyek-Pusztakócs complex. Vegetation was surveyed at randomly selected 2-m × 2-m plots in alkali steppes and loess grasslands. We used data only from plots located in *Artemisio-Festucetum pseudovinae* or *Achilleo-Festucetum pseudovinae* (alkali steppes) or in *Salvio-Festucetum rupicolae* (loess grasslands) associations. Further details of botanical field methods are given in Török et al. (2010) and Vida et al. (2010).

Variables and data analysis

We compared the species composition of restored alkali steppes and loess grasslands using non-metric multidimensional scaling (NMDS) with Sørensen similarity, by the 'metaMDS' function of the R package 'vegan' (The R Foundation for Statistical Computing, Vienna, AT). We evaluated the effect of restoration conditions on vegetation variables in a space-for-time substitution approach, in which we used data from 2009 to compare response variables across sampling units on fields restored in different years. Response variables were species number, species diversity and total vegetation cover. Species diversity was quantified with both the Shannon and the Simpson indices of diversity because the former is more sensitive to the occurrences of rare species, whereas the latter is more influenced by abundances of dominant or common species (Tóthmérész 1995; Magurran 2004). Cover values for species were pooled over the four 1-m^2 subplots to obtain mean cover values per species for 2-m × 2-m plots. Species were classified into weed and non-weed species groups according to Grime's CSR strategy types (Grime 1979), modified and adapted to Hungarian conditions by Borhidi (1995). We used Borhidi's (1995) categories W (short-lived weeds), RC (ruderal competitors) and AC (adventive competitors) to define weeds. We considered non-weed species that are regularly present in the target-state alkali and loess grasslands in the Hortobágy area as 'target' species and calculated each of the four response variables both for all species and for target species only, resulting in a total of eight response variables.

Restoration conditions (independent variables) considered were restoration age, last crop type, seed mixture used in restoration and distance to the target vegetation. Restoration age was defined between one and four, as the number of years that had passed between the year a site was restored (2005–2008) and the year of the survey (2009). Last crop was either alfalfa (*Medicago sativa*, n = 18 plots), cereal (wheat *Triticum* spp. or barley *Hordeum vulgare*, n = 15) or sunflower (*Helianthus annuus*, n = 12). Restoration was carried out by the same methodology in each field, but with two seed mixtures (alkali and loess, see above). Finally, we measured distance to target vegetation using digitized habitat maps prepared for other studies and verified extensively on the ground. We first delineated patches of target-state alkali and loess vegetation in the Egyek-Pusztakócs landscape and then used ArcGIS 10.0 for Windows to measure the distances (±1 m) between the centre of the permanent plots and the border of the nearest patch of corresponding (alkali or loess) target-state vegetation (Fig. 1).

We examined the influence of restoration conditions on vegetation variables by analysing data with generalized linear mixed-effects models (GLMM). GLMM is a powerful analytical tool capable of detecting the influence of one or a few main effects (factors and covariates) on the response variable, even when the within-group errors are correlated and/or have unequal variances (R Development Core Team 2011, Vienna, Austria). The use of GLMM was also necessary because of the hierarchical nature of the data. There were two permanent plots at 22 sampling sites and there was one plot at one site, and sampling sites (total n = 45) were nested in 17 fields, introducing non-independence at the field level. GLMMs are capable of controlling for such non-independence because they allow the inclusion of hierarchical random factors. Because our sampling sites were a 'sample' of an unknown number of potential sampling sites in a 'sample' of fields restored, we used a hierarchical random factor with two levels (Sites nested within Fields). We constructed full GLMMs containing the four fixed effects, the hierarchical random effect and all two-way interactions between the four fixed effects. We then progressed by eliminating non-significant ($P > 0.05$) interactions one by one. Our final GLMMs contained the fixed effects, the random effect and any significant ($P < 0.05$) interaction. We evaluated the influence of the two levels of the random factor (Site, Field) by comparing the intercept SD of each level to the residual SD (Pinheiro & Bates 2000) and inferred substantial influence of any or both of the two levels if their intercept SD was larger than or similar (same order of magnitude) to the residual SD. All statistical calculations were performed in R, version 2.13.0. We specified GLMMs using function 'lme' in package 'nlme' and used Tukey's HSD procedure for *post-hoc* mean comparison for categorical variables, as implemented in the 'multcomp' package.

Results

Restoration results and early vegetation development

Grassland restoration was implemented on 760 ha of cropland between 2005 and 2008 (Fig. 1), of which loess grasslands were restored on 95 ha and alkali steppes on 665 ha. Four fields where the spontaneous regeneration of vegetation had started were not actively restored and were designated as controls.

Festuca seedlings germinated 2–3 wk after sowing and in greater numbers in the spring, but were soon overgrown by weeds. Short-lived weeds on former alfalfa fields included *Capsella bursa-pastoris*, *Matricaria inodora*, *Polygonum aviculare*, *Descurainia sophia* and *Stellaria media*, whereas on former sunflower and cereal fields, *Matricaria inodora*, *Anthemis arvensis*, *Capsella bursa-pastoris* and *Galium spurium* dominated. The sown perennial grasses became dominant in the second or third year, depending on site. Some unsown perennial grasses and target herbs (e.g. *Achillea collina*, *Alopecurus pratensis*, *Trifolium angulatum*, *T. striatum*, *Vicia hirsuta*, *V. angustifolia*) established on former alfalfa fields by the third year. This process was slower on former sunflower and cereal fields, where the perennial weed *Cirsium arvense* also increased in cover (>40% on three sunflower fields by Year 3).

In 2009, we recorded 100 species of flowering plants in the permanent plots. Most of these species (63%) were classified as weeds, and 37 species were non-weed 'target' species. An NMDS ordination indicated a clear difference in plant species composition between plots restored with loess and alkali seed mixtures (Fig. 2). Within alkali restored fields, NMDS scores differed by restoration age along the second axis ($F_{3,41} = 32.062$, $P < 0.001$), and *post-hoc* testing showed significant differences between all pairs ($P < 0.05$) of years except between 1- and 2-yr-old restored grasslands (2007 and 2008). Scores for alkali restored fields did not differ along the first NMDS axis ($F_{3,41} = 2.005$, $P = 0.128$), and there was little progress towards the target alkali steppes (Fig. 2). Most loess restoration was in 2005 and some in 2006, and no trend could be observed for restored loess grasslands (Fig. 2). An

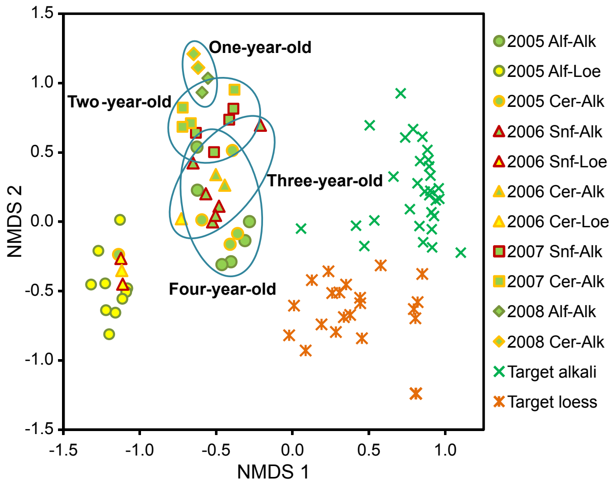

Fig. 2. Species composition of flowering plants on fields restored in different years and surveyed in 2009 ($n = 45$) and on target-state grasslands surveyed in 2007 ($n = 30$). The site plot was obtained by NMDS ordination using Sørensen similarity of presence/absence data (final stress: 17.13%). Restoration age is indicated by elliptoids (for alkali restorations only) and symbol shape (rhomboid – 1-yr-old, square – 2-yr-old, triangle – 3-yr-old, circle – 4-yr-old), whereas last crop type is indicated by symbol outline colour (Alf – alfalfa: green, Cer – cereal: orange, Snf – sunflower: dark red) and seed mixture is indicated by symbol fill colour (Alk – alkali: green, Loe – loess, yellow).

NMDS analysis using data from the restored plots showed that the species composition of alkali-restored plots appeared to become more heterogeneous with time, and plots restored with alkali seed mixture in 2005 had already separated into two groups by 2009 (Figs S1, S2). The species composition of loess-restored plots, however, was similar, regardless of the last crop cultivated on the field (Figs S1, S2).

Several herb species of conservation importance were observed to establish on the restored fields but were not detected in the regularly monitored permanent plots, such as *Salvia nemorosa* on loess restoration, *Aster sedifolius* and *Limonium gmelinii* on alkali restoration and *Dianthus pontederae* on both (Fig. S3).

The influence of last crop type, seed mixture and distance to target vegetation on vegetation development

Generalized linear models fitted to the data from 2009 (i.e. 1- to 4-yr-old restored fields) suggested that restoration age, last crop type and seed mixture each affected vegetation variables, whereas distance to the target vegetation was less important.

Restoration age significantly influenced the number of all species, the Shannon and Simpson diversity of all species, and the number and total cover of target species (Tables 1 and 2). The number of all species and Shannon

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Table 1. Major vegetation variables (mean ± SE) by year of restoration as measured on restored grasslands in 2009.

Species Group	Restoration Year	N	Species Number *	Shannon Diversity	Simpson Diversity	Total Cover
All Species	2008	4	26.0 ± 2.45[a]	2.00 ± 0.050[a]	0.26 ± 0.033[ab]	97.6 ± 6.12
	2007	8	21.8 ± 2.06[a]	1.68 ± 0.080[a]	0.30 ± 0.023[bc]	86.5 ± 4.13
	2006	12	9.7 ± 0.99[b]	1.22 ± 0.085[b]	0.39 ± 0.042[bc]	107.6 ± 5.73
	2005	21	7.8 ± 0.84[b]	1.09 ± 0.049[b]	0.42 ± 0.020[cd]	93.4 ± 4.50
Target Species Only	2008	4	5.3 ± 0.48[(ab)]	0.98 ± 0.088	0.49 ± 0.033	16.8 ± 6.49[a]
	2007	8	5.8 ± 1.16[(b)]	0.63 ± 0.153	0.68 ± 0.092	34.4 ± 7.70[ab]
	2006	12	3.3 ± 0.31[(ac)]	0.61 ± 0.097	0.64 ± 0.061	71.3 ± 8.44[b]
	2005	21	3.5 ± 0.25[(ac)]	0.82 ± 0.048	0.51 ± 0.029	82.5 ± 5.59[b]

*Groups not sharing a letter are significantly different according to Tukey's HSD procedure ($P < 0.05$; marginal non-significance, $P < 0.1$, is indicated by parentheses) following generalized linear mixed-effects models (Table 2).

diversity of all species were high in 1-yr-old grasslands, and decreased dramatically from 2- to 3-yr-old grasslands. In contrast, the Simpson diversity of all species increased steadily from 1- to 4-yr-old grasslands. Finally, the total cover of target species, including the sown grasses, increased from 17% on average in the first year to ca. 83% in the fourth (Table 1).

Last crop type influenced the number and Shannon diversity of all species (Table 2). The number and Shannon diversity of all species was higher on former sunflower and cereal fields than on alfalfa fields (Fig. 3a, b). Because there was no significant difference in the number or diversity of target species between the three crop types (Fig. 3a, b), these results show that non-target weeds made up a larger proportion of species on former sunflower and cereal fields than on former alfalfa fields.

Seed mixture influenced the number and Shannon diversity of all species and the Simpson diversity of target species (Table 2). Alkali restorations had more species (mean 15.0 ± 8.36 (SD), $n = 30$) than loess restorations (7.1 ± 1.96, $n = 15$; F statistic in Table 2). The Shannon diversity of all species and the Simpson diversity of target species were also higher in alkali than in loess restorations (Fig. 4a, Table 2). In contrast, the total cover of both all species and target species was higher in loess restorations than in alkali restorations (Fig. 4b, Table 2).

Distance to the target vegetation did not directly affect the studied vegetation variables. However, there was a significant interaction between distance to target vegetation and last crop type for the number and diversity of target species (Table 2). This was mostly because the number of species was unexpectedly high (11) in two plots very close to both a target alkali grassland and a newly formed depression and meadow (see below), which resulted in high species numbers and a negative relationship between distance and number of target species for former cereal fields but not for alfalfa and sunflower fields (Fig. S4a). Because most of the 11 species had low cover, this interaction was less pronounced but was still significant for both diversity indices for target species (Fig. S4b, c).

Spatial variability in vegetation development

The evaluation of the hierarchical random factor used in the GLMM analysis showed that the level of Field was influential in five of the eight response variables (number of all species, Simpson diversity of all species, total cover of all species, number of target species, total cover of target species), and Site was similarly influential with Field in two of these cases (number and total cover of all species) (Table 2). These results show that spatial variability in the diversity and cover of vegetation was substantial and that most of this variation existed among fields and some existed also between sites.

Discussion

Restoration and early vegetation development

To our knowledge, the grassland restoration implemented is currently the largest by surface area in Europe. The early results of this large-scale grassland restoration have provided several insights into the development of vegetation when similar low-input restoration is implemented at numerous sites within a landscape.

The high cover of short-lived weeds found in the first year is well-known from other studies of secondary succession (e.g. Lawson et al. 2004; Lepš et al. 2007). Weed cover was probably beneficial to *Festuca* growth by providing a more stable, humid microclimate and protection from the sun to the seedlings. This role of weed cover in facilitation of the germination and establishment of the sown grass species, however, is much less frequently reported (Callaway & Walker 1997; Pywell et al. 2002; Brooker et al. 2008; Pueyo et al. 2009). Early observations suggested that weed species composition was related to the last crop cultivated on the fields (Török et al. 2010). *Matricaria inodora* and *Capsella bursa-pastoris* were dominant in both types of restoration, with *Descurainia sophia* and *Stellaria media* being common on former alfalfa fields, and *Anthemis arvensis* and *Galium spurium* on cereal/sunflower fields. The rapid achievement of

Table 2. Results of generalized linear mixed-effect models testing the effect of last crop type (alfalfa/cereal/sunflower), seed mixture (alkali/loess), distance to target vegetation and restoration age (1–4 yr) on vegetation variables on restored fields. 'Location' was a hierarchical random factor, with 45 permanent plots surveyed in 2009 and nested within site (n = 23 sites, 22 sites with two plots, one site with one plot) and with sites nested within fields (n = 17 fields, 11 fields with one site, six fields with two sites). Significant effects are shaded in grey.

Response Variable	Independent Variables	Coefficient ± SE	*F*	*P*	Influential 'Location'
Number of All Species	**Restoration Age**	−6.17 ± 0.986	39.104	0.000	Field = Site
	Last Crop Type, Cereal–Sunflower	−3.01 ± 2.467	10.880	0.002	
	Alfalfa–Sunflower	2.00 ± 2.384			
	Seed Mixture	−0.03 ± 1.772	6.196	0.022	
	Distance to Target Vegetation	−0.00 ± 0.002	0.133	0.720	
Shannon Diversity, All Species	**Restoration Age**	−0.32 ± 0.042	57.716	0.000	None
	Last Crop Type, Cereal–Sunflower	−0.19 ± 0.097	8.520	0.004	
	Alfalfa–Sunflower	0.01 ± 0.098			
	Seed Mixture	0.07 ± 0.092	6.090	0.023	
	Distance to Target Vegetation	−0.00 ± 0.000	0.266	0.612	
Simpson Diversity, All Species	**Restoration Age**	0.07 ± 0.020	11.555	0.005	Field
	Last Crop Type, Cereal–Sunflower	0.02 ± 0.047	1.194	0.334	
	Alfalfa–Sunflower	−0.00 ± 0.047			
	Seed Mixture	−0.06 ± 0.043	0.015	0.905	
	Distance to Target Vegetation	0.00 ± 0.000	0.087	0.771	
Total Cover, All Species	Restoration Age	−1.99 ± 3.527	0.317	0.583	Field = Site
	Last Crop Type, Cereal–Sunflower	10.10 ± 8.502	0.292	0.752	
	Alfalfa–Sunflower	13.53 ± 8.459			
	Seed Mixture	23.15 ± 7.341	13.396	0.002	
	Distance to Target Vegetation	0.00 ± 0.006	0.089	0.768	
Number of Target Species	**Restoration Age**	−0.10 ± 0.359	6.259	0.027	Field
	Last Crop Type, Cereal–Sunflower	−1.60 ± 1.353	3.874	0.048	
	Alfalfa–Sunflower	2.56 ± 1.125			
	Seed Mixture	1.48 ± 0.515	3.354	0.084	
	Distance to Target Vegetation	−0.00 ± 0.001	0.930	0.348	
	Last Crop × Distance to Target	0.00 ± 0.001	8.380	0.003	
Shannon Diversity, Target Species	Restoration Age	−0.05 ± 0.048	1.109	0.312	None
	Last Crop Type, Cereal–Sunflower	−0.19 ± 0.141	3.542	0.059	
	Alfalfa–Sunflower	0.19 ± 0.148			
	Seed Mixture	0.35 ± 0.132	4.120	0.057	
	Distance to Target Vegetation	−0.00 ± 0.000	0.124	0.729	
	Last Crop × Distance to Target	−0.21 ± 0.289	5.250	0.016	
Simpson Diversity, Target Species	Restoration Age	−0.00 ± 0.030	0.000	0.991	None
	Last Crop Type, Cereal–Sunflower	0.07 ± 0.088	2.754	0.100	
	Alfalfa–Sunflower	−0.13 ± 0.093			
	Seed mixture	−0.20 ± 0.083	4.613	0.046	
	Distance to Target Vegetation	−0.00 ± 0.000	0.245	0.627	
	Last Crop × Distance to Target	−0.09 ± 0.182	4.083	0.035	
Total Cover, Target Species	**Restoration Age**	19.17 ± 4.455	18.524	0.001	Field
	Last Crop Type, Cereal–Sunflower	11.99 ± 10.740	3.511	0.060	
	Alfalfa–Sunflower	10.09 ± 10.687			
	Seed Mixture	25.96 ± 9.465	25.094	0.000	
	Distance to Target Vegetation	0.00 ± 0.008	0.020	0.888	

abundance of these weeds suggested that they established from the seed bank in the restored fields, indicating that deep ploughing may not be 100% efficient in eliminating their seed banks. The restored fields were also heavily treated with fertilizers and pesticides in the 1960s and 1970s, but less so since the 1980s, when regulations for Hortobágy National Park limited chemical use in protected areas. The nutrient load of the soil was still high before the restoration, especially due to high concentrations of phosphorus (mean 370 ± 459.0 (SD) mg·kg^{-1}, n = 45 plots) and potassium (552 ± 320.2 mg·kg^{-1}) (Deák et al. 2008). The high availability of nutrients may have also contributed to the early success of short-lived weeds and may be related to the increase of perennial weed cover, particularly of *C. arvense*, which occurred on some former sunflower fields in our study and in

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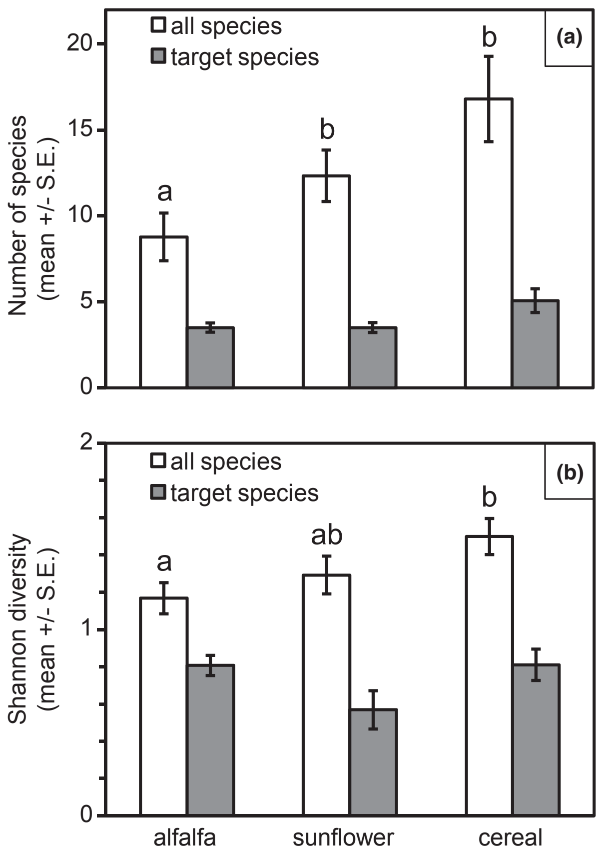

Fig. 3. Number (**a**) and Shannon diversity (**b**) of all species and target species on former alfalfa, sunflower or cereal fields restored to grasslands, based on data collected in n = 45 permanent plots in 2009. Groups not sharing a letter are significantly different (Tukey HSD following GLMM in Table 2, $P < 0.05$).

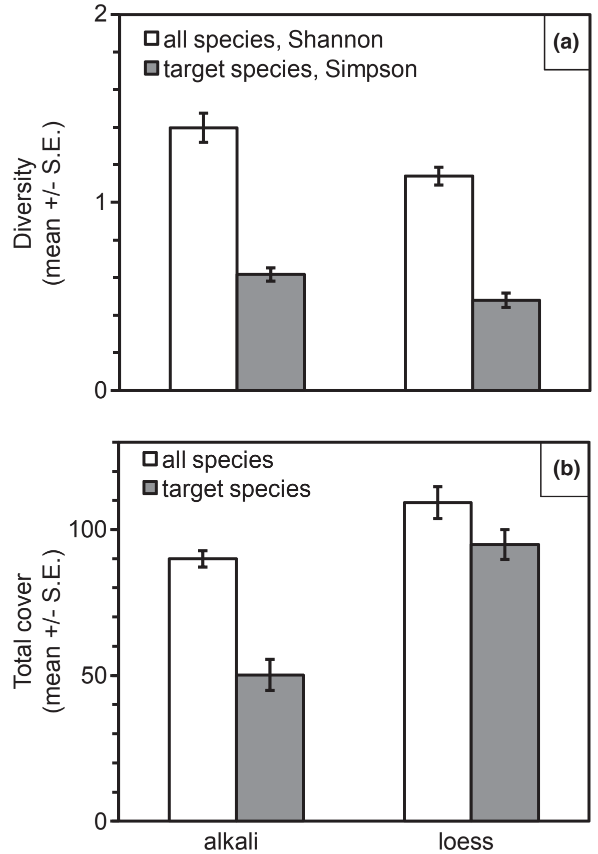

Fig. 4. Shannon diversity of all species and Simpson diversity of target species (**a**) and total cover of all species and target species (**b**) on former croplands restored by sowing alkali or loess seed mixture, based on data collected in n = 45 permanent plots in 2009. Differences between the two seed mixtures are significant for both diversity indices (Tukey HSD following GLMM in Table 2, $P < 0.05$) and for total cover ($P < 0.001$).

previous studies (Ruprecht 2005; Jongepierova et al. 2007; Prach et al. 2007).

Differences according to last crop

Our results suggest that there were proportionally more weedy species in restorations on former sunflower and cereal fields, which could thus be more prone to weed infestation than former alfalfa fields. Alfalfa is a perennial hay crop, which means lower below-ground disturbance (no ploughing for 3–4 yr) and higher above-ground disturbance (cutting for hay several times in a year) in alfalfa fields compared with fields of annual crops such as sunflower and cereal. These effects, coupled with alfalfa being a strong competitor and producer of allelopathic compounds, effectively suppress weeds that are known to cause problems on fields of annual crops (Meiss et al. 2010). Furthermore, the natural senescence of alfalfa creates microsites available for germination and establishment of other species, creating conditions for forbs to colonize older alfalfa fields and to develop a seed bank there (Török et al. 2011a). Restoration on alfalfa fields, therefore, may be more successful than on sunflower or cereal fields. One disadvantage of restoration on former alfalfa fields, however, is that the restoration process may be threatened by the accumulation of litter due to increased plant productivity (Deák et al. 2011), which in turn may be related to the farming practice of keeping high levels of phosphorus and potassium in alfalfa fields (Meiss et al. 2010).

Differences according to seed mixture

We found significant differences between sites restored by the two seed mixtures in species composition, diversity and total cover (Figs 2 and 4). Alkali-restored fields harboured more heterogeneous vegetation and had higher Shannon diversity of all species than loess-restored fields. The difference in Simpson diversity of target species

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further suggested that common target species were more frequent in alkali-restored fields. These results suggest that secondary succession started in several different directions over the large alkali-restored fields. Loess-restored fields, although they were usually smaller in area than alkali-restored fields, still had higher total cover, both for all species and target species. In fact, the difference in cover between the two species groups was much less in loess-restored fields than in alkali restoration (Fig. 4b). The contrasting patterns, i.e. more species with lower total cover on larger alkali-restored fields and fewer species with higher total cover on smaller loess-restored fields, could indicate that loess-restored fields provide better resources for the fewer colonizing species that are thus capable of developing higher cover.

Distance to target vegetation

We did not find any evidence that distance to the target vegetation influenced vegetation variables, which is contrary to the findings of many previous studies (Bakker et al. 1996). One explanation is that 1–4 yr after restoration may be too early to detect any effect of proximity to target-state natural grasslands. Although there are no physical barriers between target and restored grasslands, the lack of livestock vectors for seed dispersal (cattle, sheep) may have also presented a dispersal barrier in some areas. Finally, it is also possible that because most areas are relatively close to target vegetation (Fig. 1), the rate of immigration of target species varies little in the landscape.

Spatial variability in post-restoration vegetation development

The findings that vegetation variables differed both by last crop type and seed mixture suggested the possibility that vegetation development started along multiple pathways of succession on fields scattered within the landscape. Our result that the hierarchical random factor of ‘Location’ in the GLMM was influential in five of eight variables suggested much variability in vegetation variables at the level of Fields. In lower-lying, wetter areas, meadows dominated by either *Alopecurus pratensis* or *Carex melanostachya* formed (Fig. S5). On drier, higher plateaus *Festuca* grasslands with *Achillea* and *Artemisia* species became characteristic, occasionally with re-sprouting alfalfa (Fig. S6). Although it certainly requires more years of study to fully evaluate whether multiple pathways were initiated by our restoration using low-diversity seed mixtures over larger areas, our results point towards this possibility. The variability in such alternative successional routes or stages may contribute to the increase in diversity of vegetation and habitat types within the landscape, which is characteristic for the Egyek-Pusztakócs grasslands (Fig. S7).

Additional processes may also have contributed to vegetation differences among fields. The fields used to be ploughed regularly with heavy machinery, which smoothed the ground surface. Restoration also implied the termination of ploughing, which led to rapid changes in microtopography because soil in some parts of fields collapsed and sank, forming small depressions. The depressions were inundated with water from groundwater seepage and rainwater run-off, and were soon colonized by wetland plant species (e.g. *Bolboschoenus maritimus*) as early as the second year (Fig. S8). In the absence of ploughing, increased salinization (upward movement of sodium salts in the soil) and soil erosion occurred in several sites near these alkali depressions, which processes will presumably lead to the formation of alkali microforms characteristic on Pannonic salt steppes. These areas became very similar in physiognomy and plant species composition to the target alkali steppes as early as the second year (Fig. S9).

Temporal processes

Restoration age had a large influence on vegetation variables, indicating that vegetation development occurred rapidly after restoration. The number and Shannon diversity of all species declined with time due to a suppression of early-successional short-lived weeds, whereas the Simpson diversity of all species increased with time (Table 1). This tendency can be interpreted as the cover values of common species becoming more even from 1- to 4-yr-old grasslands. The cover of target species also increased significantly with time. These two findings suggest that target species were gradually colonizing the restored fields from the first through the fourth year. This process could also be observed in arthropod assemblages, the naturalness of which increased gradually throughout the years (Déri et al. 2011).

The need for post-restoration management

To enable further favourable development of the vegetation of restored grasslands, it will be essential in the future to ensure the removal of the accumulating litter and to facilitate the colonization of forbs characteristic of the target habitat types. Restored grasslands thus need to be managed primarily through grazing or mowing, where grazing is not feasible. Non-intensive grazing is the preferred option because livestock can be effective agents of seed dispersal from nearby natural grasslands to the restored sites (Poschlod et al. 1998; Mann & Tischew 2010). Grazing can also lead to a further increase in the diversity of the insect fauna (Kruess & Tscharntke 2002) and the colonization of rare, alkali grassland nesting birds. To this end, we also

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made adjustments to the grazing system and provided support (e.g. in rental contracts, applications to agri-environmental schemes) to livestock farmers for development of grazing infrastructure and increasing livestock numbers so as to extend grazing to as many natural and newly restored grasslands as possible.

Conclusion

In summary, our large-scale restoration decreased the fragmentation of grasslands and the areal extent of arable lands within the protected area, reduced chemical load on grasslands and marshes by establishing important buffer zones near the remaining croplands, and started successional pathways that may lead to semi-natural grasslands with time. As an implicit result, regular human disturbance arising from agricultural cultivation has decreased considerably within the national park area. We observed rapid favourable changes in the vegetation in the first 4 yr following restoration, but also noted processes that could threaten restoration success at some sites. Our restoration can be viewed as a large-scale experiment in which the same early push, i.e. sowing of low-diversity seed mixtures, is allocated to a number of sites within a landscape with slight variation in soil characteristics, water balance and other factors, to create opportunities for the operation of natural ecological processes in the post-restoration period. Our project thus provides an example for restoration and management to enhance spatial variability in vegetation and habitat diversity, which can potentially lead to higher total species diversity in the landscape.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Details of restored fields, sites and plots used in the study.

Table S2. Names and abbreviations of plant species recorded in the restored plots in 2009.

Table S3. Table of target species and their mean cover on fields restored in different years.

Figure S1. Species composition of flowering plants on fields restored in different years.

Figure S2. The site plot of Fig. S1 redrawn with plant species names.

Figure S3. Examples of herb species establishing in the restored fields outside the permanent plots.

Figure S4. The relationship between number or diversity of target species and distance to target vegetation for the three types of last crop.

Figure S5. Loess grassland restoration on a former alfalfa field, dominated by *Alopecurus pratensis* in Year 2 (top), and alkali steppe restoration on a former alfalfa field, dominated by *Carex melanostachya* in Year 3 (bottom). Both photos by Szabolcs Lengyel.

Figure S6. Alkali steppe restoration on a former alfalfa field. Photo by Szabolcs Lengyel.

Figure S7. Mosaic structure of vegetation characteristic in the Egyek-Pusztakócs landscape. Photo by Szabolcs Lengyel.

Figure S8. A depression formed by soil collapse and filled from rainwater and colonised by *Bolboschoenus maritimus* in Year 2 in an alkali steppe restoration on a former sunflower field. Photo by Szabolcs Lengyel.

Figure S9. A natural alkali steppe (top) and an alkali steppe restoration on a former sunflower field in Year 2 (bottom). Both photos by Szabolcs Lengyel.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.This paper describes early vegetation development following Europe's largest active grassland restoration, in which two or three grass species were sown over 760 ha cropland to allow vegetation regeneration by succession dependent on local conditions. The results mostly show favourable changes, including landscape-scale differences in vegetation development, but also suggest potential threats such as buildup of litter and perennial weeds.