RESEARCH ARTICLE

Succession in soil seed banks and its implications for restoration of calcareous sand grasslands

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Spontaneous succession is increasingly involved in grassland restoration, because it offers a cost-effective solution compared to technical reclamation methods. This topic is especially important nowadays, as large areas of marginal croplands are being abandoned on poor soils of Central and Eastern Europe, which offers a possibility for the spontaneous recovery of typical target grasslands. Studying the vegetation composition, aboveground biomass, and seed bank in old fields of different age and target calcareous sand grasslands using the chronosequence method, we aimed to answer the following questions: (1) Which species contribute to the seed banks of old fields and reference grasslands? (2) Does the direction of vegetation and seed bank succession trend toward the reference grasslands? (3) How are the vegetation changes in spontaneous succession reflected by the soil seed banks of old fields? In reference grasslands on the dune tops only sporadic seed banks were detected, while several hygrophytes had dense seed banks in reference grasslands in dune slacks. Similarity between the species composition of vegetation and seed banks was low. The development of vegetation and seed banks in old fields progressed toward that of target grasslands and the proportion of weedy species (e.g. indigenous weeds and invasive species) also decreased with time. The cryptogam biomass correlated significantly negatively, while the soil phosphorus significantly positively with the weedy species seed bank density. Our results indicated that the role of persistent seed banks in the regeneration of calcareous sand grasslands from old fields is rather limited and promising vegetation changes are mostly driven by spatial dispersal.

Key words: dispersal, grassland restoration, land abandonment, passive restoration, vegetation recovery, weed

Implication for Practice

- Restoration of calcareous sand grasslands from old fields is weakly supported by the soil seed bank as persistent seeds of characteristic species are mostly lacking both in old fields and in reference grasslands.
- Low similarities between vegetation and seed banks stress that promising vegetation changes are most likely driven by spatial dispersal.
- Landscape-scale patterns, such as availability and the spatial configuration of reference grasslands, should be evaluated and the support of spatial dispersal should be prioritized.
- Fast recovery of cryptogam cover would suppress the establishment of weedy species and might enable the considerable reduction of their seed banks in the long run.

Introduction

Grassland ecosystems are facing large-scale degradation worldwide. The most crucial drivers of their biodiversity deterioration are area loss and altered management (i.e. cessation of former management or intensification; Bakker & Berendse 1999). In many Western European countries, the area loss of seminatural grasslands was higher than 90% (Diemer et al. 2001; Critchley

et al. 2004; Dengler et al. 2014). The area loss is also high in the Western Palaearctic steppe zone; the loss of steppe vegetation is alarmingly high, e.g. in Ukraine, Russia, and Hungary (Deák et al. 2016; Wesche et al. 2016). Grassland fragments in mountain regions are threatened by cessation of former management (Valkó et al. 2012), while in the lowlands by both cessation and intensification (e.g. high-stocking rates, frequent mowing, over seeding, and/or use of fertilizers; Dengler et al. 2014). As grasslands highly contribute to the landscape-scale biodiversity, their conservation and restoration is an essential task.

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Passive restoration and technical reclamation represent two alternatives of restoration activities (Prach & Hobbs 2008). During passive restoration, grassland recovery is exclusively based on natural regeneration processes, that is, spontaneous succession. In technical reclamation, seed sowing or plant material transfer with subsequent site preservation and management is frequently applied (Kiehl et al. 2010; Török et al. 2011). Passive restoration is increasingly involved in grassland restoration, as it offers a cost-effective solution compared to technical reclamation (Prach & Hobbs 2008). It was stressed, however, that the application of passive restoration has some constraints (Bakker & Berendse 1999) and can be considered to be the most promising in sites where both the propagule sources of grassland plants and dispersal vectors are available nearby, and the soil of the sites is moderately loaded with nutrients (Török et al. 2011; Valkó et al. 2017). The topic is especially important nowadays, as large areas of marginal croplands are being abandoned in Central and Eastern Europe, which offers a possibility for the spontaneous recovery of formerly typical target grasslands (Valkó et al. 2016). While there are vast numbers of theory-based experimental studies on spontaneous succession, much less attention is given to their applicability in practical restoration (Török & Helm 2017).

It was found in several grassland types that most of the characteristic species have at most sporadic persistent seed banks (Halassy 2001; Donath et al. 2003; Hölzel & Otte 2003; Bossuyt & Honnay 2008; Kiss et al. 2016), while some other studies indicated that the role of seed banks in sustainment or recovery of grassland biodiversity is more promising (Valkó et al. 2011; Kalamees et al. 2012). However, it was also stressed that the restoration potential of seed banks is generally increasing from dry to wet habitats and was found to be quite promising in floodplain meadows or fen meadows (Pfadenhauer & Maas 1987; Valkó et al. 2011; Metsoja et al. 2014). Species of early successional stages generally build up persistent seed banks, thus, the seed bank can hamper restoration progress in grasslands as a source of some weedy species (Török et al. 2012). As in spontaneous succession, species colonization and establishment can be based on seed rain and on local seed banks, and seed banks can have a vital role in recovery (Halassy 2004). In spite of this, only a few studies analyzed the compositional changes in seed banks and their possible role in vegetation recovery during spontaneous succession (but see Milberg 1992; Kalamees & Zobel 1998; Mitlacher et al. 2002). Studies analyzing grassland vegetation and seed bank development in secondary succession are especially scarce (but see Bossuyt & Hermy 2001; Ma et al. 2009). Our overall aim was to evaluate the role of soil seed banks in the spontaneous recovery of calcareous sand grasslands. Studying old fields using the chronosequence method including abandoned fields of different age and target grasslands, we aimed at answering the following questions: (1) Which species contribute to the seed banks of old fields and reference grasslands? (2) Does the direction of vegetation and seed bank succession trend toward the reference grasslands? (3) How are the vegetation changes in spontaneous succession reflected by the soil seed banks of old fields?

Methods

Study Sites and Sampling

The Kiskunság calcareous sand region is situated in the center of the Pannonian Biogeographic region in Central Hungary. Kiskunság is characterized by a continental climate with a marked sub-Mediterranean influence. The mean annual temperature is 10°C, mean annual precipitation is 500–550 mm with high year-to-year fluctuations, characterized by a semiarid period in summer (Borhidi 1993). The region is covered by calcareous sandy soils (with a moderately alkaline pH up to 8.1, and relatively high $CaCO_3$ content up to 7.3%; Csecserits et al. 2011). The abandonment of croplands started in the 1960s and became very intensive in the few years after the collapse of the communist regime and continued until present days (Biró et al. 2008). Primary grassland types are open-sand grasslands near to the top of dunes (characterized by low cover of perennial species and high amount of bare soil), and closed-sand grasslands (characterized by high cover of perennial species and low amount of bare soil) are at lower elevations, typical near to dune slacks.

Data Collection and Analyses

We selected altogether 12 old fields for the study. The old fields were assigned to the following four age groups (three fields in each group, geo-coordinates in Table S1, Supporting Information): AG1: <10 years old, AG2: 10–20 years old, AG3: 20–40 years old, and AG4: >40 years old. Classification of old fields was based on historical aerial photographs and maps and was refined by the local knowledge of site managers. We also sampled seminatural grasslands in dune slacks (closed reference grasslands) and dune top (open reference grasslands), three sites of both types. Percentage cover of vascular plant species was recorded in 2×2−m sized plots, five in each old field and reference grassland stand in early May 2012 (altogether 90 plots were recorded).

We also collected 20 biomass samples from 20×20−cm plots in each field near to the surveyed plots (altogether 360 samples). We dried the biomass samples (3 weeks, at room humidity and temperature); sorted into litter, graminoid, forb, moss, and lichen fractions and weighted with an accuracy of 0.01 g. To obtain crucial abiotic parameters for seed bank and vegetation analyses the basic soil characteristics for the upper 10 cm soil layers of the old fields and reference grasslands were assessed in HL-LAB accredited laboratory (NAT-1-1654/2011). The following soil characteristics were analyzed: $CaCO_3$ (MSZ-08-0206-2:1978 2.2 section; m/m %; Labor MIM calcimeter), humus (MSZ 08-0210:1977, MSZ-08-0452: 1980; m/m %; Spectronic Genesys 5 Milton Roy spectrophotometer), phosphorus (mg/kg; MSZ 20135:1999 4.2.1 and 5.1 section, ammonium lactate soluble P_2O_5−P, Thermo Jarrell Ash Polyscan 61E ICP), and potassium content (mg/kg; MSZ 20135:1999. 4.2.1 and 5.1 section, ammonium lactate soluble K_2O−K, Thermo Jarrell Ash Polyscan 61E ICP).

Seed bank was sampled in the year after vegetation sampling, in the early days of April 2013. From each vegetation plot, six soil cores were collected by a vacuum-corer (4 cm in diameter,

10 cm in depth, 126 cm^3 volume each sample). The soil cores from the same plot were pooled during sample processing. We used the seedling emergence method with sample concentration introduced by Ter Heerdt et al. (1996). Collected samples were concentrated with sieves (3 and 0.18 mm mesh size). Retained concentrated samples were spread in a 2- to 4-mm-thick layer on the surface of trays previously filled with steam-sterilized potting soil. Air-borne seed contamination was monitored with control trays filled only with steam-sterilized potting soil. Germination lasted in total 32 weeks, with a 4-week-long watering break (used to mimic natural conditions for the driest period of the year typical in study sites). Trays were regularly watered; emerged seedlings were regularly counted and removed. Unidentified seedlings were transplanted and grown till their identification. During the germination experiment 72 seedlings, mostly forbs, died before identification to species level (1.2% of the total number of seedlings), which is a typical ratio in such studies.

The typical greenhouse weed *Oxalis stricta* (common yellow woodsorrel) and seedlings of wind-dispersed trees (*Populus* spp. [poplar species] and *Ailanthus altissima* [tree of heaven]) were removed from the trays and not considered in the analyses. We pooled *Typha latifolia* (broadleaf cattail) and *Typha angustifolia* (narrowleaf cattail) as *T. angustifolia* (it affected in total 19 seedlings), *Bromus hordeaceus* (soft brome) and *Bromus squarrosus* (corn brome) as *B. squarrosus* (1 seedling), and *Stipa borysthenica* (bunchgrass species) and *Stipa capillata* as *S. borysthenica* (8 seedlings) in analyses as we were not able to distinguish these in the seedling stage. In vegetation and seed bank comparisons, *Equisetum ramosissimum* (branched horsetail) was not considered as it produces no seeds. In the analyses of seed bank densities all seed bank samples of a respective old field or reference grassland stand were pooled to obtain the required minimum volume (i.e. 6 samples were collected from each of the 5 plots per old field or reference grassland, in total 30 samples with a volume of 3770 cm^3 per old field or reference grassland stand).

We identified weedy species using the Social Behavior Type classification of Borhidi (1995), which is an updated and refined system based on the Grime CSR classification (Grime 2001). Weeds (W), ruderal and adventive competitors (RC and AC, respectively) were considered as weedy species (frequent weedy species were marked with boldface in Table S2). Vegetation and seed banks of old fields and reference grasslands were compared using DCA ordination (Detrended Correspondence Analysis) on cumulative presence–absence datasets (for each old field and reference grassland stand, the frequency of a respective species was five if the species was present in all of the vegetation plots or seed bank samples). Effect of vegetation and environmental characteristics on the species composition of seed banks in old fields and reference grasslands were assessed by CCA ordination (Canonical Correspondence Analysis) based on seedling numbers. The differences in total seed bank density and weedy species density in seed banks between old fields and reference grasslands were analyzed by one-way analysis of variance and Tukey test (Zar 1999). In the comparisons of the composition of vegetation and seed banks we used Jaccard similarity. Effect of

environmental factors (i.e. soil parameters and biomass) on total seed bank and weedy species seed bank density were assessed using Spearman rank-correlation. Statistical analyses were calculated using CANOCO 4.5 (Lepš & Šmilauer 2003) and SPSS 17.0 (SPSS, Inc., Chicago, IL, U.S.A.; Released 2008). Nomenclature follows Király (2009).

Results

Vegetation Composition

The vegetation of both reference grassland types was characterized by high-percentage cover of stress-tolerant grasses (e.g. *Stipa borysthenica*, *Festuca vaginata* [fescue], *Koeleria glauca* [blue hair grass] and *Bothriochloa ischaemum* [yellow bluestem]). In addition to this, in the vegetation of closed reference grasslands, some generalist and disturbance-tolerant graminoids such as *Calamagrostis epigeios* (wood small-reed), *Cynodon dactylon* (Bermuda grass), *Poa angustifolia* (narrow-leaved meadow-grass), and *Scirpoides holoschoenus* (round-headed club-rush) were also present. Both types of reference grasslands were characterized by the presence of stress-tolerant forbs such as *Fumana procumbens* (sprawling needle sunrose), *Euphorbia seguieriana* (spurge species), and *Syrenia cana* (Brassicaceae). We found that the vegetation composition of old fields progressed toward the reference grasslands during succession (Fig. 1). Young age groups were mainly characterized by disturbance-tolerant graminoids and forbs (e.g. *P. angustifolia*, *C. dactylon*, or *Verbascum lychnitis* [white mullein]) and weedy species (e.g. *Ambrosia artemisiifolia* [common ragweed], *Elymus repens* [couch grass], or *Asclepias syriaca* [common milkweed]). The only exception was *S. borysthenica*, which was present with relatively high cover in some old fields of the young age groups (Table S2). In the older age groups, the cover of stress-tolerant grasses (*F. vaginata*, *K. glauca*) and forbs (*Dianthus serotinus* [Caryophyllaceae]*, E. segueriana*) was increased (Table S2 and Fig. 1).

Seed Bank Composition and Density

Altogether 5,778 seedlings of 92 species emerged from the seed banks. The seed banks of closed and open reference grasslands were distinct both in species composition and seed bank densities. The high-density seed banks of closed reference grasslands were characterized by the dominance of *Scirpoides holoschoenus* (76–86% of total seed bank density), followed by other two hygrophytes, *Juncus articulatus* (jointleaf rush) and *Centaurium pulchellum* (lesser centaury). The latter two species were only detected in the seed banks. The open reference grasslands had only low-density seed banks, characterized mostly by short-lived forb species (*Arenaria serpyllifolia* [thyme-leaf sandwort] and *Cerastium semidecandrum* [fivestamen chickweed], see more species in Appendix S1). The seed bank densities of old fields were somewhat higher than that of open reference grasslands with a trend of decreasing total seed bank density with increasing field age (Fig. 2). *Conyza*
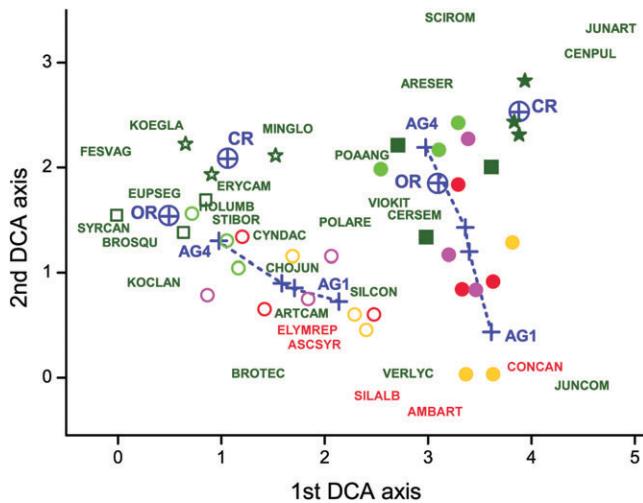
Figure 1. Vegetation and seed banks of old fields and reference grasslands. DCA ordination on cumulative presence–absence dataset (for each field and reference grassland the frequency of a respective species was 5 if the species was present in all of the plots or seed bank samples). Gradient lengths are 3.927 and 2.833, cumulative percentage variance of species data are 15.4 and 21.6 for the first and second axis, respectively). Notations: Empty symbols, vegetation; Full symbols, seed banks. Old fields: Age group 1 = orange, Age group 2 = red, Age group 3 = lilac, Age group 4 = light green. Open reference grassland = rectangle in dark green. Closed reference = asterisk in dark green. Centroids of each age group for vegetation and seed banks, respectively, were denoted by blue crosses. The centroids of reference grasslands were marked with blue-crossed circles. The species codes were generated using three letters of genus and three letters of species names (i.e. *Achillea collina* is abbreviated as ACHCOL), for the full list of abbreviations for species see Appendix S1. Weedy species were marked by red color.

canadensis (*Canadian horseweed*), *Portulaca oleracea* (little hogweed), *Chenopodium album* (common lambsquarters), *Ambrosia artemisiifolia*, and *Oenothera biennis* (common evening-primrose) were the weedy species detected in the highest density in the seed banks of old fields. Out of these species only *Conyza canadensis* and *Chenopodium album* were detected in the seed banks of reference grasslands. The density of weedy species in the seed banks was significantly lower in older age groups of old fields and reference grasslands compared to young age groups (Fig. 3).

Vegetation and Seed Banks

In total, 152 species were found in the study sites in vegetation and/or in the soil seed banks. The vegetation and seed banks shared 51 species; 60 species were detected only in the vegetation, while 41 species only in the seed banks. Species present with a minimum total frequency score of 5 in vegetation and/or seed banks are listed in Table S2. The DCA ordination revealed that the vegetation and seed bank composition were quite distinct in all sampled fields and reference grasslands (Fig. 1). In the DCA the gradient lengths were 3.927 and 2.833; cumulative percentage variance of species data were 15.4 and 21.6 for the first and second axis, respectively. We found low similarity
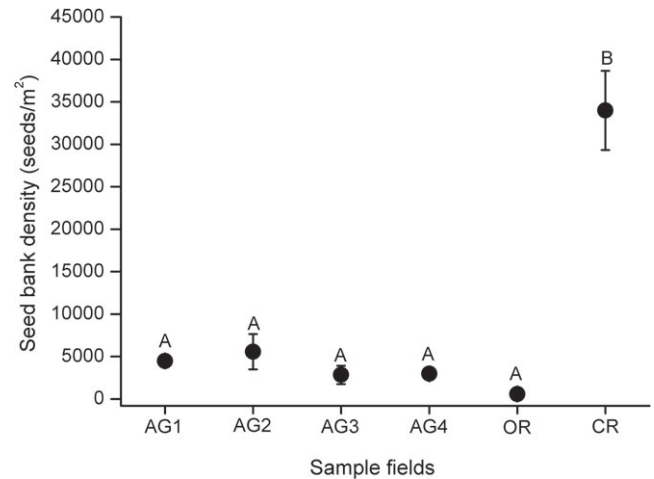

Figure 2. Total seed bank density in old fields and reference grasslands (mean ± SE). Significant differences were denoted by capital letters (one-way analysis of variance and Tukey test; $p < 0.001$). Notations: AG1–AG4 = old-field age groups; 1: <10 years, 2: 10–20 years, 3: 20–40 years; 4: >40 years. OR, open reference grasslands near to dune top, CR, closed reference grasslands near to dune slacks.
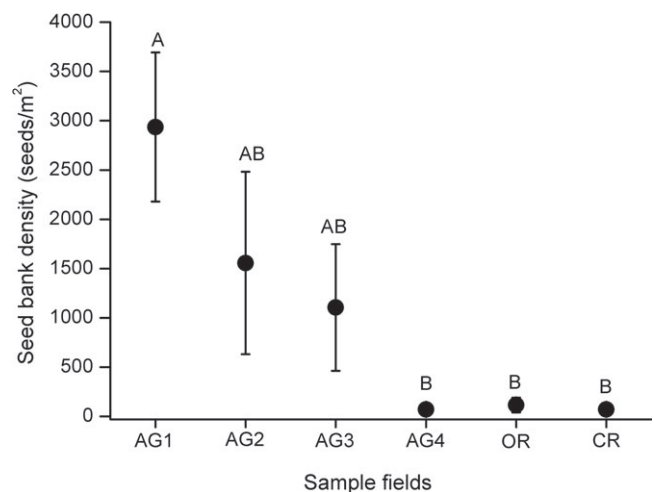

Figure 3. Seed bank density of weedy species in old fields and reference grasslands (mean ± SE). Significant differences were denoted by capital letters (one-way analysis of variance and Tukey test; $p = 0.018$). Notations are the same as for Fig. 2.

between vegetation and seed banks; the lowest Jaccard similarity scores between vegetation and seed banks were found in the reference grasslands (a mean of 0.09 in the open and 0.11 in the closed reference grasslands, respectively), while the highest similarity was detected in the two younger age groups of old fields (0.21 and 0.19, in Age groups 1 and 2, respectively), but the differences were not significant.

Changes in Environmental Factors and Seed Banks

The Monte Carlo permutation tests for the CCA were significant for the first axis $p = 0.006$, and for all canonical axes $p = 0.026$.
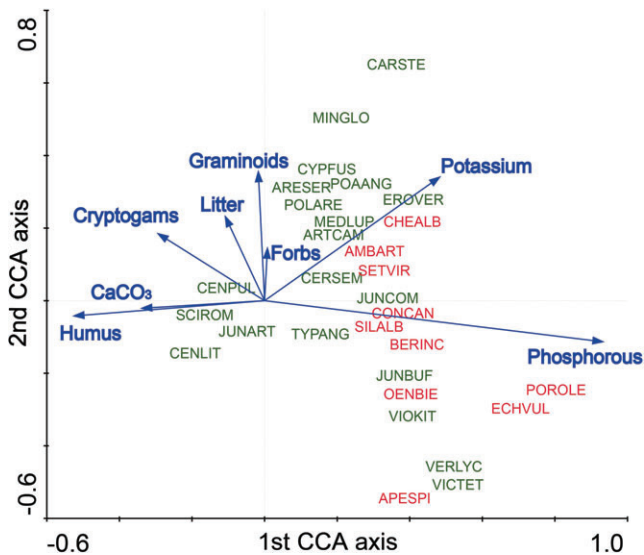
Figure 4. Effect of vegetation and environmental characteristics on the composition of seed banks in old fields and reference grasslands. CCA ordination based on seedling numbers. Monte Carlo permutation test for the first axis $p = 0.006$, for all canonical axes $p = 0.026$. Cumulative percentage variances of species data were 22.5 and 33.8, species-environmental relation 38.9 and 58.5 for the first and second axis, respectively. For the vegetation characteristics pooled biomass data of 20 biomass samples per each field or reference grassland were used. The arrows of vegetation and environmental factors were added using weighted averaging. The species codes were generated using three letters of genus and three letters of species names (i.e. *Achillea collina* is abbreviated as ACHCOL), for the full list of abbreviations for species see Appendix S1. Weedy species were marked by red color.

Cumulative percentage variances of species data were 22.5 and 33.8, species-environmental relation 38.9 and 58.5 for the first and second axis, respectively. Most of the factors were not correlated with the total and weedy species seed bank densities. We found a positive but marginally significant correlation between litter and total seed bank density. There were high fluctuations in abiotic parameters ($CaCO_3$, humus, phosphorus, and potassium contents) of sampled old fields and reference grasslands; and no significant differences were detected between reference grasslands and old-field age groups. The biomass of cryptogams correlated significantly negatively ($r = -0.504$, $p = 0.032$), while the soil phosphorus content significantly positively ($r = 0.608$, $p = 0.007$) with the weedy species seed bank density (Table S3). These correlations were also well displayed by the CCA ordination, where weedy species, especially *Portulaca olearcea*, *Echium vulgare* (viper's bugloss), *Apera spica-venti* (common windgrass), and *Oenothera biennis*, were positively correlated with the phosphorus content and negatively with the biomass of cryptogams (Fig. 4).

Discussion

We found that the role of persistent seed banks in the regeneration of the studied calcareous sand grasslands from old fields is rather limited. Most species had at most low seed bank densities, with the exception of some hygrophytes and weedy species. The most characteristic species both in reference grasslands and old fields did not build up persistent seed banks, which is well reflected by the low similarity scores in all studied old fields and reference grasslands. These are in line with the conclusions of Bossuyt and Honnay (2008) and Jentsch and Beyschlag (2003), and also supported by other findings of Karlík and Poschlod (2014) in calcareous grasslands. However, these results are in contrast with the findings of Kalamees et al. (2012) where they detected dense and species-rich persistent soil seed banks in all of their study sites in calcareous alvar vegetation. In an acidic sand grassland region of Hungary using the same seed bank analysis method, a bit higher seed density scores were reported from secondary grasslands (10,300–40,900 seeds/m^2; Török et al. 2009) and natural open dry sand grasslands (13,900–24,600 seeds/m^2; Matus et al. 2005). The most likely explanation could be that the climate of the study site is more continental with lower precipitation than in the acidic sand grassland region; and it was also proven that higher humidity supports the build-up of persistent seed banks (Bossuyt & Honnay 2008). It is also possible that the detected differences are caused by the differences in the presence of seed pathogens in calcareous and acidic soils found by Basto et al. (2015). They found that the abundance of seed pathogens is higher in calcareous soils, which can cause a lower soil seed bank density.

We found a marked difference between aboveground vegetation and seed banks along the whole chronosequence similar to other studies comparing vegetation and seed banks along temporal gradients (Kalamees & Zobel 1998; Halassy 2004; Metsoja et al. 2014). Analyzing the primary succession chronosequence it was found that the seed bank density is increasing (Bossuyt & Hermy 2001; Marcante et al. 2009). In contrast, we found a decreasing trend in the density of total seed banks (in exception of the closed reference grasslands) and a significant decrease in the seed bank density of weedy species during secondary succession validating the results of other studies (Bossuyt & Hermy 2001). We detected the highest seed bank density for hygrophyte species (e.g. *Scirpoides holoschoenus*, *Juncus articulatus*, and *Centaurium pulchellum*). These results were well in line with most seed bank studies where especially for Cyperaceae and Juncaceae species rather high densities were reported (see the review of Bossuyt & Honnay 2008).

The similarity of vegetation and seed banks showed a decreasing trend with succession, and the lowest similarity scores were found in reference grasslands. These results are well in line with the trends described in Bossuyt and Honnay (2008) and explained by the increasing stability of successional communities. Explained by the slowing-down-succession theory (Lepš 1987), the increasing vegetation canopy during secondary succession resulted a decreased level of species turnover (Török et al. 2009; Albert et al. 2014) and decreased gap availability for the regeneration of short-lived and weedy species (Peco et al. 1998; Török et al. 2012).

It was found that the increase in litter was positively correlated with the total seed bank density, and cryptogam biomass was negatively correlated with the seed bank of weedy species.

It was argued by Kwiatkowska-Falińska et al. (2011) that the high cover of cryptogams as an effective seed trap can mitigate the speed or even prevent the arrival of seeds on the soil surface and thus their incorporation into the soil seed bank, which is one likely explanation for the correlation found between cryptogam biomass and the seed bank density of weedy species. For litter it was published in the literature that accumulated litter can also act as a seed trap for grassland species (Donath & Eckstein 2010; Ruprecht & Szabó 2012), but can help retain soil humidity and decrease the temperature fluctuations on the soil surface which can have positive effects on the preservation of soil seed banks, especially in dry communities (Eckstein & Donath 2005). The latter assumption provides an explanation for the correlation found between litter and total seed bank density in the studied dry grassland stands.

In spite of the limited contribution of the seed banks to the regeneration process, we found that vegetation recovery was promising toward the reference grasslands. Thus, promising vegetation changes are likely driven by spatial dispersal of grassland species. We stress that in restoration decisions the landscape-level availability and the spatial pattern of reference grasslands should be evaluated. As argued by Brudvig (2011), restoration approaches often consider only local aspects and neglect the importance of landscape context, land use changes, or habitat history. Consideration of landscape-scale patterns of seed dispersal can considerably improve the restoration success as pointed out by Török and Helm (2017). To facilitate the spontaneous recovery processes the support of spatial dispersal and dispersal vectors should be prioritized (Ozinga et al. 2009). Our results also suggest that the fast restoration of cryptogam cover might suppress the establishment of weedy species (especially gap strategist ones) and might enable the reduction of their seed banks in the long run.

Acknowledgments

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Geo-coordinates of sample sites.
Table S2. Frequent species in the vegetation and seed banks of reference grasslands and old fields.
Table S3. Correlation between seed bank densities, biomass fractions, and environmental factors.