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RESEARCH ARTICLE

Restoration Potential in Seed Banks of Acidic Fen and Dry-Mesophilous Meadows: Can Restoration Be Based on Local Seed Banks?

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Abstract

A crucial question in ecological restoration is whether target species that are missing from aboveground vegetation are represented in the seed bank. We evaluated the role of persistent seed banks in the restoration of species richness, and the relative value of managed and unmanaged grasslands, by studying closely located and floristically similar mown and abandoned stands of fen and dry-mesophilous meadows. We found that a higher proportion of the target species detected in aboveground vegetation possessed persistent seed banks in fen meadows than in dry-mesophilous ones (44 and 29%, respectively). The proportion of target species found exclusively in the seed bank was much lower (11% for both meadow types). Conversely, common rushes (*Juncus conglomeratus* and *J. effusus*), mostly missing from the vegetation, dominated the seed banks in all fen meadow plots (50–94% of total seed densities) and were also detected in seed banks of dry-mesophilous meadows. We found that resumed mowing on previously abandoned meadows has promoted species richness and the flowering success of several species in comparison with unmanaged ones in both meadow types. Vegetation type had a stronger influence on seed bank richness and density than management status and we detected much higher seed bank densities in fen meadows (64,000–94,000 seeds/m^2) than in dry-mesophilous ones (4,400–6,300 seeds/m^2). Therefore, restoration of former richness could not be based exclusively on the local seed banks in the studied meadow types. Further management, such as hay transfer or seeding of target species, is required to increase species richness.

Key words: abandonment, ***Brachypodium***, grassland, ***Juncus***, ***Molinia***, mowing.

Introduction

Extensively managed hay meadows in mountain regions of Europe were originally created by forest cutting and maintained extensively by low intensity mowing (Fischer & Wipf 2002; Zeiter et al. 2006). Due to the changes in agro-environmental schemes in the last few decades, an increased abandonment of these meadows was reported from many regions in Central–Europe (Stampfli & Zeiter 1999; Diemer et al. 2001; Poschlod et al. 2005). The mountain hay meadows are among the most species-rich communities in Europe and harbor many threatened plant and animal species (Losvik 1999; Stampfli & Zeiter 1999; Ilmarinen et al. 2009). They are therefore considered to be habitats of outstanding conservational value (Dietschi et al. 2007). Restoration of former biodiversity and conservation of the remaining, often fragmented meadow stands, are high priorities from a nature conservation perspective (Smith et al. 2002).

The abandonment of hay meadows is often followed by declining species richness (Bekker et al. 1997; Stampfli & Zeiter 1999; Stammel et al. 2006). Litter accumulation following cessation of management leads to an increasing dominance of a few competitive graminoids and often results in the disappearance of most subordinate herbs due to increased shading (Billeter et al. 2007; Rudmann-Maurer et al. 2008). Still there are open questions regarding the success of restoration of species richness; e.g. are there any target species already missing from aboveground vegetation of abandoned stands still present in the soil seed banks, and how does their persistence vary in different grassland types with similar history and management?

There are contrasting views on the possible role of soil seed banks in grassland restoration. Several studies emphasize that soil seed banks form an important source for re-colonization (Bakker & Berendse 1999), particularly when species dispersal is limited (Rosenthal 2006; Simmering et al. 2006). However, other investigations have found that target species often lack persistent seed banks (Kalamees & Zobel 1998; Bossuyt & Honnay 2008). Still there is a shortage of seed bank records, especially for species of high conservational value. Under-representation of target species in databases may hamper the understanding of the seed banks' role in community regeneration (Thompson et al. 1997; Csontos 2001).

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To address some of these issues, we studied mown and abandoned stands of acidic fen and dry-mesophilous meadows with the aim of evaluating the following questions: (1) What proportion of total species richness is represented in the seed banks of different meadow types? (2) Do the seed banks contain species that are not represented in the aboveground vegetation? (3) What is the size of the seed bank for restoration target species? (4) Does the density and species richness of the seed banks differ between mown and abandoned stands within the same meadow type? (5) Does management status or vegetation type have more of an effect on seed bank richness and density?

Methods

Study Site

The study site, called the "Gyertyán-kúti-rétek," is located in the Zemplén Mountains between the villages of Telkibánya and Regéc (NE Hungary; 48°26.1–26.7′N; 21°21.6–22.3′E) on a plateau with a height of 640–720 m a.s.l. It is surrounded by oak (*Quercus petrea*) hornbeam (*Carpinus betulus*), beech (*Fagus sylvatica*) forests and spruce plantations (*Picea abies*). The bedrock is amphibol-rich andesite on which podzolic brown forest soil with heavy, clayey, humus-rich, and acidic topsoil was formed (Appendix S1). Mean annual temperature of the site is about 7.5–8.0°C, whereas mean annual precipitation is 750–800 mm with a midsummer maximum. The meadows were established in the eighteenth century; their area was approximately 100 ha in the past. They were managed by mowing with scythe then removing the hay by hand raking once a year in July. Traditional management created and maintained highly species-rich vegetation which harbored more than 350 vascular species, including more than 40 legally protected ones. Management has gradually been abandoned since the 1960s, resulting in the colonization of wind-dispersed tree species (mostly *Betula pendula* [birch] and *Carpinus betulus* [hornbeam]). Large stands of young birch forests were cut and traditional management was gradually resumed since 1985 (Simon et al. 2007).

Stands of the two most widespread acidic meadow types, fen meadows and dry-mesophilous meadows were studied (for detailed site characteristics, see Appendix S1). Fen meadows (*Junco-Molinion*) are located in lower elevations and on humus rich soils. They are dominated by *Molinia arundinacea* (purple moorgrass). Dry-mesophilous meadows (*Cirsio pannonicae-Brachypodion pinnati*) are located in higher elevations and on less fertile soils. Typical graminoids in these meadows include *Brachypodium pinnatum* (heath falsebrome), *Calamagrostis arundinacea* (reed grass), and *Carex montana* (mountain sedge) (Borhidi 2003; Appendix S2).

Sampling

Four stands (two mown and two abandoned) from each meadow type were studied. In mown stands traditional management was resumed in 1993 while abandoned stands were left unmanaged. In each stand aboveground vegetation was recorded in five 2 × 2–m sized permanent plots in July 2004. A species list was compiled for each plot and the number of flowering shoots was recorded. Soil seed banks were studied with the seedling emergence method, as follows: Six soil samples (4-cm in diameter and 10-cm in depth) per plot were drilled after snowmelt in 2005 (fen meadows) and in 2006 (dry-mesophilous meadows). Two vertical segments (0–5 cm and 5–10 cm) were separated; then identical segments from the same plot were pooled. This sampling design enabled the detection of a species with a 95% probability, provided it had at least 80 seeds/m^2 and a nonaggregated seed bank (Thompson et al. 1997). Sample concentration was used to reduce sample volume and to promote germination (ter Heerdt et al. 1996). Concentrated samples were spread in a maximum of 3–4 mm thick layer on trays, previously filled with 5-cm of steam-sterilized potting soil. Trays were illuminated with natural light in a greenhouse and watered daily from April to October. More than 1,600 specimens of unidentified taxa were transplanted and grown till identification. Accidental seed rain was monitored in sample-free control trays filled with sterilized soil.

Data Processing and Analysis

Species were grouped into "graminoids" that is Poaceae, Cyperaceae, and Juncaceae and "herbs" that is dicots and nongraminoid monocots (including Liliaceae, Typhaceae, Iridaceae, and Orchidaceae), reflecting their contrasting responses to mowing. Seedlings of *Juncus conglomeratus* (compact rush) and *J. effusus* (common rush) were pooled because of identification difficulties. The vast majority (circa 90%) of their transplants proved to be *J. conglomeratus*. Greenhouse weeds and wind-dispersed pioneers detected in control trays were excluded from analyses. Seedlings that died before being identified (0.3% of totally emerged seedlings) were also excluded.

Species were classified into seed bank type categories based on Thompson et al. (1997) using vegetation records and vertical distribution data of the seed bank (density records for the 0–5 and 5–10 cm layer, respectively). The proportion of species with a persistent seed bank type was then calculated. Species with low frequency in the established vegetation (detected in a maximum of 3 plots from a total of 20 within a meadow type) and with low seed numbers (less than three viable seeds detected in a meadow type) were not classified into seed bank types; thus they were excluded from persistency calculations. Accidentally occurring ferns (forming no seeds) and orchids (with generally acknowledged cultivation difficulties; Thompson et al. 1997) were similarly excluded. Nonwoody stress tolerant species characteristic to the studied meadow types (according to Grime 1979; Borhidi 1995), including legally protected ones were considered as target species.

The effects of management and meadow type on important vegetation and seed bank variables were analyzed using two-way analysis of variance (ANOVA); these variables were $\ln(x + 1)$ transformed prior to statistical analyses (variables: total species richness and herb species richness both in the vegetation and seed banks; flowering species richness, flowering herb species richness and number of flowering shoots of herbs for vegetation only; number of seedlings, number of seedlings excluding *Juncus*, and number of herb seedlings for seed banks only). The mean numbers of flowering shoots and seed densities of frequent species were compared with t test on $\ln(x + 1)$ transformed data, between mown and abandoned meadow stands (Zar 1999). Species were considered frequent when they had more than 50 flowering shoots in the vegetation, and/or at least 50 viable seeds detected in the seed bank of at least one meadow type. Vegetation and seed bank composition were compared between mown and abandoned stands of the two meadow types with Sørensen similarity using multidimensional scaling (MDS) ordination (Legendre & Legendre 1998). Correlations between the number of flowering species in the vegetation and the species richness in the seed banks, as well as the correlation for the number of flowering herbs and the number of herb species in seed banks were analyzed by Spearman rank correlation.

Results

Vegetation

In total, 158 species (32 graminoids and 126 herbs) were recorded in the study plots. A larger diversity of herbs was detected in dry-mesophilous meadows (100 herb species, 79% of total herbs) than in fen meadows (80 species, 63% of total herbs). The species richness of graminoids was approximately the same in both meadow types (25 and 26 species, respectively). The studied meadow types shared 73 species; these species displayed different frequencies and levels of flowering success in the two meadow types (Appendix S2).

In both meadow types species richness, richness of herb species and flowering shoots of herbs proved to be significantly higher in mown stands than in abandoned ones. Higher mean scores of total and of herb species richness were detected in the dry-mesophilous meadows than in the fen meadows (Table 1). Mowing had a positive effect on all the studied vegetation characteristics in both meadow types (Table 2).

Of the 24 frequent flowering species in fen meadows, 6 had significantly higher flowering success in mown stands (*Briza media* (perennial quaking grass) $t = 2.473$, $p = 0.024$, $n = 10$; *Festuca ovina* (sheep fescue) $t = 5.648$, $p < 0.001$, $n = 10$; *Luzula multiflora* (common woodrush) $t = 2.762$, $p = 0.013$, $n = 10$; *Plantago lanceolata* (narrowleaf plantain) $t = 3.904$, $p < 0.001$, $n = 10$; *Thymus pulegioides* (lemon thyme) $t = 3.904$, $p = 0.001$, $n = 10$; and *Viola canina* (dog violet) $t = 5.515$, $p < 0.001$, $n = 10$). In abandoned stands only *M. arundinacea* ($t = 4.367$, $p < 0.001$, $n = 10$) reached significantly higher flowering success. In dry-mesophilous meadows, 4 of the 14 frequent flowering species had a significantly higher number of flowering shoots in mown plots (*Helianthemum ovatum* (common rock-rose) $t = 3.476$, $p = 0.003$, $n = 10$, *Thesium linophyllon* (flaxleaf) $t = 2.511$, $p = 0.022$, $n = 10$, *Thymus pulegioides* $t = 2.853$, $p = 0.011$, $n = 10$, and *Veronica officinalis* (common gipsyweed) $t = 3.711$, $p = 0.002$, $n = 10$). Only

Table 1. Vegetation and seed bank characteristics of the meadow stands (mean ± SE). Vegetation characteristics were calculated for 4 m^2 sized plots ($n = 5$ in each stand). Number of seedlings scores were calculated for seeds/m^2 density ($n = 5$ for each stand).

	Fen Meadow Stands				*Dry-Mesophilous Meadow Stands*			
	Mown I	*Mown II*	*Abandoned I*	*Abandoned II*	*Mown I*	*Mown II*	*Abandoned I*	*Abandoned II*
Vegetation								
Species richness	50.0 ± 1.8	53.0 ± 1.4	31.4 ± 4.1	49.4 ± 3.9	59.8 ± 2.0	62.2 ± 1.2	42.0 ± 3.5	53.2 ± 1.4
Herb species richness	32.6 ± 1.1	38.4 ± 1.1	25.4 ± 3.4	35.6 ± 2.8	47.0 ± 2.1	48.4 ± 0.9	33.0 ± 2.9	41.2 ± 1.7
Flowering species richness	30.6 ± 1.5	37.0 ± 1.8	12.8 ± 2.7	34.6 ± 3.0	23.0 ± 1.6	24.0 ± 1.4	16.0 ± 2.3	26.4 ± 2.2
Flowering herb species richness	17.2 ± 0.7	25.2 ± 1.1	9.0 ± 2.1	22.2 ± 1.8	14.2 ± 1.2	14.8 ± 0.7	9.8 ± 1.7	18.2 ± 2.5
Number flowering shoots of herbs	102.2 ± 7.8	270.2 ± 19.2	29.2 ± 7.9	166.6 ± 31.2	85.2 ± 5.5	163.4 ± 16.4	31.0 ± 6.6	107.0 ± 16.8
Seed bank								
Species richness	20.0 ± 1.3	27.0 ± 2.1	18.2 ± 1.2	27.2 ± 1.6	15.2 ± 2.8	14.2 ± 1.6	14.6 ± 0.7	15.0 ± 1.9
Herb species richness	11.2 ± 0.7	14.8 ± 1.0	9.8 ± 1.4	14.2 ± 1.7	7.2 ± 1.4	7.2 ± 1.1	10.4 ± 0.9	7.0 ± 1.4
Number of seedlings	91,700 ± 14,337	83,344 ± 10,306	63,980 ± 3,602	94,034 ± 10,839	5,543 ± 744	4,350 ± 797	6,339 ± 465	5,862 ± 748
Number of seedlings without *Juncus*	15,968 ± 1,701	16,791 ± 1,678	12,334 ± 878	15,862 ± 1,701	5,437 ± 758	4,138 ± 816	6,313 ± 449	5,703 ± 705
Number of herb seedlings	11,034 ± 1,461	12,573 ± 1,360	8,090 ± 984	9,284 ± 1,410	3,474 ± 505	2,466 ± 738	4,907 ± 671	3,342 ± 734

Table 2. Two-way ANOVA of the vegetation and seed bank characteristics of the meadows ($n = 10$). Significant effects ($p < 0.05$) are denoted by boldface.

	Meadow Type			Management			Type × Management		
	$F_{1,36}$	MS	p	$F_{1,36}$	MS	p	$F_{1,36}$	MS	p
Vegetation									
Species richness	8.702	0.324	**0.006**	19.362	0.720	**<0.001**	0.045	0.002	0.834
Herb species richness	18.776	0.631	**<0.001**	14.153	0.475	**<0.001**	0.470	0.016	0.497
Flowering species richness	2.310	0.321	0.137	7.225	1.003	**0.011**	2.115	0.294	0.155
Flowering herb species richness	2.385	0.386	0.131	4.286	0.694	**0.046**	1.410	0.228	0.243
Number of flowering shoots of herbs	1.105	0.627	0.300	13.370	7.588	**<0.001**	0.154	0.087	0.697
Seed bank									
Species richness	34.735	1.825	**<0.001**	0.008	0.001	0.931	0.198	0.010	0.659
Herb species richness	21.031	1.867	**<0.001**	0.106	0.009	0.746	2.004	0.178	0.166
Number of seedlings	861.011	72.784	**<0.001**	0.615	0.052	0.438	3.406	0.288	0.073
Number of seedlings excluding *Juncus*	138.739	10.979	**<0.001**	0.492	0.039	0.488	5.713	0.452	**0.022**
Number of herb seedlings	71.828	12.216	**<0.001**	0.023	0.004	0.881	6.382	1.085	**0.016**

Calamagrostis arundinacea ($t = 5.776$, $p < 0.001$, $n = 10$) had significantly higher mean numbers of flowering shoots in abandoned than in mown dry-mesophilous meadow stands.

Seed Banks

Altogether 94 species (38 graminoids and 56 herbs) were found in soil samples. In fen meadows 44% of aboveground species possessed any seed banks, whereas in dry-mesophilous meadows the same figure was 26%. These proportions for target species were 44 and 29%, respectively, whereas the proportion of target species detected only in seed banks was 11% in both meadow types. Of the 31 species detected in soil seed banks of both meadow types, only two species (*L. multiflora* and *Campanula patula* [spreading bellflower]) were similarly frequent (Appendix S2). Samples from different meadow types proved to be similarly rich in species, but a lower number of herbs were detected in the seed banks of dry-mesophilous meadows compared to fen meadows. Mean seed densities were about 10–20 times higher in fen meadows than in dry-mesophilous ones (Table 1). Total seed densities excluding the dominant *Juncus* species, and the seed density of herbs were also two to four times higher in fen meadows, than these scores in the dry-mesophilous meadows (Table 1). All studied seed bank characteristics were significantly affected by the meadow type. No overall effect of management on the seed banks was revealed on the density of persistent seed banks (Table 2). In fen meadows, *M. arundinacea* had much higher densities in the abandoned plots ($t = 9.709$, $p < 0.001$, $n = 10$), whereas *Agrostis canina* (common bentgrass) ($t = 4.041$, $p < 0.001$, $n = 10$) and *Lychnis flos-cuculi* (ragged robin) ($t = 3.920$, $p = 0.001$, $n = 10$) possessed more dense seed banks in the mown stands. None of the detected species had significantly different seed densities in differently managed dry-mesophilous meadow stands.

Similarity of Above and Belowground Samples

The MDS ordination showed a clear distinction between vegetation and seed banks (Fig. 1). Similarities between vegetation and seed banks differed greatly according to the vegetation type (Sørensen similarities for fen meadows: 0.41–0.53, whereas for dry-mesophilous meadows 0.28–0.36). Based on specific vegetation and seed bank data, we were able to classify seed longevity of 84 species in fen and 88 species in dry-mesophilous meadows, respectively. Persistent records in fen meadows comprised 49% of all classified species and 33% in dry-mesophilous meadows. In fen meadows, a strong positive correlation was revealed between the number of flowering species in the vegetation and the species richness in the seed banks (Spearman rank correlation; $p < 0.001$ $n = 20$, $r = 0.68$) and the same holds for the herbs ($p < 0.001$, $n = 20$, $r = 0.70$). No such correlations were found in dry-mesophilous meadows.

In fen meadows almost all frequent graminoids of the vegetation had a considerable number of viable seeds, whereas in dry-mesophilous meadows only *Sieglingia decumbens* (common heathgrass) and *L. multiflora* had relatively dense seed banks (a mean seed density over 250 seeds/m^2, Fig. 1, Appendix S2). In contrast to graminoids, 25% of herbs detected in vegetation of fen meadows had any seed banks, and 18% were persistent. In dry-mesophilous meadows, these scores were only 15 and 6%, respectively. Although some target species were only found in seed banks (e.g. some sedges like *Carex pilulifera* [pill sedge] or *C. nigra* [black sedge]) these were significantly outnumbered by those ones which were exclusively found in vegetation. In fen meadows 31 species (incl. protected species as *Achillea ptarmica* [sneezewort], *Gladiolus imbricatus* [wild gladiolus], *Gentiana pneumonanthe* [marsh gentian]) were exclusively found in aboveground vegetation, whereas in dry-mesophilous meadows this figure was 46 (incl. protected species such as *Carlina acaulis* [steemless carline thistle], *Gentianella austriaca* [austrian gentian] [Appendix S2]). Overall, most of the detected legally protected target species (Király 2007) in both meadow types lacked persistent seed banks (9 of 11 species). Only *Hypericum maculatum* (spotted St. Johnswort) (20–500 seeds/m^2) and *Carex hartmannii* (Hartmann's sedge) (one seedling) had a detectable seed bank. Conversely, common rushes

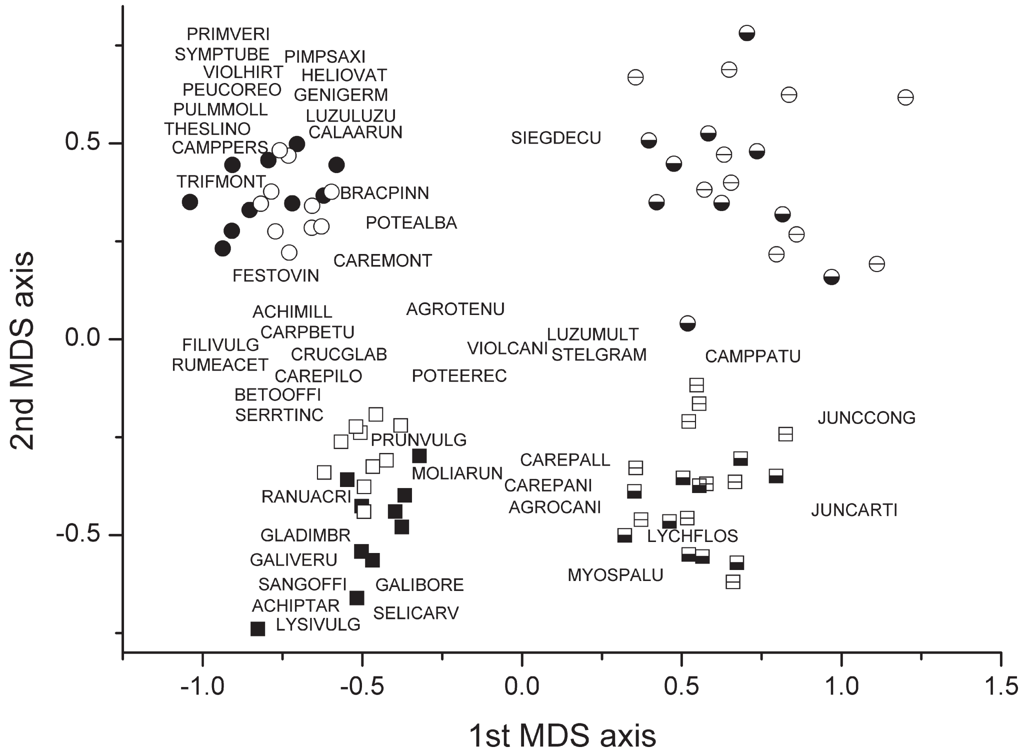

Figure 1. The similarity of vegetation and seed banks of fen meadow and dry-mesophilous meadow stands based on presence–absence of species (Sørensen similarity and MDS ordination, stress = 12.64). Notations: □, fen meadow, vegetation, abandoned; ⊟, fen meadow, seed banks, abandoned; ■, fen meadow, vegetation, mown; ⬓, fen meadow, seed banks, mown; ○, dry-mesophilous meadow, vegetation, abandoned; ⊖, dry-mesophilous meadow, seed banks, abandoned; ●, dry-mesophilous meadow, vegetation, mown; ◒, dry-mesophilous meadow, seed banks, mown. Additional data for the plotted species and species abbreviations are found in Appendix S2.

(*J. conglomeratus* and *J. effusus*), that were mostly missing from the vegetation, dominated the seed banks in all fen meadow plots (50–94% of total seed densities). These rush species were also present in the seed bank in dry-mesophilous plots. Further rush species (*Juncus articulatus* [jointleaf rush], *J. bufonius* [toad rush]), several sedges (*Carex pilulifera*, *C. nigra, C. remota* [remote sedge]), and a number of hygrophyte herbs (*Peplis portula* [spatulaleaf loosestrife], *Scrophularia umbrosa* [water figwort], *Typha angustifolia* [narrowleaf cattail]) were exclusively detected in the seed banks.

Discussion

Vegetation and Seed Bank

The low-to-medium similarity between vegetation and seed banks reported here fit well in the range formerly detected in grasslands (Hopfensperger 2007; Bossuyt & Honnay 2008). Seed bank densities detected in the acidic dry-mesophilous meadows proved remarkably higher than in most analyzed dry-mesophilous calcareous grasslands (about 200–900 seeds/m^2; e.g. Kalamees & Zobel 1998; Willems et Bik 1998; Bossuyt et al. 2006), but somewhat lower than in some chalk grasslands in Germany (6,000–7,000 seeds/m^2; e.g. Poschlod & Jackel 1993).

We detected seed densities in the soil of the fen meadows of an order of magnitude higher than in dry-mesophilous ones, which coincides with results of former studies conducted in similar wet meadow types (Bekker et al. 2000; Matus et al. 2003; Jutila 2001). The enormously high seed density of the fen meadows was caused by the *Juncus* seeds. As in other wet meadows rushes comprised the largest part (50–94%) of the seed banks (most often *J. conglomeratus* and *J. effusus*; Bekker et al. 2000; Matus et al. 2003; Jutila 2001). High loads of *Juncus* seed banks can threaten restoration but evidence is missing in what circumstances they really hamper the establishment of other species.

In contrast to the fen meadow stands the percentage of rushes in acidic dry-mesophilous meadows, measures as low as 2.2% of the seed bank (about a maximum of 130 seeds/m^2), similar to levels reported in previous studies on calcareous meadow types (Kalamees & Zobel 1998; Willems & Bik 1998). Total density of herbs was three to four times higher in fen meadows than in dry-mesophilous ones. This group contained the most target species and is often subject to extinction after abandonment (Stampfli & Zeiter 1999; Stammel et al. 2006). Furthermore, a much smaller proportion of these species had persistent seed banks in dry-mesophilous meadows than in fen meadows. These results suggest that soil seed banks can only play a subordinate role in restoration of this meadow type.

Management

Resumed traditional management is usually considered to promote species richness in vegetation of abandoned grasslands (Losvik 1999; Stampfli & Zeiter 1999; Williams et al. 2007). Our study also supports these findings. The picture, however, is less clear concerning reproductive success (flowering and seed banks). The flowering success of several species was apparently influenced by management. It was difficult to judge whether or not resumed management could affect specific seed bank densities. The most likely reason is that the alteration of persistent seed bank is much slower than changes in vegetation (Ghorbani et al. 2007). Therefore, the seed bank structure and composition as a long-term "successional memory" reflects the former stages of the vegetation development (Török et al. 2009).

Conclusions

Irrespective of the vegetation type, only a small number of target species built up detectable seed banks. The same holds for the legally protected target species, which possessed at most sparse seed banks in both meadow types. Consequently, these species can become extinct locally when they disappear from the aboveground vegetation. Restoration of former species richness is therefore not possible from local seed banks. Our results showed that in spite of the similar site conditions and vegetation, seed banks in the two meadow types were remarkably different. Consequently, restoration prospects also differ markedly. Regeneration of dominant grasses, sedges and several common herbs from local seed banks is promising in fen meadows, but it is still unknown whether or not high densities of pioneer *Juncus* seeds could hamper restoration aims. Poorly developed seed banks of dry-mesophilous meadows do not guarantee the regeneration of species-rich vegetation.

Spontaneous regeneration processes are increasingly integrated as restoration tools in ecological restoration (Prach & Hobbs 2008; Prach & Řehounková 2008). However, further case studies are needed to explore in which communities and circumstances could restoration actions be based on spontaneous recovering processes (e.g. spontaneous recovery from seed banks). Our results have shown that even closely positioned stands of contrasting hay meadows require distinct restoration measures. In fen meadows, one can rely on a spontaneous recovery of relatively species-rich stands resuming the former management. In contrast, propagule import is a further requirement for dry-mesophilous meadows (e.g. hay transfer from remaining species-rich stands; Donath et al. 2007; Wallin et al. 2009). Our results underline the importance of regular management for the species-rich hay meadows, as the most economic way of conservation. These stands also can serve as donor sites for improving degraded ones (Donath et al. 2007; Liu et al. 2009).

Implications for Practice

- Our study showed that the role of seed banks in restoration is remarkably different in closely located and floristically similar fen and dry-mesophilous meadows.
- A higher proportion of target species possess seed banks in fen meadows than in dry-mesophilous ones.
- In fen meadows, one can rely on a partial spontaneous recovery from the seed bank, that is establishment of most graminoids and several common herbs is possible from the seed bank.
- Low propagule densities in the soil of dry-mesophilous meadows suggest poor restoration prospects.
- Species poor stands of both meadow types should rely at least partially on hay or propagule transfer from species-rich stands to increase diversity. Therefore, traditionally managed species-rich meadows of the region should have conservation priority as potential donor sites.

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Supporting Information

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

Appendix S1. Major site and soil charecteristics of the studied meadow stands ($n = 5$).

Appendix S2. The frequent species in vegetation and seed banks of the meadows. Species present in the vegetation of at least 80% of the plots (16) or had at least 50 emerged seedlings in total are listed; number of flowering shoots and germinated seedlings were pooled at the stand level. Vegetation: **Vf**: frequency (I–V = 1–5 plots), **F**: number of flowering shoots. Seed banks: **Sf**: frequency (I–V = 1–5 plots) **S**: number of seedlings (each seedling found corresponds with 26.53 germinable seeds/m2), **SBT:** seed bank type; **T**: transient, **SP**: short term persistent; **LP**: long-term persistent (Thompson et al. 1997). Target species, defined as stress tolerant taxa (specialists and generalists; Grime 1979; Borhidi 1995), including legally protected ones (Király 2007) are denoted by "*".