Ecological Applications, 32(1), 2022, e02463

Post-restoration grassland management overrides the effects of restoration methods in propagule-rich landscapes

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Citation: Tölgyesi, C., C. Vadász, R. Kun, A. I. Csathó, Z. Bátori, A. Hábenczyus, L. Erdős, and P. Török. 2022. Post-restoration grassland management overrides the effects of restoration methods in propagule-rich landscapes. Ecological Applications 32(1):e02463. 10.1002/eap.2463

Abstract. Grassland restoration is gaining momentum worldwide to tackle the loss of biodiversity and associated ecosystem services. Restoration methods and their effects on ecological community reassembly have been extensively studied across various grassland types, while the importance of post-restoration management has so far received less attention. Grassland management is an important surrogate for natural disturbances, with which most ancient grasslands have coevolved. Thus, without the reintroduction of management-related disturbance, restoration targets are unlikely to be achieved in restored grasslands. In this study, we aimed to explore how 20 yr of management by mowing once a year or light cattle grazing affects restoration success in Palearctic meadow-steppe grasslands restored by either sowing native grasses (sown sites), applying *Medicago sativa* as a nurse plant (*Medicago* sites), or allowing spontaneous succession (spontaneous sites). We found that, following mowing, sown sites maintained long-lasting establishment limitation, while *Medicago* sites experienced a delay in succession. These limitations resulted in low total and target species richness, low functional redundancy, and distinct species and functional composition compared to reference data from ancient grasslands. Spontaneous sites that were mowed reached a more advanced successional stage, although they did not reach reference levels regarding most vegetation descriptors. Sown and *Medicago* sites that were grazed had higher total and target species richness than those that were mowed, and showed restoration success similar to that of spontaneous sites, on which grazing had only moderate further positive effects. Grazed sites, irrespective of the restoration method, were uniformly species rich, functionally diverse, and functionally redundant, and thus became important biodiverse habitats with considerable resilience. We conclude that an optimally chosen post-restoration management may have an impact on long-term community reassembly comparable to the choice of restoration method. Restoration planners may, therefore, need to put more emphasis on future management than on the initial restoration method. However, our findings also imply that if local constraints, such as potentially high invasive propagule pressure, necessitate the application of restoration methods that could also hinder the establishment of target species, the long-term recovery of the grassland can still be ensured by wisely chosen post-restoration management.

Key words: abandonment; community reassembly; competition; establishment limitation; functional diversity; grassland management; grassland restoration; grazing; mowing; old field.

INTRODUCTION

Ancient grasslands are increasingly recognized as biodiversity-rich habitats and vital sources of ecosystem services (Bengtsson et al. 2019, Dengler et al. 2020, Nerlekar and Veldman 2020). Grasslands provide for most of our sustainable meat and dairy production and can sequester considerable amounts of atmospheric carbon into the soil (Zhao and Liu 2020). However, grasslands are among the most threatened habitats worldwide, due to conversion into arable fields, built-up areas, and tree plantations, and changes in management intensity, including both under and over use. For instance, some formerly grassland-rich regions, such as

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Manuscript received 1 February 2021; revised 3 May 2021; accepted 24 May 2021; final version received 27 September 2021. Corresponding Editor: Alison K. Brody.
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Eastern Europe or the American Midwest, have lost over 90% of their grasslands (mostly tallgrass and mixed prairie [Samson and Knopf 1994] and European steppe [Dengler et al. 2020]). However, as global awareness of the values of nature is increasing, societal demand for the reconstruction of natural ecosystems, including grasslands, is also gaining momentum (United Nations Environment Agency 2019, Fischer et al. 2021). The highest number of habitat reconstruction projects have targeted grasslands (Wainwright et al. 2017), contributing to an increasing body of knowledge on practical methodology and the underlying mechanisms of ecological community reassembly.

The choice of grassland restoration method largely depends on how various filters inhibiting the dispersal and establishment of target species can be best overcome. Thus, there is no one-size-fits-all method, but method selection heavily depends on pre-restoration degradation levels, landscape features, and the devised targets (Cramer and Hobbs 2008, Laughlin 2014, Waldén et al. 2017). The most frequently applied method is sowing seeds of native species (Barr et al. 2017). High seed diversity is often favored (Prach et al. 2014), but managers of large-scale restoration projects seldom have access to satisfactory quantities of the seeds of all desired species. Using only a few dominant and easily accessible species has also been shown to yield a favorable outcome, namely a natural-looking grassy matrix with few weeds (Török et al. 2011). Sown grasses, however, can arrest succession by hindering the colonization of rare target species (Tölgyesi et al. 2019). The initial sowing of a perennial nurse crop, such as *Medicago sativa*, is a commonly applied approach, as it inhibits early successional weeds but thins out spontaneously later on, providing small-scale colonization gaps for target species (Li and Xu 2008, Kelemen et al. 2017). Spontaneous recovery can also be feasible if the surrounding landscape is rich in source populations of target species and no competitively superior exotic or native species hinder the establishment of late colonizers (Prach and Hobbs 2008).

Grassland restoration, however, does not end with the implementation of the optimal restoration method if the targeted grassland community is to be sustained on a permanent basis. Although grassland composition and structure are largely determined by climatic and edaphic factors, most grassland communities have also coevolved with natural disturbances, mainly fire and herbivory (Feurdean et al. 2018, Nerlekar and Veldman 2020). These disturbances, if not too intense, can keep competitively superior species at bay and prevent the accumulation of litter, thereby facilitating the coexistence of higher numbers of species and functional groups. Without a certain level of disturbance, this species-rich steady state is no longer sustained, and the grassland either degrades or turns into alternative vegetation types, such as forest or shrubland (Feurdean et al. 2018, Staal et al. 2018). It has been shown, for instance, that tall-grass prairie restored by sowing high-diversity seed mixtures tends to lose species over time, and require re-sowing, if an appropriate disturbance regime is not implemented (Barber et al. 2019). Disturbance dependency thus poses a major challenge to restoration practitioners, as they need to continuously or periodically manage the restored communities with a certain type and intensity of disturbance.

Economic grassland management techniques, such as livestock grazing and mowing, can be considered widely feasible, sustainable, and even profitable surrogates of natural disturbances (Pykälä 2000). Ecologists have given much attention to the effects of livestock grazing and mowing on biodiversity, but mostly on long-established grasslands and rarely in the context of restoration on ex-arable fields (Tälle et al. 2016). However, it has been shown that both of these management methods are likely to have positive effects compared to abandonment after restoration, due to suppression of competitively superior species (Barber et al. 2019, Dowhower et al. 2020). There is also evidence that grazing can promote dispersal to restored sites via zoochory (Kapás et al. 2020), possibly rendering grazing a more effective post-restoration management option than mowing. A remaining challenge is to understand how mowing and grazing interact with the successional trajectories set forth by different initial restoration methods, and how this affects the long-term success of restoration.

In this study, we aimed to assess how two management types, annual mowing once a year and low-intensity cattle grazing, interact with the effects of three different initial restoration methods: the sowing of native grasses; using a perennial nurse crop (*Medicago sativa*); and spontaneous succession, over a 20-yr period. We applied both species- and trait-based evaluation methods, because high species richness is a well-documented target feature of ancient grasslands (Wilson et al. 2012) and functional traits provide further insight into the intricate assembly mechanisms of grasslands (Wainwright et al. 2017). Specifically, we tested the effect of the two post-restoration management types on the recovery of (1) species richness, (2) functional diversity, (3) functional redundancy, and (4) species and functional composition in differently restored grasslands.

MATERIAL AND METHODS

Study site

The study was carried out near the village of Kunpeszér, central Hungary (47.04°–47.13° N, 19.22°–19.32° E), in a lowland forest-steppe region, where forest and grassland could form a natural mosaic. Wild ungulates and fire used to have a decisive role in keeping the landscape open, but they have been replaced by traditional grassland management for centuries (Erdős, 2018). The climate of the region is moderately continental with a slight sub-Mediterranean influence, characterized by a mean annual precipitation of 550–600 mm (peak in early summer) and a mean temperature of 11°–12°C (Tölgyesi et al. 2016). Ancient grasslands are species rich meadow-steppes and mesic meadows. Characteristic species include *Chrysopogon gryllus*, *Festuca rupicola*, *Galium verum*, *Molinia caerulea*, and *Poa angustifolia*. The soil is relatively humus-rich calcareous sand. A significant proportion of the former ancient grassland in the region was converted into arable fields during the socialist era. However, at the turn of the millennium (mostly between 1998 and 2001), nearly 2000 ha were reclaimed to increase habitat quality for species with high conservation priority, such as the Great Bustard (*Otis tarda*) and the meadow viper (*Vipera ursinii rakosiensis*). Grassland restoration was done by using three methods: (1) sowing the seeds of a few native grasses (*Bromus inermis*, *Dactylis glomerata, Festuca arundinacea*, *Molinia caerulea*, and *Poa angustifolia*) of local provenance (henceforth sown sites); (2) sowing *Medicago sativa* as a short-lived perennial nurse crop, which spontaneously thins out and gives way to recolonizing target grass and forb species (*Medicago* sites); and (3) allowing spontaneous succession without any other initial restoration measure (spontaneous sites). The methods were used on a trial-and-error basis as little previous information was available on their efficacy in the region. Sites with different methods of restoration were randomly distributed among former land parcels, and all were adjacent to ancient grasslands, species rich dirt road verges or ditches, suggesting that dispersal limitation was likely low. Immediately following restoration, grasslands were integrated into the regional grassland management practice and subject either to mowing once a year late in the season, or low intensity pastoral or fenced cattle grazing (~0.5–0.8 animal units/ha) throughout the vegetation period (Vadász et al. 2016).

Data collection

We surveyed six two-decade-old sites for each of the three restoration methods; three having been grazed and three mowed annually since their restoration (Fig. 1). We also selected three grazed and three mowed ancient grassland localities for sampling as reference (henceforth reference sites). In each site, we surveyed the vegetation on 4-m^2 random plots, once in late summer but before mowing in 2016 (286 plots), and once in spring in 2017 (292 plots). Plots were not placed at the same locations on the two sampling dates. The number of plots per site ranged between 6 and 23, depending on the size of the sites (Appendix S1: Table S1). We identified all plants to species level and assessed their cover in percent. We applied two sampling dates because highly competitive, noxious native and invasive plant species (e.g., *Calamagrostis epigejos*, *Solidago gigantea*, and *S. canadensis*) reach peak cover late in the season, so we could account for their effect with late sampling, while several target species, such as orchids and other geophytes, are detectable only in the first half of the vegetation period, requiring an early sampling. Furthermore, we can also expect seasonal differences in the effects of the two management methods. Light grazing may be a continuous low-intensity disturbance evenly distributed over the vegetation season, while mowing is a single high-intensity disturbance taking place late in the vegetation season. As a result, aboveground competition in mowed sites is expected to be low early in the season, due to limited regrowth outside the vegetation period, but high later in the season, until the next mowing event.

Data processing

We used the number of vascular plant species in the plots (henceforth species richness) as a taxon-based measure of restoration success. We considered both total species richness and target species richness. Target species were derived from the total species pool by ruling out ruderal species, common disturbance-tolerant grassland species and early spring ephemerals, following Borhidi (1995), as well as woody species and sown species (Appendix S1: Table S2). To assess species compositional patterns, we prepared a nonmetric multidimensional scaling (NMDS) on the plots × species abundance matrix, and calculated the average Bray-Curtis distance of each restored plot from the reference plots.

To characterize functional diversity, we used Rao's quadratic entropy, which measures the average functional distance between two randomly chosen species in the plots and accounts also for their abundances (Botta-Dukát 2005). We calculated functional diversity using seven traits encompassing the entire life history of species. Traits included vegetative height, specific leaf area, absolute leaf area, Raunkiaer's life form, rate of clonal growth, pollination type, number of seeds per shoot, and seed mass. Sources and data types of traits are shown in Appendix S1: Table S3. We chose Rao as the functional diversity metric because it can be used for further calculations expressing functional redundancy with the following formula: $FR = 1 - Q/D$, where FR is the functional redundancy, Q is Rao's functional diversity, and D is the Simpson diversity of species (Ricotta et al. 2016). The rationale behind this calculation is that Rao's functional diversity converges to Simpson's diversity as the functional dissimilarity of species reaches a maximum, so in redundant communities, where species resemble each other functionally, Q/D becomes low, and FR becomes high.

We assessed functional composition with NMDS performed on the plots × traits matrix as the source data set (Tölgyesi et al. 2019). Records in the matrix were the community weighted means of quantitative traits, while categorical traits were split up into dummy traits of each trait level. We calculated Gower distances for plot pairs using the matrix. Quantitative traits received a weight of

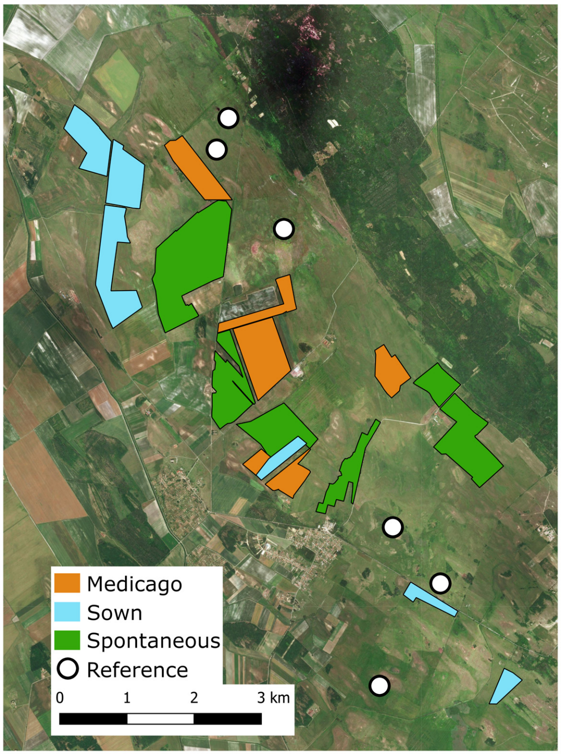

FIG. 1. Map of the restored grassland sites and the location of the reference sites in the matrix of ancient grasslands. One-half of the sites were managed by annual mowing late in the season, while the other half by low-intensity cattle grazing.

one in the calculation, while the dummy traits had weights equaling the inverse of the number of the original levels of the categorical trait. The resulting distance matrix was used as the input data for the NMDS. Using the functional distance matrix, we also calculated the mean distance of each restored plot from the reference plots.

We prepared linear mixed-effects models for the univariate descriptors of the vegetation, i.e., total species richness, target species richness, mean species compositional distance from references, Rao's functional diversity, functional redundancy and mean functional distance from references. The fixed factors were restoration method (three levels: sown, *Medicago*, spontaneous) and management (mowing and grazing) with interaction; site was used as a random factor. We used a Poisson error term for total and target species richness, and Gaussian for the rest of the models. When significant interaction was detected between the fixed factors, we split the models and tested restoration method separately in the two management types and tested management type separately in the three restoration methods.

All analysis was implemented separately for spring and late summer data using R version 4.0.3. Rao's functional diversity and functional redundancy were calculated with the rao.diversity function of the *SYNCHA* package (Debastiani and Pillar 2012), while we used the gowdis function of the *FD* package (Laliberté et al. 2014) to calculate the Gower distance matrix. We used the metaMDS function of the *vegan* package (Oksanen et al. 2019) to prepare the NMDS ordinations. We tested the linear mixed-effects models with the Anova function of the *car* package (Fox and Weisberg 2019), and when restoration method was found to have a significant effect, pairwise comparisons were made with the emmeans function of the *emmeans* package (Lenth 2020).

RESULTS

Species richness

We observed a total of 309 plant species in the restored and reference sites. The average total species richness in the plots was 23.6 and 20.0 in spring and late summer, respectively. In spring, restoration method had no effect on the total species richness (Fig. 2, Table 1), whereas two decades of grazing resulted in significantly increased values compared to mowing in the case of all grassland restoration methods. Reference sites had markedly higher total species richness than restored sites; grazing had the same positive effect on reference sites as on restored sites.

In late summer, mowed spontaneous sites had higher total species richness than mowed sown and *Medicago* sites. Compared to mowing, grazing had a significant positive effect on total species richness in the sown and *Medicago* sites but not in spontaneous sites, leading to uniform species richness levels in the grazed restored sites. Reference sites had significantly higher total species richness than any of the restored sites, but management had no effect in their case. Target species richness showed a similar pattern to total species richness. The only difference was that *Medicago* sites had lower target species richness in spring than either sown or spontaneous sites (Fig. 2, Table 1).

Functional diversity and redundancy

In spring, functional diversity did not differ among restoration methods or management types (Fig. 3, Table 2). Compared to restored sites, reference sites had somewhat lower functional diversity, but this difference was significant only for *Medicago* sites. Management did not affect functional diversity in reference sites. In late summer, mowed spontaneous sites were functionally more diverse than sown sites, while *Medicago* sites were in between. Compared to mowing, grazing had a significant positive effect on functional diversity in sown and *Medicago* sites but not in spontaneous ones, leading to uniformly high functional diversity in all restored sites, equaling that of reference sites. Management did not

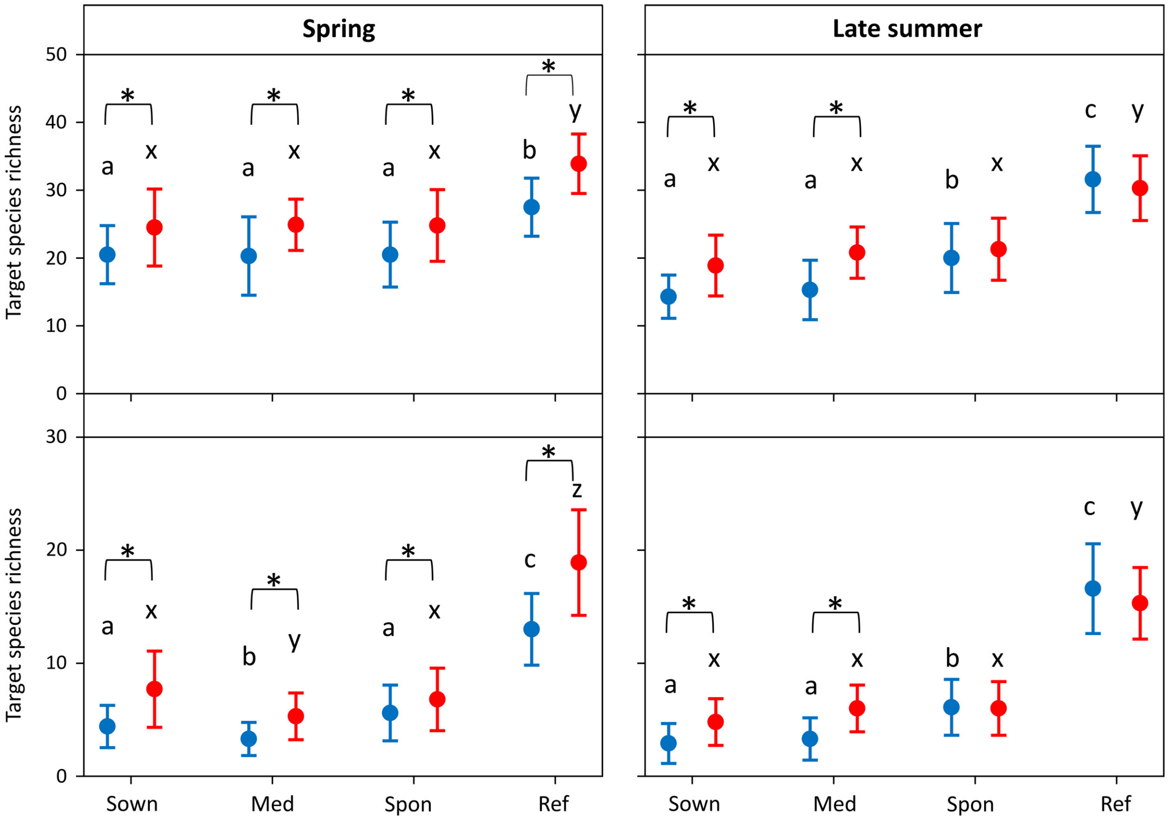

FIG. 2. Total and target species richness of the studied grassland types in spring and late summer (mean ± SD). Blue, mowed; red, grazed; Sown, sown sites; Med, *Medicago* sites; Spon, spontaneous sites; Ref, reference sites. Lowercase letters from a to c and x to z refer to significantly different groups within mowed and grazed sites, respectively. Asterisks indicate significant difference between mowed and grazed sites within the four types of grassland ($P < 0.05$). Comparisons were based on linear mixed-effects models.

affect the functional diversity of reference sites in late summer either.

In spring, functional redundancy did not differ among restoration methods (Fig. 3, Table 2). Following grazing, sown and *Medicago* sites showed a similar level of functional redundancy to spontaneous sites, which were themselves not influenced by grazing. Mowed reference sites had higher functional redundancy than mowed sown and *Medicago* sites. In late summer, grazed *Medicago* sites had higher functional redundancy than mowed ones, leading again to uniform redundancy levels in all grazed restored sites. Reference sites were more redundant than sown and *Medicago* sites, irrespective of management, whereas spontaneous sites were more similar to reference levels. Management had no effect on the functional redundancy of reference sites in late summer.

Compositional dissimilarities

According to the NMDS of species composition, grazed and mowed reference sites formed a single distinct group (Fig. 4). These reference sites were located farther away from restored sites in the ordination space, although grazed restored sites appeared closer to reference sites than mowed restored sites. In spring, grazing compared to mowing pulled the species composition closer to the reference sites along the first axis in all types of restored sites. This was also the case in late summer, but for sown and spontaneous restored sites only. *Medicago* sites showed more similarity to the reference sites along the second axis. These patterns are confirmed with the statistics prepared on the mean Bray-Curtis dissimilarities of the restored and reference grasslands, as restoration type had no significant effect on the dissimilarity values, but management type decreased them significantly.

The functional composition of restored and reference sites was not as distinct as their species composition (Fig. 4). However, grazing had a similar effect as for species composition, as grazed restored sites appeared closer to reference sites along the first NMDS axis in both seasons. Statistics also confirmed some of these tendencies (Fig. 5, Table 3), as functional distances between

TABLE 1. Test results of the linear mixed-effects models prepared for the total and target species richness scores of restored and reference grassland types in spring and fall.

	Total species richness			Target species richness		
Tested variables and comparisons	χ^2	z	P	χ^2	z	P
Spring						
Grassland type	**54.94**		**<0.001**	**130.36**		**<0.001**
Management	**34.90**		**<0.001**	**20.06**		**<0.001**
Interaction	0.17		0.982	2.06		0.560
Ref vs. Spon		**6.20**	**<0.001**		**7.77**	**<0.001**
Ref vs. Med		**6.14**	**<0.001**		**10.56**	**<0.001**
Ref vs. Sown		**6.40**	**<0.001**		**8.41**	**<0.001**
Spon vs. Med		0.06	0.999		**3.20**	**0.008**
Spon vs. Sown		0.12	0.999		0.64	0.918
Med vs. Sown		0.06	0.999		**−2.59**	**0.048**
Fall						
Grassland type	**179.42**		**<0.001**	**275.55**		**<0.001**
Management	**20.27**		**<0.001**	**10.00**		**0.002**
Interaction	**15.95**		**0.001**	**17.69**		**<0.001**
Mowed sites						
Ref vs. Spon		**5.03**	**<0.001**		**6.06**	**<0.001**
Ref vs. Med		**8.42**	**<0.001**		**9.98**	**<0.001**
Ref vs. Sown		**10.08**	**<0.001**		**11.91**	**<0.001**
Spon vs. Med		2.92	**0.018**		**3.48**	**0.003**
Spon vs. Sown		3.90	**<0.001**		**4.44**	**<0.001**
Med vs. Sown		0.74	0.883		0.63	0.921
Grazed sites						
Ref vs. Spon		**6.08**	**<0.001**		**8.01**	**<0.001**
Ref vs. Med		**5.96**	**<0.001**		**7.26**	**<0.001**
Ref vs. Sown		**7.35**	**<0.001**		**8.74**	**<0.001**
Spon vs. Med		0.44	0.972		−0.06	0.999
Spon vs. Sown		2.19	0.125		1.79	0.277
Med vs. Sown		1.61	0.372		1.71	0.321
Sown sites						
Grazed vs. Mowed	**17.87**		**<0.001**	**4.76**		**0.029**
Medicago sites						
Grazed vs. Mowed	**30.77**		**<0.001**	**20.57**		**<0.001**
Spontaneous sites						
Grazed vs. Mowed	0.81		0.368	0.05		0.830
Reference sites						
Grazed vs. Mowed	0.15		0.699	0.36		0.548

Notes: If significant interaction was detected, reduced models, containing only one factor level of one of the fixed effects (grassland type or management) and all levels of the other factor, were checked for significant differences. In the absence of interaction, pairwise comparisons of the factor levels of grassland type were calculated from the full models. Significant results are shown in boldface type ($P > 0.05$). Ref, reference sites; Med, *Medicago* sites; Spon, spontaneous sites.

grazed restored and reference sites were smaller than between mowed restored and reference sites in sown (spring and late summer) and spontaneous (spring) sites.

DISCUSSION

In this study, we assessed how long-term grassland management interacts with the success of initial grassland restoration methods. We addressed multiple facets of grassland community reassembly, because these patterns in isolation can be explained by alternative mechanisms (Laughlin et al. 2017), leaving unresolved questions and limiting the relevance of conclusions for other environments (Laughlin 2014, Engst et al. 2016). Our findings, however, covered different facets and could be used to supplement each other to make an in-depth interpretation of community reassembly.

Competitive sown grasses can suppress early successional, non-target species (Prach et al. 2014) due to their tall stature and/or clonal growth, but can also persist in high abundances for long periods, and mowing may not always be an efficient method to adequately suppress them (Tölgyesi et al. 2019, Valkó et al. 2020). Our data suggest that the competitive effect of these grasses in mowed sites is less pronounced in spring, following the removal of their

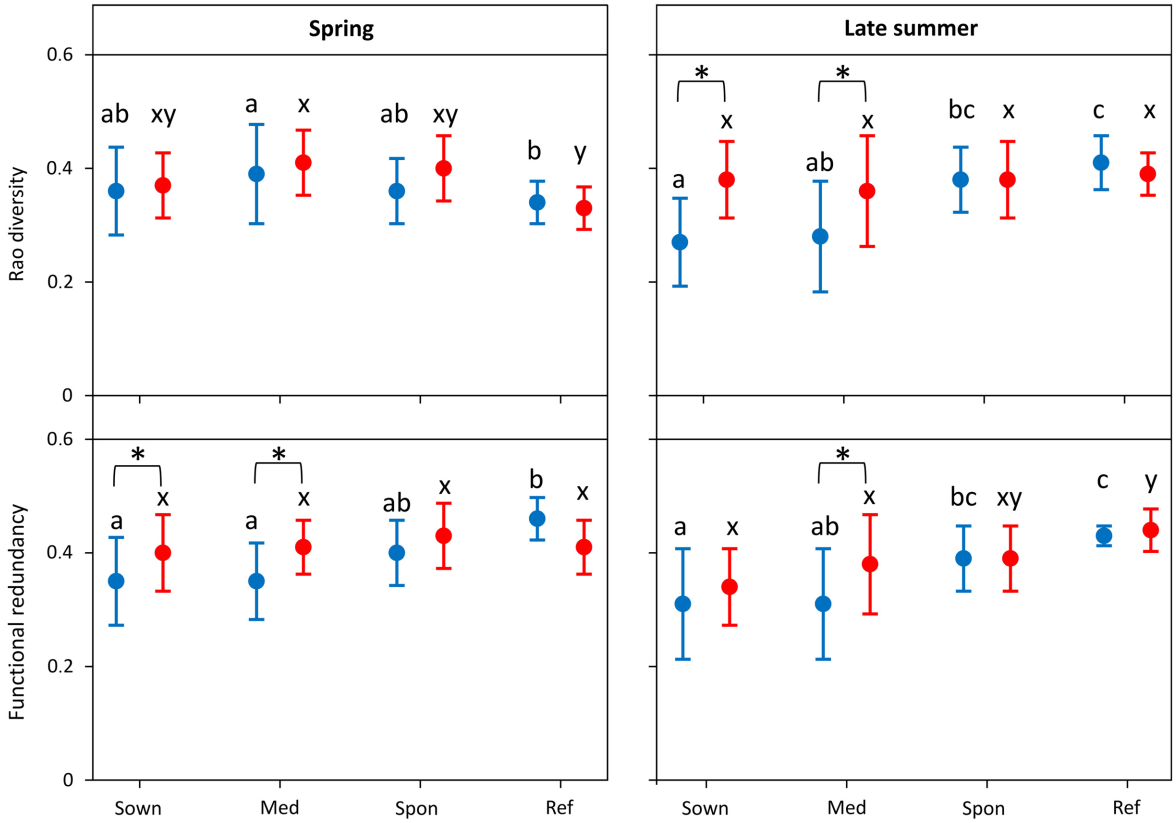

FIG. 3. Rao's functional diversity and functional redundancy of the studied grassland types in spring and late summer (mean ± SD). Blue, mowed; red, grazed; Sown, sown sites; Med, *Medicago* sites; Spon, spontaneous sites; Ref, reference sites. Lowercase letters from a to c and x to y refer to significantly different groups within mowed and grazed sites, respectively. Asterisks indicate significant difference between mowed and grazed sites within the four types of grassland ($P < 0.05$). Comparisons were based on linear mixed-effects models.

biomass at the end of the previous growing season. In contrast, late summer species richness scores, total and target alike, were lower in mowed sown sites than in spontaneous ones, as dominant grasses could reach their maximum biomass and, hence, competitive effect by late summer.

Medicago was also expected to help suppress non-target species in early successional stages, characterized by non-target species, and to give way to colonizing target species later on (Kelemen et al. 2017). However, our data do not fully confirm this trajectory but suggest that succession is simply delayed in mowed *Medicago* sites, indicated by the high non-target species richness in spring. Target (and total) species richness was also low in late summer, too, but, unlike in sown sites, this cannot be explained by a current competitive effect of *Medicago*, as it was virtually absent from the plots. Earlier though, it may have held back the colonization of incoming species, and the current pattern may be caused by a delay in recovery, determined by the time *Medicago* needed for thinning out. Increased soil nitrogen content brought about by the nitrogen-fixing ability of *Medicago* may have also contributed to this trend, since high nitrogen content can delay recovery by sustaining ruderal conditions and promoting competitive species (Maron and Jeffries 2001, Averett et al. 2004).

The undesirable conditions, i.e., high establishment limitation in sown sites and the delay in the succession of *Medicago* sites, were mostly absent when the management was light grazing. Grazing could lead to this positive effect via two mechanisms, i.e., continuous suppression of competition and zoochorous dispersal (Kapás et al. 2020). Our data suggest that the former was more influential as sites with introduced competitive species (sown and *Medicago* sites) were more enhanced by grazing than spontaneous sites (see late summer data in Fig. 2). If zoochory had a high importance, we should have detected its effect on spontaneous sites, too. Sperry et al. (2019) showed that the colonization of new species is increasingly difficult in species-rich restored grasslands due to competition associated with the lack of vacant niches. They propose grazing as a means to tackle this problem, but our data only partially support the mitigating effect of light grazing in spontaneous sites, i.e., in the most species rich type of restored sites. From our study, it appears that even light

TABLE 2. Test results of the linear mixed-effects models prepared for Rao's functional diversity and functional redundancy values of restored and reference grassland types in spring and fall.

	Rao				FRedund			
Tested variables and comparisons	χ^2	*t*	*z*	*P*	χ^2	*t*	*z*	*P*
Spring								
Grassland type	1.74			0.187	**4.48**			**0.034**
Management	**14.64**			**0.002**	**15.41**			**0.001**
Interaction	1.79			0.617	**10.28**			**0.016**
Mowed sites								
Ref vs. Spon		−2.52		0.087		2.54		0.109
Ref vs. Med		**−3.64**		**0.008**		**4.39**		**0.005**
Ref vs. Sown		−1.47		0.472		**4.35**		**0.006**
Spon vs. Med		−1.26		0.602		−2.13		0.228
Spon vs. Sown		1.16		0.658		2.02		0.277
Med vs. Sown		2.41		0.119		−0.20		0.997
Grazed sites								
Ref vs. Spon							−0.63	0.920
Ref vs. Med							0.16	0.998
Ref vs. Sown							0.41	0.976
Spon vs. Med							0.85	0.831
Spon vs. Sown							1.12	0.690
Med vs. Sown							0.26	0.993
Sown sites								
Grazed vs. Mowed					**4.61**			**0.031**
Medicago sites								
Grazed vs. Mowed					**8.65**			**0.003**
Spontaneous sites								
Grazed vs. Mowed					1.14			0.287
Reference sites								
Grazed vs. Mowed					3.19			0.074
Fall								
Grassland type	**23.28**			**<0.001**	**53.67**			**<0.001**
Management	**12.67**			**0.004**	**6.53**			**0.011**
Interaction	**14.74**			**0.002**	**5.76**			**0.024**
Mowed sites								
Ref vs. Spon			0.62	0.923			1.38	0.537
Ref vs. Med			**3.34**	**0.030**			**4.56**	**0.002**
Ref vs. Sown			**4.20**	**0.006**			**5.01**	**<0.001**
Spon vs. Med			2.53	0.125			3.53	0.053
Spon vs. Sown			**3.27**	**0.044**			**4.01**	**0.027**
Med vs. Sown			0.50	0.956			0.24	0.995
Grazed sites								
Ref vs. Spon			0.49	0.961			2.80	0.058
Ref vs. Med			1.36	0.540			**3.05**	**0.036**
Ref vs. Sown			0.47	0.964			**4.72**	**0.001**
Spon vs. Med			1.17	0.660			0.55	0.945
Spon vs. Sown			0.02	1.000			2.66	0.109
Med vs. Sown			−1.04	0.731			1.93	0.285
Sown sites								
Grazed vs. Mowed	**16.31**			**<0.001**				
Medicago sites								
Grazed vs. Mowed	**4.67**			**0.031**				
Spontaneous sites								
Grazed vs. Mowed	0.05			0.817				
Reference sites								
Grazed vs. Mowed	0.50			0.481				

Notes: If significant interaction was detected, reduced models, containing only one factor level of one of the fixed effects (grassland type or management) and all levels of the other factor, were checked for significant differences. In the absence of interaction, pairwise comparisons of the factor levels of grassland type were calculated from the full models. Significant results are shown in boldface type ($P > 0.05$). Ref, reference sites; Med, *Medicago* sites; Spon, spontaneous sites.

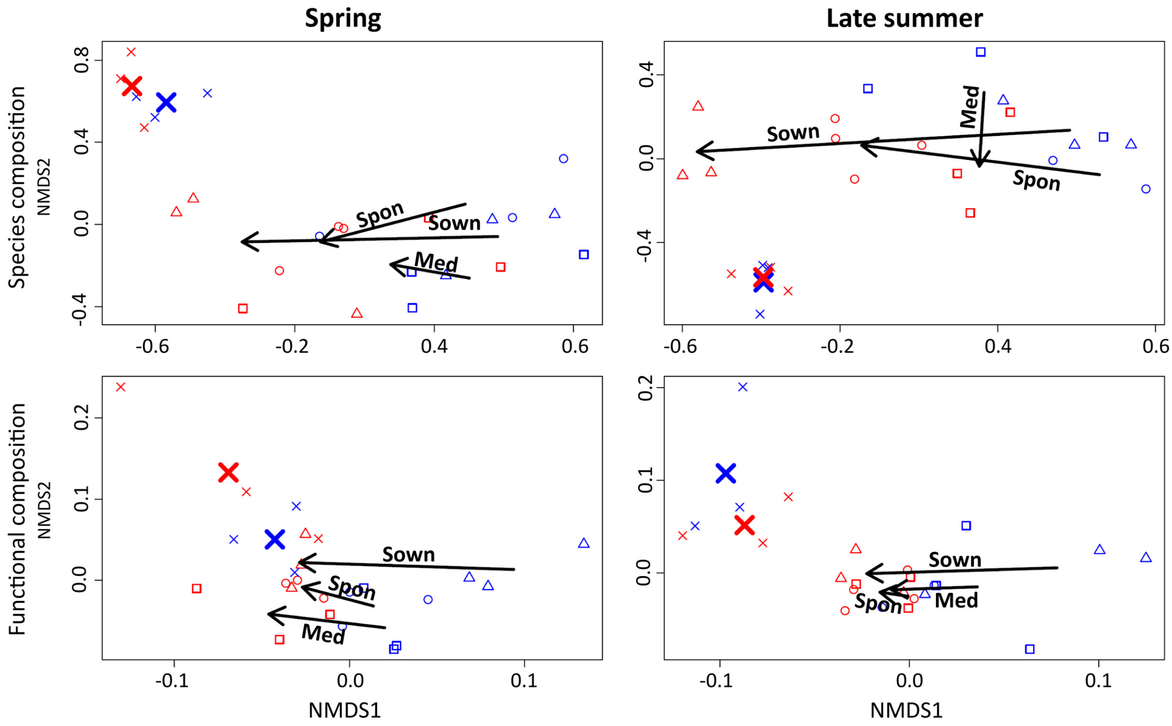

FIG. 4. Nonmetric multidimensional scaling (NMDS) scatterplots illustrating the species composition of the studied grassland types in spring (stress = 0.21) and late summer (stress = 0.22), and their functional composition in spring (stress = 0.19) and late summer (stress = 0.18). Blue, mowed sites; red, grazed sites; triangle, sown sites; square, *Medicago* sites; circle, spontaneous sites; ×, reference sites. Small symbols are centroids of each site derived from 6–23 plots. Large crosses mark the global centroids of mowed and grazed reference sites. Arrows show the effect of management on each restored grassland type by pointing from the global centroids of each type of mowed restored sites to their grazed counterparts. Individual plots are not shown.

grazing has a limit in aiding the recovery of species richness, and, even when post-restoration management is optimal, reaching the reference level of species richness may take a very long time, as also concluded by many authors (Öster et al. 2009, Nerlekar and Veldman 2020). To speed up the recovery of species richness in adequately restored and subsequently managed grasslands, more specific interventions may be required, including the reintroduction of species groups other than vascular plants, such as mycorrhiza-forming fungi (Koziol and Bever 2017).

In contrast to species richness, the functional diversity of restored sites was closer to that of reference sites. Where mowed sites had lower scores (sown and *Medicago* sites in late summer), grazing brought them up to the reference level. Grazing did not improve spontaneous sites, that is, the effect of grazing was similar to our findings for species richness, regarding the limitations of management optimization. Nevertheless, ecological functions can be expected to recover more quickly than species richness (Engst et al. 2016), and the higher than reference scores in *Medicago* sites are also in good agreement with the mechanism outlined for their species richness relations. That is, species of early and later successional stages, which may have contrasting traits due to their contrasting life history strategies (Kelemen et al. 2017), may coexist in *Medicago* sites, boosting functional diversity. Communities that combine subsets of the native species pool and disturbance-tolerant, functionally distinct groups of species also show this pattern compared to intact communities (Bátori et al. 2020). This indicates that high functionality is not necessarily a good indicator of restoration success or intactness, even though recommended by some studies (Laughlin 2014). However, when coupled with other community metrics, functional diversity aids valuable interpretation of community reassembly (see also Peco et al. 2012). In our case, the high species richness and comparatively lower functional diversity of reference sites suggest high functional redundancy, which we could also confirm. This enables the community to sustain functions when exposed to perturbations, thereby building resilience (Biggs et al. 2020). Where redundancy was comparably low in mowed sites, grazing tended to bring it up to the level of reference sites. We suggest that, similar to species diversity, the continuous suppression of competition by grazing allows for the coexistence of functionally similar species. Grazing, however, can also increase overall functional redundancy by selectively removing species, allowing for the persistence of a few, functionally similar,

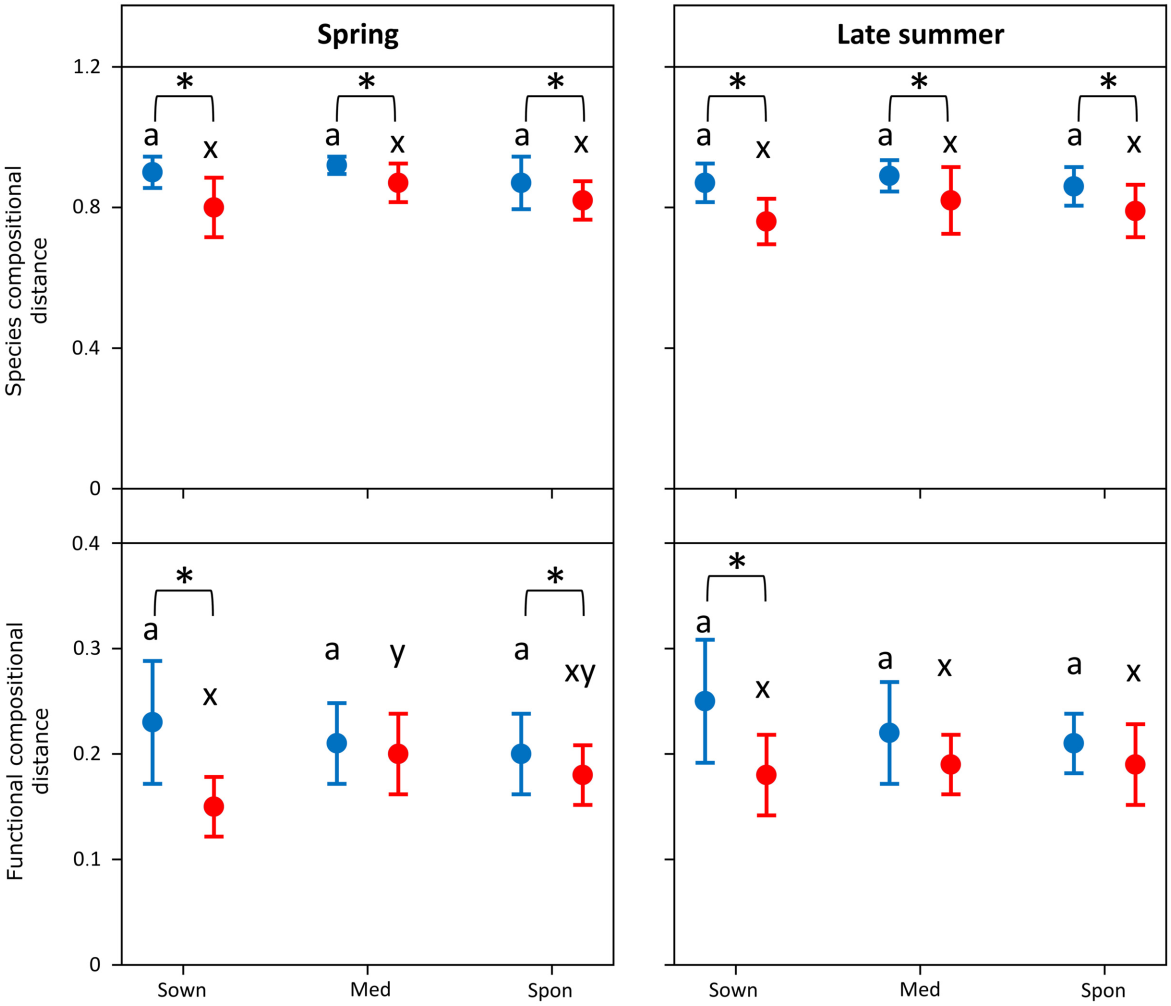

FIG. 5. Mean species and functional compositional distances of restored sites from references (mean ± SD). Blue, mowed; red, grazed; Sown, sown sites; Med, *Medicago* sites; Spon, spontaneous sites; Ref, reference sites. Mowed restoration sites did not differ from each other in any of the four cases (indicated with a). Markings x and y refer to significantly different groups among grazed sites. Asterisks indicate significant difference between mowed and grazed sites within the three restored grassland types ($P < 0.05$). Comparisons were based on linear mixed-effects models.

grazing-tolerant, prostrate or rosette-forming species (Sasaki et al. 2009). Given the high species richness we observed, our data do not support this alternative explanation and are fully in favor of a beneficial improvement of functional redundancy when light grazing is the post-restoration management.

Similar species richness scores can be attained by different sets of species and similar functional diversity scores by different individual functional characteristics of the species (Laughlin et al. 2017). Therefore, the beneficial effects of light grazing on species richness and functionality do not necessarily result in a shift towards target species and functional composition. Instead, grazing management may also divert the successional trajectory and delay full recovery in the long run. This potential misguidance of recovery can be ruled out with the patterns we found for species composition. Restored sites were highly distinct in species composition from reference sites but grazing pulled them closer in the ordination space, and significantly decreased the compositional distances from the reference sites.

The arrangement of restored sites in the functional ordination space provides further support for the outlined mechanisms. The effect of management was less pronounced compared to the effect on species composition, which may be due to the advanced state of the functional recovery in most restored sites, as also indicated by the functional diversity relations. Furthermore, in sown sites, which were the most constrained by competition, grazing significantly pulled functional composition closer to the reference sites, while we did not detect this effect in *Medicago* sites, corroborating

Table 3. Test results of the linear mixed-effects models prepared for the mean compositional and functional distances of restored grassland types from reference grasslands in spring and fall.

	SDist		FDist		
Tested variables and comparisons	χ^2	P	χ^2	t	P
Spring					
Grassland type	4.77	0.092	3.17		0.205
Management	**9.61**	**0.002**	**21.56**		**<0.001**
Interaction	1.06	0.590	**9.29**		**0.010**
Mowed sites					
Spon vs. Med				−0.84	0.694
Spon vs. Sown				−1.79	0.259
Med vs. Sown				−0.89	0.666
Grazed sites					
Spon vs. Med				−1.72	0.272
Spon vs. Sown				1.78	0.257
Med vs. Sown				**3.48**	**0.030**
Sown sites					
Grazed vs. Mowed			**42.81**		**<0.001**
Medicago sites					
Grazed vs. Mowed			0.63		0.427
Spontaneous sites					
Grazed vs. Mowed			**5.17**		**0.024**
Fall					
Grassland type	3.00	0.223	2.24		0.327
Management	**26.88**	**<0.001**	**22.13**		**<0.001**
Interaction	1.28	0.527	**7.05**		**0.029**
Mowed sites					
Spon vs. Med				−0.76	0.741
Spon vs. Sown				−2.12	0.154
Med vs. Sown				−1.46	0.362
Grazed sites					
Spon vs. Med				−0.22	0.975
Spon vs. Sown				1.21	0.485
Med vs. Sown				1.30	0.434
Sown sites					
Grazed vs. Mowed			**16.01**		**<0.001**
Medicago sites					
Grazed vs. Mowed			3.81		0.051
Spontaneous sites					
Grazed vs. Mowed			3.76		0.052

Notes: If significant interaction was detected, reduced models, containing only one factor level of one of the fixed effects (grassland type or management) and all levels of the other factor, were tested for difference. In the absence of interaction, pairwise comparisons of the factor levels of grassland type were calculated from the full models. Significant results are shown in boldface type ($P > 0.05$). SDist, species compositional distance; FDist, functional compositional distance; Ref, reference sites; Med, *Medicago* sites; Spon, spontaneous sites.

that reasons other than competition also delayed recovery.

Conclusions

Our findings highlight that carefully chosen management can be a more important determinant of long-term restoration success than initial restoration methods; thus, restoration planners may need to put more emphasis on management than on the choice of initial restoration method. On the other hand, if local constraints, such as potentially high invasive species pressure, necessitate the application of an establishment-limiting initial method, the recovery of the grassland is not necessarily doomed by the side effects of the method but they may be counterbalanced if the post-restoration management is wisely chosen. In our case, the most suitable choice of management was low intensity grazing, and, we expect, it may be appropriate for a variety of other restored grasslands, too. However, light grazing does not always have more favorable effects on grassland biodiversity than mowing, so it is possible that in some other grassland types, particularly those that have not coevolved with large ungulates, mowing may support recovery more efficiently. Planners may thus need to carefully choose the appropriate long-term management, including its type, intensity, and timing, to attain best possible restoration results in the long run.

Acknowledgments

We thank the support of the Hungarian Ministry of Agriculture, the Kiskunság National Park Directorate and the Hungarian National Research, Development and Innovation Office (grant numbers: K124796 and PD19 132131). We are also grateful to Emmeline Topp for proofreading the manuscript.

Literature Cited

Averett, J. M., R. A. Klips, L. E. Nave, S. D. Frey, and P. S. Curtis. 2004. Effects of soil carbon amendment on nitrogen availability and plant growth in an experimental tallgrass prairie restoration. Restoration Ecology 12:568–574.

Barber, N. A., A. K. Farrell, R. C. Blackburn, J. T. Bauer, A. M. Groves, L. A. Brudvig, and H. P. Jones. 2019. Grassland restoration characteristics influence phylogenetic and taxonomic structure of plant communities and suggest assembly mechanisms. Journal of Ecology 107:2105–2120.

Barr, S., J. L. Jonas, and M. W. Paschke. 2017. Optimizing seed mixture diversity and seeding rates for grassland restoration. Restoration Ecology 25:396–404.

Bátori, Z., P. J. Kiss, C. Tölgyesi, B. Deák, O. Valkó, P. Török, L. Erdős, B. Tóthmérész, and A. Kelemen. 2020. River embankments mitigate the loss of grassland biodiversity in agricultural landscapes. River Research and Applications 36:1160–1170.

Bengtsson, J., J. M. Bullock, B. Egoh, C. Everson, T. Everson, T. O'Connor, P. J. O'Farrell, H. G. Smith, and R. Lindborg. 2019. Grasslands–more important for ecosystem services than you might think. Ecosphere 10:e02582.

Biggs, C. R., et al. 2020. Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. Ecosphere 11:e03184.

Borhidi, A. 1995. Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. Acta Botanica Hungarica 39:97–181.

Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. Journal of Vegetation Science 16:533–540.

Cramer, V. A., R. J. Hobbs, and R. J. Standish. 2008. What's new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology and Evolution 23:104–112.

Debastiani, V. J., and V. D. Pillar. 2012. SYNCSA - R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. Bioinformatics 28:2067–2068.

Dengler, J., I. Biurrun, S. Boch, I. Dembicz, and P. Török. 2020. Grasslands of the palaearctic biogeographic realm. Pages 617–637 *in* M. I. Goldstein, D. A. DellaSala, and D. A. DiPaolo, editors. Encyclopedia of the world's biomes. Volume 3: Forests—trees of life. Grasslands and shrublands—sea of plants. Elsevier, Amsterdam, the Netherlands.

Dowhower, S. L., W. R. Teague, K. Steigman, and R. Freiheit. 2020. Texas Blackland Prairie restoration on old-field vegetation using seeding, mowing, and burning. Arid Land Management 35(1):66–82.

Engst, K., A. Baasch, A. Erfmeier, U. Jandt, K. May, R. Schmeide, and H. Bruelheide. 2016. Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. Journal of Applied Ecology 53:751–764.

Erdős, L., et al. 2018. The edge of two worlds: A new review and synthesis on Eurasian forest-steppes. Applied Vegetation Science 21:345–362.

Feurdean, A., E. Ruprecht, Z. Molnár, S. M. Hutchinson, and T. Hickler. 2018. Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. Biological Conservation 228:224–232.

Fischer, J., M. Riechers, J. Loos, B. Martin-Lopez, and V. M. Temperton. 2021. Making the UN Decade on Ecosystem Restoration a social-ecological endeavour. Trends in Ecology and Evolution 36:20–28.

Fox, J., and S. Weisberg. 2019. An R Companion to Applied Regression. Third edition. Sage, Thousand Oaks, California, USA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Kapás, R. E., J. Plue, A. Kimberley, and S. A. O. Cousins. 2020. Grazing livestock increases both vegetation and seed bank diversity in remnant and restored grasslands. Journal of Vegetation Science 31:1053–1065.

Kelemen, A., B. Tóthmérész, O. Valkó, T. Miglécz, B. Deák, and P., Török. 2017. New aspects of grassland recovery in old-fields revealed by trait-based analyses of perennial-crop-mediated succession. Ecology and Evolution 7:2432–2440.

Koziol, L., and J. D. Bever. 2017. The missing link in grassland restoration: arbuscular mycorrhizal fungi inoculation increases plant diversity and accelerates succession. Journal of Applied Ecology 54:1301–1309.

Laliberté, E., P. Legendre, and B. Shipley. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. https://cran.r-project.org/web/packages/FD/index.html

Laughlin, D. C. 2014. Applying trait-based models to achieve functional targets for theory-drive ecological restoration. Ecology Letters 17:771–784.

Laughlin, D. C., R. T. Strahan, M. M. Moore, P. Z. Fulé, D. W. Huffman, and W. W. Covington. 2017. The hierarchy of predictability in ecological restoration: are vegetation structure and functional diversity more predictable than community composition? Journal of Applied Ecology 54:1058–1069.

Lenth, R. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.2-1. https://CRAN.R-project.org/package=emmeans

Li, J.-H., D.-H. Xu, and G. Wang. 2008. Weed inhibition by sowing legume species in early succession of abandoned fields on Loess Plateau, China. Acta Oecologica 33:10–14.

Maron, J. L., and R. L. Jeffries. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecological Applications 11:1088–1100.

Nerlekar, A. N., and J. V. Veldman. 2020. High diversity and slow assembly of old-growth grasslands. Proceedings of the National Academy of Sciences USA 117:18550–18556.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2019. vegan: Community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan

Öster, M., K. Ask, S. A. O. Cousins, and O. Eriksson. 2009. Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. Journal of Applied Ecology 46:1266–1274.

Peco, B., C. P. Carmona, I. de Pablos, and F. M. Azcárate. 2012. Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. Agriculture, Ecosystems and Environment 152:27–32.

Prach, K., and R. J. Hobbs. 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restoration Ecology 16:363–366.

Prach, K., I. Jongepierová, K. Rehunková, and K. Fajmon. 2014. Restoration of grasslands in ex-arable land using regional and commercial seed mixtures and spontaneous succession: Successional trajectories and changes in species richness. Agriculture, Ecosystems and Environment 182:131–136.

Pykälä, J. 2000. Mitigating human effects on european biodiversity through traditional animal husbandry. Conservation Biology 14:705–712.

Ricotta, C., F. de Bello, M. Moretti, M. Caccianiga, B. E. L. Cerabolini, and S. Pavoine. 2016. Measuring the functional redundancy of biological communities: a quantitative guide. Methods in Ecology and Evolution 7:1386–1395.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44:418–421.

Sasaki, T., S. Okubo, T. Okayasu, U. Jamsran, T. Ohkuro, and K. Takeuchi. 2009. Two-phase functional redundancy in plant communities along a grazing gradient in Mongolian rangelands. Ecology 90:2598–2608.

Sperry, K. P., H. Hilfer, I. Lane, J. Petersen, P. M. Dixon, and L. L. Sullivan. 2019. Species diversity and dispersal traits alter biodiversity spillover in reconstructed grasslands. Journal of Applied Ecology 56:2216–2224.

Staal, A., E. H. van Nes, S. Hantson, M. Hantson, S. C. Dekker, S. Pueyo, C. Xu, and M. Scheffer. 2018. Resilience of tropical tree cover: The roles of climate, fire, and herbivory. Global Change Biology 24:5096–5109.

Tälle, M., B. Deák, P. Poschlod, O. Valkó, L. Westerberg, and P. Milberg. 2016. Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. Agriculture, Ecosystems and Environment 222:200–212.

Tölgyesi, C., P. Török, R. Kun, A. I. Csathó, Z. Bátori, L. Erdős, and C. Vadász. 2019. Plant composition and diversity at edges in a semi-natural forest-grassland mosaic. Land Degradation and Development 30:1083–1094.

Tölgyesi, C., C. Vadász, R. Kun, A. Csathó, Z. Bátori, A. Hábenczyus, L. Erdős, and P. Török. 2021. Post-restoration grassland management overrides the effects of restoration methods in propagule-rich landscapes. Dryad, Data Set. https://doi.org/10.5061/dryad.jq2bvq88q

Tölgyesi, C., M. Zalatnai, L. Erdős, Z. Bátori, N. R. Hupp, and L. Körmöczi. 2016. Unexpected ecotone dynamics of a sand dune vegetation complex following water table decline. Journal of Plant Ecology 9:40–50.

Török, P., E. Vida, B. Deák, S. Lengyel, and B. Tóthmérész. 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. Biodiversity and Conservation 20:2311–2332.

United Nations Environment Agency. 2019. Resolution 73/284: United Nations Decade on Ecosystem Restoration (2021–2030). https://undocs.org/A/RES/73/284

Vadász, C., A. Máté, R. Kun, and V. Vadász-Besnyői. 2016. Quantifying the diversifying potential of conservation usement systems: an evidence based conceptual model for managing species-rich grasslands. Agriculture, Ecosystems and Environment 234:134–141.

Valkó, O., B. Deák, P. Török, K. Tóth, R. Kiss, A. Kelemen, T. Miglécz, J. Sonkoly, and B. Tóthmérész. 2020. Dynamics in vegetation and seed bank composition highlight the importance of post-restoration management in sown grasslands. Restoration Ecology, 29(S1). https://doi.org/10.1111/rec.13192

Wainwright, C. E., T. L. Staples, L. S. Charles, T. C. Flanagan, H. R. Lai, X. Loy, V. A. Reynolds, and M. M. Mayfield. 2017. Links between community ecology theory and ecological restoration are on the rise. Journal of Applied Ecology 55:570–581.

Waldén, E., E. Öckinger, M. Winsa, and R. Lindborg. 2017. Effects of landscape composition, species pool and tie on grassland specialists in restored semi-natural grasslands. Biological Conservation 214:176–183.

Wilson, J. B., R. K. Peet, J. Dengler, and M. Pärtel. 2012. Plant species richness: the world records. Journal of Vegetation Science 23:796–802.

Zhao, Y., Z. Liu, and J. Wu. 2020. Grassland ecosystem services: a systematic review of research advances and future directions. Landscape Ecology 35:793–814.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2463/full

Open Research

Data (Tölgyesi et al. 2021) are archived in the Dryad digital repository: https://doi.org/10.5061/dryad.jq2bvq88q