





## RESEARCH ARTICLE

# Recovery of species richness lags behind functional recovery in restored grasslands

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## Abstract

Restoration of grasslands on abandoned croplands is a major opportunity for land development in degraded landscapes. In this study, we compared the success of three restoration measures, spontaneous recovery, perennial-crop-mediated restoration, and sowing native grasses, by using a unique combination of species-based and trait-based approaches. We sampled 373 4-m<sup>2</sup> plots in nearly 1,000 ha of 20-year-old-restored grasslands and 72 4-m<sup>2</sup> plots in three neighbouring ancient grasslands. Species richness and target species cover were higher in spontaneously recovered sites than in other restored sites, but reference sites had higher scores than all restored sites. Spontaneous sites had higher functional diversity than the other restored sites. Spontaneous and reference sites showed little difference in their functional diversity and in the community-weighted means of relevant traits. Our findings indicate that the establishment limitation effect of the initial application of perennial crops or sowing competitive grasses can last for decades, hindering the recolonization of target species and the recovery of functional diversity; thus, they should be applied in landscapes with high cover of natural habitats only when inhibiting undesirable species is of paramount importance. The similar levels of functional niche saturation in spontaneous and reference sites may also indicate a self-developed establishment-limited situation after 20 years of succession. In combination with this, the lagging recovery of species richness entails lower functional redundancy in spontaneous sites. Our results underline the necessity of postrestorative management methods that reduce establishment limitation and contribute to the recolonization and subsequent coexistence of functionally similar species.

## KEYWORDS

community reassembly, establishment limitation, functional diversity, functional ordination, grassland restoration, spontaneous recovery

## 1 | INTRODUCTION

Temperate grasslands harbour high biodiversity and are also among the most threatened ecosystems in the world (Dengler, Janišová, Török, & Wellstein, 2014; Hoekstra, Boucher, Ricketts, & Roberts,

2005; Ren & Zhou, 2018). The overwhelming majority of natural grasslands in Eurasia and North America have been tilled and converted into croplands (Habel et al., 2013; Mao, Wang, Zeng, Luo, & Zhang, 2018; Samson & Knopf, 1994; Wesche et al., 2016), whereas extensively used seminatural grasslands of NW and central Europe

have also suffered serious reductions both in area and biodiversity (Török & Dengler, 2018). A reverse trend, that is, land abandonment, has also become a major driver of landscape change in the past decades due to social economic changes, such as the collapse of the socialist block (Hobbs & Cramer, 2007). This reduction in land use intensity provides unique opportunities to recreate lost grasslands and to restore biodiversity and ecosystem functions (Batunacun, Nendel, Hu, & Lakes, 2018; Queiroz, Beilin, Folke, & Lindborg, 2014).

Several measures have been introduced for grassland restoration on former arable fields, but no one-size-fits-all method exists (Kiehl, Kirmer, Donath, Rasran, & Hölzel, 2010). Restoration planners must consider a wide array of circumstances in each individual situation to maximize restoration success and to meet the expectations of funding bodies, often within limited time frames (Prach et al., 2016). Spontaneous recovery may be a useful option if source populations of grassland species occur nearby, the seed bank of the soil has not been depleted, the risk of invasion by competitive exotic or native species is low, and soil and hydrological conditions have not been altered to such an extent that the site is no longer suitable for the target communities (Öster, Ask, Cousins, & Erikson, 2009; Prach & Hobbs, 2008). When the above biotic or abiotic thresholds are crossed, entailing severe dispersal and establishment limitations, or when restoration planners intend to speed up the process of recovery, active interventions may be necessary to support community reassembly (Bakker, van Diggelen, Bekker, & Marrs, 2012; Cramer, Hobbs, & Standish, 2008). The most straightforward method is sowing seeds of a certain set of species. The application of high-diversity seed mixtures has proven to be an efficient method (Prach, Jongepierová, Řehunková, & Fajmon, 2014; Walker et al., 2004), but mixtures like these are expensive and frequently unavailable in sufficient quantities for large-scale restorations. Sowing only a limited set of competitive grasses is easier to implement, and these grasses can suppress weeds, leading to a rapid restoration of a 'grassy matrix' of the habitats (Török et al., 2010). Another measure for early weed control is restoration using perennial crops with a relatively short lifespan, in particular *Medicago sativa*. This method is used because *Medicago* does not require annual soil disturbance (i.e., ploughing) and is competitive enough to suppress most weeds but is a relatively short-lived perennial (Kelemen et al., 2017; Török et al., 2011); therefore, it is expected to give way to recolonizing grassland species.

Once restoration is initiated by one of the above-mentioned or other methods, grassland reassembly starts, but its rate and whether it follows the desired trajectories may vary. Traditionally, restoration success is followed up with species-based measures, such as species richness (Engst et al., 2016) or similarity measures, that is, rate of established target species compared with a reference (Kiehl et al., 2010). Species-based measures, however, are not suitable for assessing functional recovery, such as the recovery of trait composition and the completeness of ecosystem functions (Engst et al., 2016; Zirbel, Bassett, Grman, & Brudvig, 2017). Although trait-based approaches have been in the spotlight of vegetation ecology over the past two decades, they have so far received little attention for

assessing restoration success in grasslands (but see, e.g., Engst et al., 2016 and Wainwright et al., 2017).

Some studies suggest that the recovery of species composition and functional trait composition does not necessarily progress with the same rate (Laughlin et al., 2017; Purschke et al., 2013) and they have different predictive power on different aspects of restoration success (Brudvig et al., 2017; Laughlin et al., 2017). Species-based measures yield easy-to-interpret results for restoration practitioners and link processes directly to species, which are the main focus of practical nature conservation. Conversely, trait-based approaches may shed light on the mechanisms that govern community reassembly, such as the relative importance of different filtering mechanisms (Török et al., 2018), and can allow comparisons across ecosystems with different flora but similar environmental conditions. These two facets of community reassembly may thus provide information on different aspects of restoration success, giving grounds for new synthesis. In light of this, we aimed to make an assessment of restored temperate grasslands by combining species-based and trait-based approaches.

Specifically, we evaluated medium-term restoration success following the application of three restoration methods, namely, (a) spontaneous recovery, (b) restoring through perennial crop, and (c) sowing competitive native grasses in a lowland landscape with low dispersal limitation due to a high abundance of ancient grassland fragments. We asked the following questions: (a) Which method was the most efficient in restoring the species composition after two decades of succession? (b) Which method resulted in the functionally most diverse grasslands? (c) Can systematic differences be confirmed between the patterns of the two facets of community reassembly?

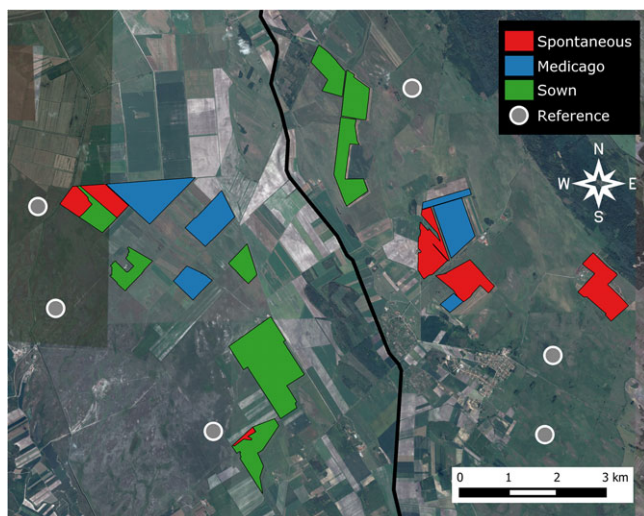
## 2 | MATERIAL AND METHODS

### 2.1 | Study areas and data collection

The study site is located in the Kiskunság National Park, central Hungary (N47°02–07' E19°09–18', 92–94 m asl). The climate is continental with an annual precipitation of 500–600 mm (maximum in June) and a mean temperature of approximately 11°C (Tölgyesi et al., 2016). Two prevailing soil types can be found in the study region: coarse-textured calcareous sandy soils in the eastern part and fine-textured soils composed of a mixture of loess and loamy alluvial deposits in the western side; the demarcation line between the two areas is sharp. The water table is close to the surface in all areas, creating habitats with a mesic or moist character. Species-rich ancient grasslands of the Festuco-Brometea and Molinio-Arrhenatheretea phytosociological classes are common in the area and have been managed by mowing once a year or by low-intensity grazing for centuries (Vadász, Máté, Kun, & Vadász-Besnyői, 2016). Arable fields were also common, but more than 1,000 hectares were reclaimed during the past two decades to increase habitat quality and connectivity for the Great Bustard (*Otis tarda*), an iconic bird species of Eurasian grasslands (Végvári et al., 2016).

Land managers applied three restoration methods in the region with more or less equal proportions: (a) spontaneous recovery, (b) perennial-crop-mediated restoration (*M. sativa*), and (c) sowing three native competitive grasses (henceforth 'spontaneous sites,' 'Medicago sites,' and 'sown sites,' respectively). The selection of a method for a particular site was random and did not depend on site-specific conditions. In *Medicago* sites, *M. sativa* was sown in the first year of restoration, but no subsequent fertilization, soil disturbance, or resowing occurred. Sown grass species of the loamy sown sites included *Alopecurus pratensis*, *Bromus inermis*, and *Festuca arundinacea*, whereas the species used on sandy soil were *Dactylis glomerata*, *F. arundinacea*, and *Molinia caerulea*. Sowing rate was 30–35 kg/ha. Seeds were obtained from local commercial distributors using only propagules of local provenance. Seeds of other competitive native grasses were not available in large enough quantities or were locally known of their low germination and survival rate on young fallows (e.g., *Chrysopogon gryllus*). Both *M. sativa* and the sown grasses were expected to suppress noxious weeds at least in the early years of succession. Weeds that land managers wanted to avoid in particular were aggressive, clonal invasive species (*Asclepias syriaca*, *Solidago canadensis*, *S. gigantea*, and *Aster* spp.) and the annual neophyte *Ambrosia artemisiifolia*, which cause public health issues due to its abundant, allergenic pollen. In all three types of sites, the postrestoration method was mowing once a year in July, supplemented with aftermath grazing from August to November. Earlier mowing was not allowed for the protection of ground-nesting birds. Furthermore, invasive plant species were also controlled by land managers to some extent at all sites.

We selected three to five sites for each restoration method on both soil types (Figure 1). Restoration took place 20 years ago in all sites. We surveyed the vegetation of the sites in randomly positioned 4-m<sup>2</sup> plots in 2017. The number of plots per sampling site ranged



**FIGURE 1** Map of the sampling sites. Sampling sites on loamy soil are located west of the Danube-valley Canal (black line), whereas those on sandy soil are on the eastern side. Restored grasslands are well-defined polygons of former arable fields, whereas reference sites are parts of vast, mostly confluent ancient grasslands [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

between 8 and 22, depending on the size of the sites. The total number of plots on restored sites were 373, and the total area of the surveyed restored sites amounted 906 ha (sown: 434 ha, *Medicago*: 249 ha, and spontaneous: 224 ha). We identified all vascular plant species in the plots and estimated their cover values in percentage. Furthermore, we also assessed the vegetation of three reference ancient grassland sites in both soil types using 12 4-m<sup>2</sup> plots per site, making a total of 72 reference plots. (Boundaries of reference sites are vague and complex; therefore, no total area can be assigned to them.)

## 2.2 | Data analysis

Reference communities differed between loamy and sandy soils; therefore, restoration success was analysed separately for each soil type. For evaluating species-based restoration success, we focussed on total species richness, the species richness of target species, and the cover of target species. We did not consider total cover because it was high in all cases. Following the habitat-specific species pool hypothesis (Török & Helm, 2017; Zobel, 2016), species of the Festuco-Brometea and Molinio-Arrhenateretea phytosociological classes were considered as target species (Horváth et al., 1995). Although usually classified as Molinio-Arrhenateretea species, *Calamagrostis epigeios* and *Elymus repens* were excluded from target species because these highly competitive, disturbance tolerant grasses are known to hinder succession (Lepš et al., 2007).

We prepared generalized linear mixed-effects models for total species richness, target species richness, and target species cover with restoration method as the fixed effect (four levels: sown, *Medicago*, spontaneous, and reference) and sampling site as the random factor. We used Poisson error term for count data (species richness) and Gaussian for cover scores. We assessed differences in species composition using principal coordinate analysis (PCoA) with Bray–Curtis dissimilarity. For a better visual representation, we combined all plots of each sampling site for the source matrix by averaging species cover scores. We applied square root transformation on the data prior to analysis.

We used nine traits, including both vegetative (plant height, specific leaf area, Raunkiaer life form, and lateral spread) and generative traits (pollination type, starting time of flowering, duration of flowering, seed mass, and seed number per ramet) for evaluating trait-based restoration success (Table 1). We used this wide array of traits to capture the entire life history of species constituting the communities. Although some of these traits show some correlation, their number is high enough to yield a reliable functional space (cf. Maire, Grenouillet, Brosse, & Villéger, 2015). Trait values were retrieved from databases; for details, see references in Table 1. Plant height was maximized to 100 cm because management does not allow higher growth in the studied grasslands.

We calculated all orthogonal components of functional diversity: functional richness, evenness, and divergence (Mason, Mouillot, Lee, & Wilson, 2005). Functional richness is a volume in functional trait space that is used by the community and, as such, is a measure

**TABLE 1** Description of the functional traits used in the study

Name of trait	Data type	Source	Note
Seed mass	Numeric	Török et al. (2013, 2016)	Log scale
Life form	Nominal with six levels: annuals, biennials, geophytes, hemicryptophytes, dwarf shrubs, and woody species	Király (2009)	
Plant height	Numeric (cm)	Király (2009)	Maximized to 100 cm
Starting time of flowering	Handled as numeric (months)	Király (2009)	
Duration of flowering	Numeric (months)	Király (2009)	
Specific leaf area	Numeric (mm <sup>2</sup> /mg)	Kleyer et al. (2008; LEDA Traitbase)	
Pollination type	Nominal with three levels: insect, wind, and self-pollination	Kühn, Durka, and Klotz (2004; BiolFlor database)	If more than one type occurs, we chose the more common one.
Lateral spread	Ordinal with three values: 1: <1 cm/year, 2: between 1 and 25 cm/year, 3: >25 cm/year	Klímesová, Danihelka, Chrtěk, de Bello, and Herben (2017; CLO-PLA database)	
Seed number per ramet	Numeric	Kleyer et al. (2008; LEDA Traitbase)	Log scale

of the exploited niche space, whereas functional evenness and divergence indicate how efficiently this space is used up by the species (Villéger, Mason, & Mouillot, 2008). We also considered community-weighted means (CWMs) for the quantitative traits (seed mass, plant height, starting time of flowering, duration of flowering, specific leaf area, and seed number per ramet), whereas nominal traits (life form and pollination type) were evaluated by analysing the cover of each level separately. For the ordinal trait (lateral spread), we also calculated CWMs to ease interpretation. Functional measures were also analysed with linear mixed-effects models in an identical design as for species-based measures. Gaussian error term was assumed in all cases. Functional composition was analysed only for the total assemblages (i.e., target species were not analysed separately).

As an analogue of the species-based PCoA, we also prepared a functional PCoA. Source data came from the plot  $\times$  trait matrix, with the values being the average CWMs of the sites for each trait. Levels of the nominal and ordinal traits were handled as separate 'dummy' traits. Because the scales of the traits varied considerably, we adjusted their range to [0:1] interval. We then calculated the average CWMs and dummy trait values for each sampling site and calculated a distance matrix using Gower distance. Dummy traits received reduced weights, inversely proportional to the number of the levels of the original traits. For example, the three dummy traits of pollination type (i.e., insect, wind, and self-pollination) received a weight of one third each. The resulting distance matrix was used for preparing the functional PCoA.

All calculations were performed in R environment (R Core Team, 2017). Functional measures were calculated with the 'dbFD' function of the *FD* package. We calculated the mixed-effects models with the 'lme' (Gaussian error term) and 'glmer' (Poisson error term) functions of the *nlme* and *lme4* packages, respectively. Significance of the full models was assessed with analysis of variance, for which we used the 'anova' function of the built-in 'stat' package (Gaussian models)

or the 'Anova' function of the *car* package (Poisson models). Pairwise comparisons of the factor levels of significant models were assisted with the 'relevel' function, and we used the false discovery rate method to correct for multiple comparisons ('p.adjust' function). Gower distance was calculated with the 'daisy' function of the *cluster* package, and the PCoAs were prepared with the 'cmdscale' function of the *vegan* package.

The nomenclature of species and plant communities follows Király (2009) and Borhidi, Kevey, and Lendvai (2012), respectively.

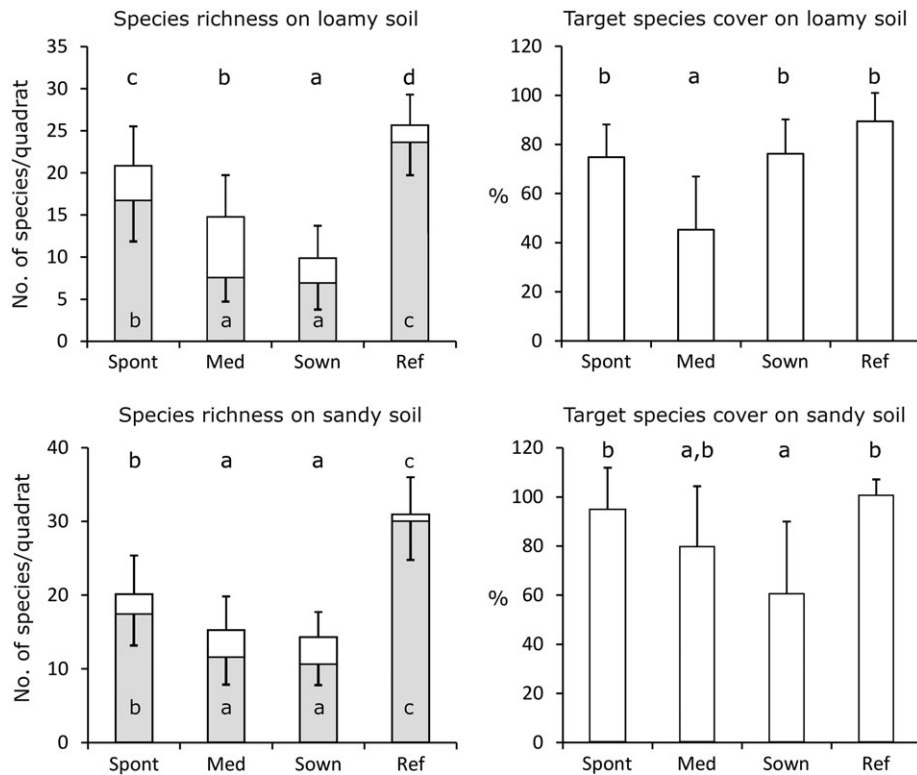
## 3 | RESULTS

### 3.1 | Species-based restoration success

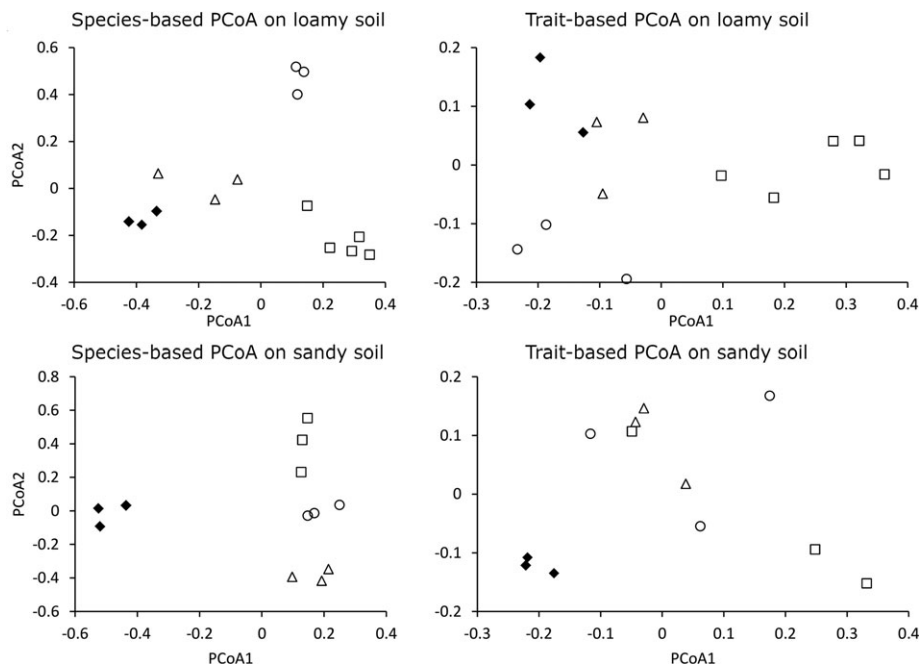
#### 3.1.1 | Loamy soil

We detected 151 species in the restored sites, of which 108 were target species. Together with reference sites, these numbers reached 185 and 142, respectively (Table S1). *M. sativa* practically disappeared from the *Medicago* sites (average cover: 0.08%). Sown grasses were abundant in sown sites (cumulative average of the three species: 50.86%), whereas these species had low average abundance in the other types of sites (*Medicago*: 2.97%, spontaneous: 2.64%, and reference: 0.56%).

The highest total species richness was found in the reference sites, followed by the spontaneous, *Medicago*, and sown sites, respectively, with significant differences between all types. The order of target species richness was similar, but *Medicago* and sown sites had identically low values. Target species cover of spontaneous and sown sites did not differ from the reference, whereas *Medicago* sites had significantly lower values than the other three types (Figure 2, Table S2). According to the species-based PCoA (Figure 3), sown and *Medicago* sites were



**FIGURE 2** Species-based measures of restoration success: Total and target species richness and target species cover on loamy and sandy soils. Groups with different lower case letters are significantly different ( $p < 0.05$ ). Shaded species richness bar sections with downward whiskers (standard deviation) and overplotted letters represent target species, whereas upward whiskers and lower case letters placed above full species richness bars are related to total species richness (i.e., nontarget species are the white column sections). Spont: spontaneous recovery sites; Med: *Medicago* sites (i.e., perennial-crop-mediated restoration); Sown: sites sown with native grasses; Ref: reference sites covered by ancient grasslands



**FIGURE 3** Scatterplots of the principal coordinate analyses prepared for the species and functional composition of the grasslands on loamy and sandy soils. Diamond: reference sites; triangle: spontaneous sites; square: sown sites; circle: *Medicago* sites. Variations covered by the first and second axes of each ordination were 34.88% and 20.84% (species-based on loamy soil), 63.38% and 15.29% (trait-based on loamy soil), 45.50% and 15.23% (species-based on sandy soil), and 49.5% and 23.29% (trait-based on sandy soil), respectively

similarly far from the reference sites in the ordination space, whereas spontaneous sites were much closer to the reference sites. Points of each site type scattered close to each other, indicating that grasslands with similar restoration methods had similar reassembly trajectories.

### 3.1.2 | Sandy soil

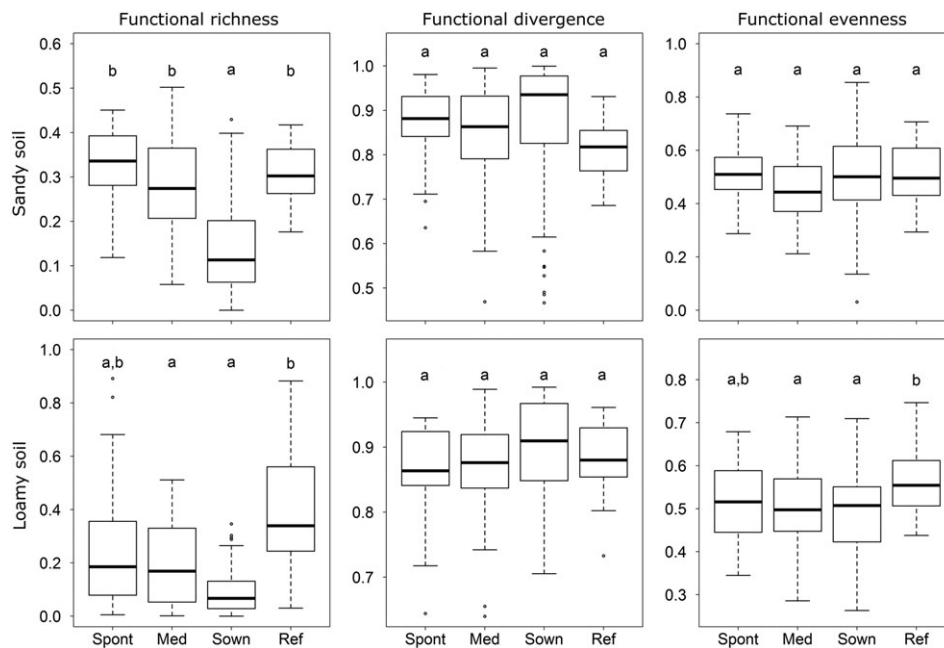
We detected 156 species in the restored sites, of which 120 were target species. Together with reference sites, these numbers reached 196 and 159, respectively (Table S1). *M. sativa* completely disappeared from the *Medicago* sites. The abundance of sown grass species on sown sites (14.11%) was comparable with that of *Medicago* and reference sites (16.47 and 11.26%, respectively), whereas these species appeared scarce in spontaneous sites (1.86%).

Species richness in the reference plots was higher than in any of the restored sites. Spontaneous sites had significantly higher species richness than *Medicago* and sown sites; the latter two sites did not differ from each other. We received the same pattern for target species; nontarget species were generally scarce. Target species cover in the reference and spontaneous sites was similar, whereas sown sites had lower cover values. We could not detect significant difference between *Medicago* sites and the other types of sites (Figure 2, Table S2). The species-based PCoA for sandy soil (Figure 3) indicated a clear separation of reference and restored sites along the first axis, whereas the differences between different restoration methods appeared along the second axis. Spontaneous sites were similarly far from the reference sites in the ordination space as the sown and *Medicago* sites. Points of each site type formed distinct triplets, as in loamy soil.

## 3.2 | Trait-based restoration success

### 3.2.1 | Loamy soil

Functional richness was similarly high in reference, spontaneous, and *Medicago* sites, but sown sites had significantly lower scores. We did not detect significant differences between the functional evenness and divergence of the studied sites (Figure 4, Table S3). The analysis of individual traits revealed a few significant differences (Table 2, Table S4). Seed mass was significantly higher in sown sites than in spontaneous sites, whereas *Medicago* and reference sites did not differ from each other or from the other two sites. Hemicryptophyte was the dominant life form; their cover did not differ among the studied sites. The cover of geophytes was significantly higher in *Medicago* sites than in the other sites; no other pairwise comparison yielded significant results for any life forms. Sown sites had the tallest vegetation and reference sites the shortest, whereas *Medicago* sites were intermediate. Spontaneous sites did not differ from reference sites in average plant height. Flowering of plants in sown sites begins 1 month later on average than in the rest of the sites, whereas the duration of flowering did not differ among sites. Specific leaf area was similar in all studied types of sites. Wind pollination was generally more common than insect pollination. Insect pollination was rare in sown sites, whereas it was significantly more common in reference sites. Self-pollination was rare in all restored sites, whereas it was significantly more common in reference sites. Lateral spread was more rapid in *Medicago* sites than in other sites. Seed number per ramet was lower in sown sites than in other sites, which in turn did not differ from each other. According to the functional PCoA (Figure 3), spontaneous sites were close to the reference sites, whereas *Medicago* and sown



**FIGURE 4** Functional richness, divergence, and evenness of the studied grasslands on loamy and sandy soils. Different lower case letters indicate significantly different groups ( $p < 0.05$ ). Spont: spontaneous recovery sites; med: *Medicago* sites (i.e., perennial-crop-mediated restoration); sown: sites sown with native grasses; ref: reference sites covered by ancient grasslands

**TABLE 2** Functional trait values (community-weighted means and level-specific cover scores) of the studied site types on sandy and loamy soils

	Loamy soil			Sandy soil			Reference	Spontaneous	Medicago	Spontaneous	Reference
	Sown	Medicago	Spontaneous	Sown	Medicago	Spontaneous					
Seed mass (log scale; mg)	<b>0.30 ± 0.87<sup>B</sup></b>	<b>-0.66 ± 1.09<sup>A, B</sup></b>	<b>-1.49 ± 0.82<sup>A</sup></b>	<b>-0.69 ± 0.37<sup>A, B</sup></b>	<b>-1.79 ± 0.94<sup>A</sup></b>	<b>-1.53 ± 0.9<sup>A</sup></b>	<b>-1.30 ± 0.57<sup>A</sup></b>	<b>0.17 ± 0.41<sup>B</sup></b>			
LFO: dwarf shrub (%)	0.00	0.00	0.00	0.06 ± 0.08	0.00	0.00	0.00	0.01 ± 0.01			
LFO: geophyte (cover%)	<b>0.04 ± 0.07<sup>A</sup></b>	<b>0.16 ± 0.19<sup>B</sup></b>	<b>0.03 ± 0.02<sup>A</sup></b>	<b>0.07 ± 0.08<sup>A</sup></b>	<b>0.03 ± 0.1<sup>A</sup></b>	<b>0.11 ± 0.12<sup>B</sup></b>	<b>0.08 ± 0.08<sup>A, B</sup></b>	<b>0.02 ± 0.02<sup>A</sup></b>			
LFO: hemipterophyte (cover%)	<b>0.92 ± 0.10<sup>B</sup></b>	<b>0.72 ± 0.23<sup>A</sup></b>	<b>0.89 ± 0.12<sup>B</sup></b>	<b>0.74 ± 0.13<sup>A</sup></b>	0.88 ± 0.21	0.82 ± 0.14	0.88 ± 0.13	0.95 ± 0.03			
LFO: biennial (cover%)	0.01 ± 0.01	0.06 ± 0.09	0.04 ± 0.04	0.03 ± 0.03	0.03 ± 0.08	0.05 ± 0.07	0.02 ± 0.03	0.01 ± 0.01			
LFO: woody species (cover%)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01 ± 0.01			
LFO: annual (cover%)	0.04 ± 0.07	0.06 ± 0.11	0.06 ± 0.09	0.10 ± 0.09	0.06 ± 0.15	0.02 ± 0.03	0.02 ± 0.04	0.00			
Height (cm)	<b>92.09 ± 22.25<sup>C</sup></b>	<b>63.14 ± 14.00<sup>B</sup></b>	<b>47.47 ± 8.13<sup>A, B</sup></b>	<b>37.92 ± 4.30<sup>A</sup></b>	66.16 ± 16.13	61.64 ± 14.45	52.72 ± 12.13	60.76 ± 5.86			
Start of flowering (month)	<b>6.34 ± 0.55<sup>B</sup></b>	<b>5.33 ± 0.40<sup>A</sup></b>	<b>5.47 ± 0.32<sup>A</sup></b>	<b>5.43 ± 0.33<sup>A</sup></b>	5.78 ± 0.34	5.66 ± 0.38	5.71 ± 0.27	5.55 ± 0.24			
Duration of flowering (month)	3.01 ± 0.29	3.58 ± 0.88	2.95 ± 0.46	3.54 ± 0.31	2.91 ± 0.71	3.51 ± 0.87	3.14 ± 0.49	3.29 ± 0.33			
SLA (mm <sup>2</sup> /mg)	19.21 ± 2.13	22.21 ± 4.05	21.92 ± 3.84	22.07 ± 1.73	20.77 ± 4.21	22.90 ± 4.02	22.01 ± 3.06	20.61 ± 1.32			
Pollination: insect (%)	<b>0.07 ± 0.10<sup>A</sup></b>	<b>0.27 ± 0.17<sup>B, C</sup></b>	<b>0.22 ± 0.17<sup>A, B</sup></b>	<b>0.41 ± 0.16<sup>C</sup></b>	0.13 ± 0.17	0.20 ± 0.16	0.35 ± 0.14	0.30 ± 0.17			
Pollination: wind (%)	<b>0.90 ± 0.11<sup>C</sup></b>	<b>0.68 ± 0.23<sup>B</sup></b>	<b>0.75 ± 0.19<sup>B</sup></b>	<b>0.48 ± 0.16<sup>A</sup></b>	0.82 ± 0.21	0.77 ± 0.18	0.62 ± 0.16	0.69 ± 0.17			
Pollination: self (%)	<b>0.03 ± 0.06<sup>A</sup></b>	<b>0.05 ± 0.12<sup>A</sup></b>	<b>0.04 ± 0.04<sup>A</sup></b>	<b>0.12 ± 0.08<sup>B</sup></b>	0.04 ± 0.12	0.02 ± 0.03	0.03 ± 0.08	0.01 ± 0.01			
Lateral spread (1–3)	<b>1.97 ± 0.19<sup>A</sup></b>	<b>2.32 ± 0.33<sup>B</sup></b>	<b>1.93 ± 0.23<sup>A</sup></b>	<b>1.92 ± 0.21<sup>A</sup></b>	<b>2.16 ± 0.45<sup>B</sup></b>	<b>2.17 ± 0.29<sup>B</sup></b>	<b>2.08 ± 0.23<sup>B</sup></b>	<b>1.49 ± 0.21<sup>A</sup></b>			
Seed/ramet (log scale)	<b>2.26 ± 0.21<sup>A</sup></b>	<b>2.99 ± 0.44<sup>B</sup></b>	<b>2.83 ± 0.28<sup>B</sup></b>	<b>2.83 ± 0.19<sup>B</sup></b>	<b>3.30 ± 0.42<sup>B</sup></b>	<b>2.94 ± 0.34<sup>A</sup></b>	<b>2.93 ± 0.35<sup>A</sup></b>	<b>2.90 ± 0.17<sup>A</sup></b>			

Note. Values are averages ± standard deviations. Bold face indicates significant differences based on linear mixed-effects models; groups with different values are marked with different upper case capitals. Exact test results are shown in Table S4. LFO: life form.

sites scattered farther. Points of each site type occupied distinct areas in the ordination space, similar to the patterns seen in the species-based PCoAs.

### 3.2.2 | Sandy soil

Functional richness was highest in reference sites and lower in *Medicago* and sown sites; spontaneous sites did not differ significantly from either site. The pattern was similar for functional evenness, but no significant difference could be detected between the functional divergence of the studied types of sites (Figure 4, Table S3). Individual traits were less variable among sites than on loamy soil (Table 2, Table S5). Reference sites had higher seed mass than the restored sites. The only life-form category that showed differences among sites was again the geophytes. *Medicago* sites had higher cover scores than sown and reference sites, whereas spontaneous sites did not differ from any sites. Reference sites had a more moderate lateral spread than the restored sites. Seed number per ramet was higher in the sown sites than in the rest of the sites. Reference sites occupied a small compact area in the functional ordination space, far from the restored sites (Figure 3). The clear separation of each restored site type we found for species-based PCoA was absent in the functional PCoA.

## 4 | DISCUSSION

The results of the species-based approach indicate that spontaneous recovery outperformed the other two restoration methods, as it yielded the highest total species richness, target species richness, and target species cover among the restored sites. Although the target species cover of sown sites on loamy soil reached that of the spontaneous sites, this was a result of the high abundance of the sown grass species.

Spontaneous succession leads to sufficient results when dispersal and establishment limitations do not hinder the recolonization of target species (Öster et al., 2009; Prach et al., 2014). In our case, all sampling sites were surrounded by communities of target species, and dispersal agents were also abundant in the landscape in the form of livestock (aftermath grazing by sheep and cattle) and wild herbivores (hares and deer). Moreover, large blocks of recovering patches are criss-crossed by dirt roads and ditches, with verges that can serve as sources of target species (cf. Cousins, 2006). Therefore, dispersal limitation was unlikely an issue for most target species in the studied landscape, allowing for a similarly high rate of seed rain in all three types of restored sites on both soils. The reason for different rates of restoration success among the studied methods may have been the differences in establishment limitation. The aim of sowing *M. sativa* or competitive native grasses was to suppress weeds in initial stages of grassland recovery by limiting their establishment success (Kelemen et al., 2017). It seems though that this effect can extend into the investigated stages (two decades) of succession and can negatively affect the recolonization of target species (for similar findings, see also

Fagan, Pywell, Bullock, & Marrs, 2008). Sowing some other, less competitive grasses, however, may have yielded different results; as in other regions, like in the White Carpathians of the Czech Republic, native grasses tend to promote the reassembly of the target communities instead of hindering it (Prach et al., 2014).

Despite the low dispersal limitation, even spontaneous sites appeared less species rich when compared with the reference sites, and the species-based PCoAs also indicated compositional differences between reference and all restored sites. Missing species in later-phase-restored grasslands are usually grassland specialists with low dispersal abilities (Riibak et al., 2015). Restored sites are generally suitable for these specialists, but their recolonization has a longer time lag compared with other species, leading to a “colonization credit” in the restored sites (Cristofeli, Piqueray, Dufrene, Bizoux, & Mahy, 2010). Colonization credit is the set of species that are available for colonization in the region but have not actually colonized yet and, as such, may be considered a special case of dark diversity (Pärtel, Szava-Kovats, & Zobel, 2011). Colonization credit may decline quickly in some cases (Engst et al., 2016; Valkó et al., 2017), but it can also persist for substantial periods of time. For instance, Öster et al. (2009) posited that half a century would not be sufficient for the full recovery of European seminatural grasslands, even with seed sources in close proximity, whereas Prach et al. (2016) predicted that reaching reference species composition may need up to two centuries. Tölgyesi, Bártori, Erdős, Gallé, and Körmöczi (2015) also found incomplete recovery after more than 50 years in abandoned old fields some 40 km south of the region discussed in the present paper. Similar to these studies, plot-scale colonization credit was high in our study after two decades of succession.

Regarding functional diversity, we found little difference between the different types of restored sites. Functional evenness and divergence did not differ on either soil type, although the functional richness of sown sites was lower than that of spontaneous and *Medicago* sites on loamy soil. Thus, the above-described differences in establishment limitation created by sown species did not hinder the recovery of functional diversity as much as for species richness. The detailed assessment of individual traits also confirmed this observation; as out of the 16 traits and trait levels we analysed, *Medicago* and spontaneous sites on loamy soil differed only in three ways: There were more geophytes and fewer hemicryptophytes, and lateral spread was more rapid in *Medicago* sites than in spontaneous sites. All of these differences can be attributed to the higher abundance of *E. repens*, a stoloniferous, highly competitive native grass, in *Medicago* sites. This species is known to perform better on old fields restored through *Medicago* than on other types of restored old fields (Kelemen et al., 2017), maybe because of the ability of *E. repens* to take advantage of the high-nitrogen content of the soil of these sites, since *M. sativa* is a nitrogen-fixing species. Individual traits on sown sites showed more differences compared with spontaneous and *Medicago* sites, but this is clearly attributable to the high abundance of the sown species, especially *F. arundinacea*, a tall wind-pollinated grass with few but heavy seeds and a brief, early flowering period (see also Table 2).



On sandy soil, we detected only two differences within individual traits: Seed number per ramet was higher in the sown sites than in the other two types of restored sites, and more geophytes were present in *Medicago* sites than in sown sites. The former is probably attributable to the high abundance of *Calamagrostis epigejos*, which has very high seed numbers. This species may have been introduced unintentionally together with the other sown grasses. Similar to loamy soil, the difference in the amount of geophytes may be caused by *E. repens*, which was more common in *Medicago* sites than in sown sites.

The difference in the functional attributes of the restored sites (spontaneous sites in particular) and reference sites was not as high as in species composition. The functional diversity of spontaneous sites recovered to the level of the reference sites, as neither component (i.e., richness, evenness, and divergence) was significantly higher in reference sites on either soil type. *Medicago* sites proved to be less complete on sandy soil, whereas sown sites performed the most poorly. However, the functional PCoA still indicated some difference between spontaneous sites and references, meaning that although these sites have similar levels of functional diversity, they achieve this with slightly different trait compositions. The analysis of individual traits confirmed only few such differences: On loamy soil, wind pollination is still more common in spontaneous sites than in reference sites, whereas on sandy soil, spontaneous sites have lower seed mass and faster lateral spread than references.

Considering species-based and trait-based approaches jointly, we can see that spontaneous sites reached similar functional diversity as reference sites with fewer species, meaning that reference sites (i.e., our target communities) are functionally more redundant than spontaneous sites. Thus, species constituting the colonization credit of spontaneous sites in fact contribute mostly to redundancy.

The volume of exploited niche space is similar in spontaneous and reference sites as indicated by their functional richness, and the communities of these sites use available resources with similar efficiency due to similar functional evenness and divergence (Villéger et al., 2008). Vacant niches are thus no more available in spontaneous sites, contributing to the development of an intrinsic form of establishment limitation well before species reassembly would be complete. This establishment limitation is also indicated by the identical target species cover values in spontaneous and reference sites.

Establishment limitation in restored grasslands is usually reported when highly competitive native or exotic species become dominant (Cramer et al., 2008), as we found in sown and partly in *Medicago* sites. Other papers approach establishment limitation from the opposite direction by stating that functionally complete communities without vacant niches in trait space are more resistant to invasions (Funk, Cleland, Suding, & Zavaleta, 2008), which is an advantageous feature of such communities. Here, we also show that vacant functional niches can run short during the recovery of grasslands without undesirable competitive species, which can not only make the communities more resistant to invasion but also slow down the recolonization rate of further target species. This mechanism entails that the time lag for the recolonization of species in the

colonization credit may be only partly caused by their low dispersal ability. They may indeed be among the last species to arrive, but they may also remain absent for longer than expected due to increasing establishment limitation as functional niche space reaches saturation. Conversely, if target communities have little functional redundancy, we may expect a fast recovery of species composition. A better understanding of old-field succession could thus be developed by relating the time needed for the complete recovery of species richness to the functional redundancy of the target communities in various grassland types.

If the target community of a restored site is functionally redundant, the recovery of ecological redundancy should be actively encouraged for community resilience against environmental perturbations (Funk et al., 2008). If some species become extinct within a functionally redundant community, it may still sustain ecological functions, but if there is little redundancy, species losses result in losses of functions (Török & Helm, 2017). Thus, even though our spontaneous sites performed well according to the functional diversity measures, lack of functional redundancy entails lower resilience with regard to ecological functions. To restore redundancy, we recommend decreasing establishment limitation in late successional stages even if no apparent limiting factors are present. There are a number of postrestoration methods that are known to have this effect; so we can recommend testing their suitability and integrating them into standard restoration schemes. Possible suitable methods include moderate levels of grazing (Auffret, 2011), mechanically opening colonization windows (Valkó et al., 2016), transplanting blocks of turf (Mudrák, Fajmon, Jongepierová, & Doležal, 2017), or sowing hemiparasitic plant species such as *Rhinanthus*, *Pedicularis*, or *Comandra* species to reduce the vitality of populations potentially hindering recolonization (Davies, Graves, Elias, & Williams, 1997; DiGiovanni, Wysocki, Burke, Duvall, & Barber, 2017).

## 5 | CONCLUSIONS

We conclude that the establishment limitation effect of sown perennial crops and competitive grasses can be detectable after decades of application, hindering the colonization of target species; thus, these measures should be applied only when inhibiting undesirable species during the first years of recovery is of paramount importance. Furthermore, our results suggest that the functional recovery of restored grasslands can be faster and more complete than the recovery of species richness. The recovery of functional diversity can create an intrinsic form of establishment limitation even without well-known limiting factors such as the dominance of exotic competitors. Once this establishment-limited stage is reached during succession, colonization credit (i.e., the set of species that are available for colonization but are yet to colonize) can persist for long time periods, keeping functional redundancy at low levels, and the community can remain susceptible to environmental perturbations, further slowing down progress towards the target species composition. A possible solution for

this stalling of succession may be the application of postrestoration methods that reduce establishment limitation.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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