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Original Research Article

What helps in the short term may hinder later: High grass abundance caused by the sowing of a competitive grass species limits meadow steppic grassland regeneration

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ABSTRACT

With the global loss of grassland ecosystems, biodiversity and ecological stability are declining at an alarming rate. One way to counteract this trend is grassland restoration on abandoned fields. A widely used method is sowing competitive native grasses at high density to rapidly establish a vegetation matrix. Here, we studied the long-term effectiveness of sowing the regionally dominant native grass species, *Festuca valesiaca*, in an abandoned field in Hungary to restore the region's natural vegetation, the endangered Pannonic loess meadow steppe. The grass was sown at high density, supplemented by additional seeding of 14 characteristic forbs. We compared vegetation development in this sown site with a neighbouring spontaneously recovering field and an adjacent ancient loess meadow steppe as reference. Vegetation was surveyed annually for 13 years in the restored sites and seven in the ancient grassland. *F. valesiaca* became dominant four years after sowing, and its cover quickly surpassed that of the ancient grassland. Regeneration was initially rapid but slowed markedly by year six after sowing, showing only small further progress thereafter. In contrast, although weed cover remained high for longer in the spontaneous site, species composition progressed steadily toward the target state, with better establishment of non-sown target forbs. Our findings indicate that a fast-emerging, dense grass cover shortens the weed-dominated phase but slows regeneration later. We highlight the importance of prioritizing long-term continuous monitoring in restoration decisions, as treatments may lead to contrasting outcomes over time.

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1. Introduction

Among the Earth's habitat types, grasslands have been converted by human activities to one of the greatest extents, primarily for agricultural cultivation and, more recently, increasingly for forestry purposes (Bond, 2021; Hoekstra et al., 2005) The majority of large intact grasslands have disappeared, and with the spread of inappropriate management practices, degradation is also becoming a growing problem (Auffret et al., 2018; Bardgett et al., 2021; Clavel et al., 2011). The remaining fragments of ancient grasslands contribute significantly to global biodiversity, providing habitat for various specialist plant and animal species (Buisson et al., 2022; Veldman et al., 2015). In addition, natural and semi-natural grassland ecosystems play a vital role in global climate regulation through water and carbon sequestration, while also offering a range of essential ecosystem services to human populations (Bengtsson et al., 2019; Egoh et al., 2018).

As the area of these grasslands further declines, there is a rising urge for rapid restoration. However, successful restoration strategies require thorough understanding of regeneration processes, which depends on temporal data (Prach, 2003). Long-term monitoring is therefore fundamental in restoration ecology, yet the term is often used inconsistently in the literature. In many cases, "long-term" refers to vegetation data collected on two occasions several years apart or resampled at irregular intervals (Lindenmayer and Likens, 2010). While these approaches can provide useful information, they capture only discrete snapshots of a continuous process. In contrast, long-term consecutive monitoring of permanent plots allows not only the detection of vegetation transitions but also their interpretation within a broader ecological context (de Bello et al., 2020). This reduces the risk of mistaking short-term vegetation patterns or other temporary fluctuations, such as climatic variability, for directional trends. Consequently, detailed time series on regeneration dynamics provide a basis for reliable conclusions and are essential for supporting evidence-based restoration decisions (Ruiz-Jaen and Aide, 2005).

Building on this need for long-term data, monitoring restoration success for a longer timespan has been identified as an important research direction (Cortina-Segarra et al., 2021; Tischew et al., 2010), and with that, the length of vegetation surveying started to increase in time (Wortley et al., 2013). Still, there are few studies covering ten or more years and we have little information on active restoration in such time scales (Kollmann et al., 2016).

Another rarely addressed key challenge in grassland restoration is the selection of appropriate reference sites. Compared to forest ecology, old-growth habitats are less commonly used as reference sites in grassland ecology (Veldman et al., 2015; Buisson et al., 2022), mainly due to their scarcity and limited data on their occurrence and characteristics. As a result, many studies rely on species-rich but relatively recent sites, and direct comparisons between ancient remnants and recovering sites remain rare (Toma et al., 2023). However, restoration outcomes are evaluated most effectively when the chosen target state represents the true reference (Wortley et al., 2013).

Sowing low-diversity seed mixtures composed predominantly of native grasses and supplemented with a few other target species is a widespread method due to its quick effects on vegetation (Török et al., 2010). Over the past decades, vast areas of former croplands have been restored by this technique as part of large-scale rehabilitation programs, particularly in the tallgrass prairies of the United States (Barr et al., 2017; Jelinski and Kulakow, 1996) and the semidry and mesic grasslands of Europe (Tischew et al., 2010; Török et al., 2011). The treatment has excellent weed control capabilities, which is also highly advantageous in the prevention of alien plant invasions (Blumenthal et al., 2005; Gornish and dos Santos, 2016), and establishes a dense vegetation matrix shortly after sowing that can reduce soil erosion (Boyd, 1942; Jelinski and Kulakow, 1996; Meissen et al., 2020). Additionally, native seed availability is limited in many regions due to a lack of species-rich donor sites and regional seed producers, further promoting the use of this restoration technique, which also has lower costs and is easier to apply than sowing a higher number of species (Török et al., 2011). However, the resulting grasslands are often species-poor, containing just a fraction of the target species besides the high abundance of the sown competitive grass (Dickson and Busby, 2009; Valkó et al., 2016a; Weber, 1999). So far, it remains unclear (1) how long the restraining effect of sown grasses persists and (2) how species assembly develops after the onset of such low-diversity states. To answer these questions, targeted monitoring studies are needed.

Loess meadow steppes formed on nutrient-rich chernozem soils have been particularly affected by cultivation (Hurka et al., 2019). In Hungary, Pannonic loess vegetation has declined by 98 % and is therefore considered as an extremely endangered habitat type (Biró et al., 2018). Beyond the extent of habitat loss, the naturalness of much of the remaining loess meadow steppes in the region has severely declined due to various degradation agents, including improper pastoral practices (both over- and undergrazing), inappropriate mowing regimes, artificial planting, poor water management practices, and further agricultural expansion (Malatinszky et al., 2013). Well-preserved primary remnants are characterized by high biodiversity, including many specialists, a high proportion of perennial forbs, and a rich insect fauna (Illyés et al., 2007a). Consequently, Pannonic loess steppic grasslands have been designated as a priority habitat type in the European Union under the Habitats Directive, making their preservation and restoration a major focus of conservation efforts.

In this study, we annually monitored vegetation development on a former cropland for thirteen years starting from 2013. The abandoned field neighboured one of the largest remaining ancient loess meadow steppes of Hungary, providing a unique opportunity to study the restoration of Pannonic lowland loess meadow steppe in direct contact with a primary, species-rich reference grassland. The ancient grassland is characterized by high species richness and a prominent abundance of forbs. Two years after abandonment, the dominant grass of the reference grassland, *Festuca valesiaca*, was sown at high density. Additionally, 14 forb species were sown at low density. Another part of the restoration site was left for spontaneous succession. We aimed to answer the following research questions: 1) How successful is high-density grass seeding in terms of species richness and composition by the end of thirteen years? 2) How does the cover of weeds, target perennial forbs and specialist species change over time in sown versus spontaneous sites, and to what extent do they converge toward the reference state? 3) How does vegetation composition develop following high-density grass sowing compared with spontaneous succession?

2. Materials and methods

2.1. Study sites

The study area was located in the Great Hungarian Plain in Hungary, within the Eurasian forest-steppe biogeographic zone. The mean annual precipitation in the region varies between 500 and 550 mm and the mean annual temperature is 10–11 °C (Bartha et al., 2024). The average elevation above sea level is 99 m. The soil in the area is chernozem, formed on loess substrate.

As reference, we chose an ancient loess meadow steppe located within Körös–Maros National Park in the south-eastern region of the country ('Tompapusztai-löszgyep', 46.360° N, 20.980° E). The grassland is of 20.9 ha and with that it is one of the largest pristine zonal meadow steppes in Hungary, meaning that vegetation development was primarily driven by climate rather than by the site's topographic or edaphic features (Illyés et al., 2007b).

In 2009, intensively managed croplands became abandoned directly adjacent to the loess meadow steppe. A field of 8.85 ha was selected for spontaneous recovery, while 5.00 ha were restored by sowing in 2011 and 2012.

(1) Reference meadow steppe

The ancient grassland was characterised by a high cover of perennial forbs (Bartha et al., 2022, 2011), and the total number of observed vascular plant species was 274 (Csathó and Csathó, 2009). The dominant species of the loess meadow steppe was *Festuca valesiaca*. Other typical grass species were *Festuca rupicola*, *Poa angustifolia*, *Carex praecox*, *Elymus hispidus*, *Alopecurus pratensis*, *Bromus inermis* and *Stipa capillata*. Common perennial forbs included *Teucrium chamaedrys*, *Galium verum*, *Fragaria viridis*, *Thalictrum minus* and *Salvia nemorosa* (Csathó and Csathó, 2009).

Historically, the ancient loess grassland was managed by cattle grazing, with management shifting to annual mowing, which continued throughout the study period (except in 2022 when the mowing did not take place due to droughty conditions and the resulting low biomass production).

(2) Sown site

To investigate the effects of grass-dominated low-diversity seed mixtures frequently used by restoration practitioners, high-density grass sowing was supplemented with a low-density forb mixture. All propagules originated from the adjacent ancient meadow steppe and were sown manually.

The dominant grass of the adjacent reference meadow steppe (*Festuca valesiaca*) was sown in 2011, two years after abandonment. This species is a competitive C_3 tussock grass and is characteristic to (sub)continental steppic grasslands of high naturalness (Conert, 1998). The seeds of *F. valesiaca* were harvested with a combine harvester on 21st June 2011, at the peak of its ripening period, and were sown on 5th October 2011. Propagules landed on open surface, as the topsoil was previously prepared by raking to remove plant debris remaining after brush cutting. The average sowing density was 33 kg/ha (Guller et al., 2022), which is generally considered as high seeding density for grasses in restorations (Török et al., 2010).

In addition, 14 forb species of the ancient grassland were sown at low densities on 4th June 2012, three years after abandonment. Seeds were collected by hand in the first days of June 2012, and stored dry at room temperature until sowing, and then evenly distributed across the five hectares. Sowing was carried out without prior cleaning, i.e., chaff and stems were not removed. The sown species were as follows: *Allium vineale*, *Astragalus cicer*, *Galium verum*, *Hypericum perforatum*, *Knautia arvensis*, *Linum austriacum*, *Plantago media*, *Ranunculus polyanthemos*, *Rumex thyrsiflorus*, *Salvia austriaca*, *Salvia nemorosa*, *Stachys recta*, *Thymus glabrescens* and *Thymus pannonicus*. In the case of *A. vineale*, bulbils were harvested and used for sowing instead of seeds.

(3) Spontaneously recovering site

This former cropland was abandoned in 2009 and has not received any kind of restoration treatment; thus, we were able to study spontaneous successional processes.

In the early period, both the sown and the spontaneous sites were managed with a brush cutter twice a year. In 2012 and 2013, there was no need for the second cutting due to extreme drought. Since 2017, as vegetation became less weedy, the management of the restored sites changed to annual mowing. The majority of young individuals of woody invasive species were removed mechanically.

2.2. Vegetation sampling

We surveyed annually eight plots of 4 m × 4 m in fixed positions at the peak of biomass production in early summer, from 2013 to 2025 in the sown and the spontaneous sites and between 2019 and 2025 in the ancient grassland. We recorded all vascular plant species and estimated their cover scores in percentages (cf., Braun-Blanquet, 1964). The nomenclature of vascular plant species follows the World Flora Online database (WFO, 2025).

2.3. Functional groups

We sorted species into functional groups of specialists, generalists and weeds. We grouped native or non-native ruderal species as weeds according to Borhidi (1995). Specialists consisted of species that belonged to the Festuco-Brometea class according to Borhidi's phytosociological classification (Borhidi, 1995). Generalists were species that were neither specialists nor weeds. *Galium verum* was classified as a specialist instead of a generalist, while *Calamagrostis epigejos* and *Elymus repens* were considered as generalists instead of weeds.

Given their particular importance in the restoration of meadow steppes, we also examined target perennial forbs separately, which we defined as the perennial forb species recorded in the ancient grassland at least once during the seven-year study period. For classification, we used Raunkiær's system combined with taxonomic classifications, where chamaephytes, hemicryptophytes, and geophytes from plant families other than Poaceae and Cyperaceae were included in this group (Király, 2009).

2.4. Data analysis

To study the long-term effect of high-density grass sowing, we compared the thirteen-year-long data series from the two restored sites. In doing so, we considered the year of abandonment as year 0 (2009), thus the first surveyed year (2013) was year 4 and the last one (2025) was year 16.

We compared vegetation attributes capturing the target state and the progress of the regeneration process across sown, spontaneous, and ancient sites over time using generalized additive mixed-effects models (GAMMs). The selected vegetation attributes were: (1) plot-level species richness, (2) cover of *Festuca valesiaca*, (3) cover of sown forb species, (4) cover of weedy species, (5) cover of generalist species, (6–8) specialist cover (total, sown, non-sown), and (9–11) target perennial forb cover (total, sown, non-sown).

In the models, "site" was added as a fixed effect, with a smoothed term for "year" incorporated, using penalized splines with a setting of 10 knots (bs = "ps", k = 10), and plot ID was included as a random intercept to account for repeated measurements within plots. For *F. valesiaca* cover, random slopes for time were additionally included to capture plot-specific temporal variation. For models (1), (2) and (3), we used global smooths for statistical inference as these provided more stable parameter estimates, while site-specific smooths were retained for visualization. The penalty order (m) was adjusted for each model (m = 1, 2, or 5) based on the temporal structure of the data to ensure appropriate smoothing. For models (3), (7–8) and (10–11), we excluded the ancient grassland to focus on comparing the sown and spontaneous sites.

To determine the degree of similarity between the species composition of the three sites and the direction of vegetation development in the restored grasslands, we used NMDS ordination (non-metric multidimensional scaling). The data were automatically square root transformed and standardized using Wisconsin double standardization to reduce the influence of highly abundant species. The analysis was performed using the Bray–Curtis similarity index with the number of iterations determined by the algorithm's convergence criteria. In addition, we calculated successional distances using the ordination regression-based approach developed by Rydgren et al. (2019), (2020) to assess the rate of compositional regeneration in both the sown and spontaneously recovering vegetation. To do this, we first computed the centroid of the ancient grassland by averaging the NMDS axis scores across all years. Next, we calculated the Euclidean distance between the ancient grassland centroid and the NMDS coordinates of the plots from both restored sites for each year, deriving the successional distances. Then we fitted a GAMM model to analyse the possible successional gradients, where distance was the dependent variable and site was the predictor variable. Time was added as a smooth term using penalized splines (with a setting of 10 knots), and plot ID was included as a random intercept.

Data processing and analysis were performed using the statistical software R version 4.5.2 (R Core Team, 2021). NMDS was computed by using the 'vegan' package (Oksanen et al., 2020), GAMMs were performed using the 'gamm4' package (Wood and Scheipl, 2025). Both NMDS and GAMM model results were visualized using the package 'ggplot2' (Wickham, 2016).

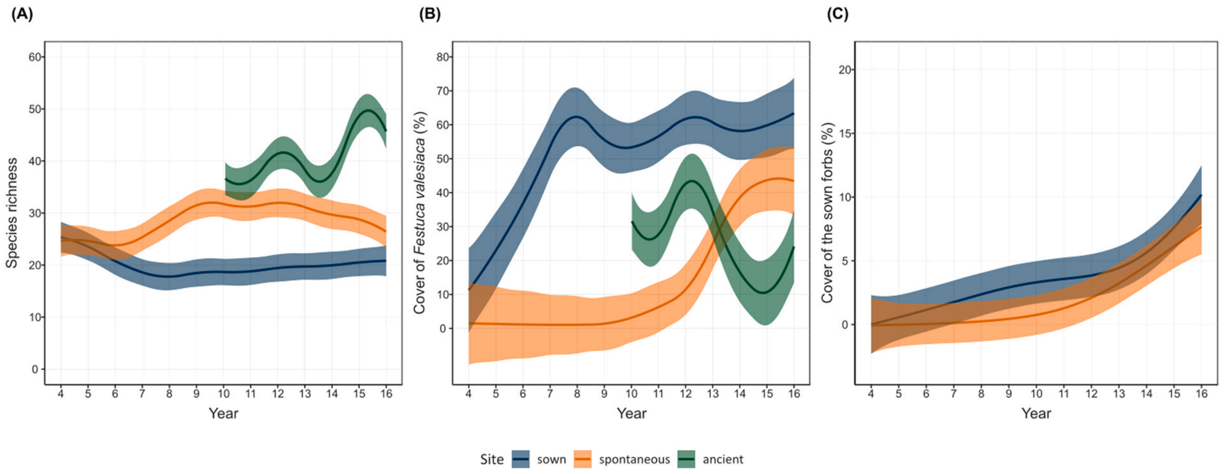

Fig. 1. Mean species richness of the grasslands (A), mean cover of *Festuca valesiaca* (B) and mean cumulative cover of the 14 additionally sown forb species (C) on 16 m^2 at the three study sites. Model lines were calculated using generalized additive mixed-effects models (GAMMs), where time was treated as a smooth term interacting with site, and plot ID included as a random effect. Year refers to years after abandonment. Shaded bands show the 95 % confidence interval.

3. Results

Over the thirteen-year study period, we recorded 111 vascular plant species at the sown site and 121 species at the spontaneous site. During the seven years of monitoring in the ancient grassland (years 10–16), 118 species were observed. Of these, 63 and 58 were recorded at least for one year in the sown and spontaneous sites, respectively. However, several of these species were weeds that occurred only occasionally at the ancient grassland (e.g. *Myosotis arvensis* and *Picris hieracioides*) or were primarily associated with small disturbed patches, such as animal burrows.

In the sown site, species richness decreased until year 8 after abandonment, followed by only a minor increase (Fig. 1A). In the

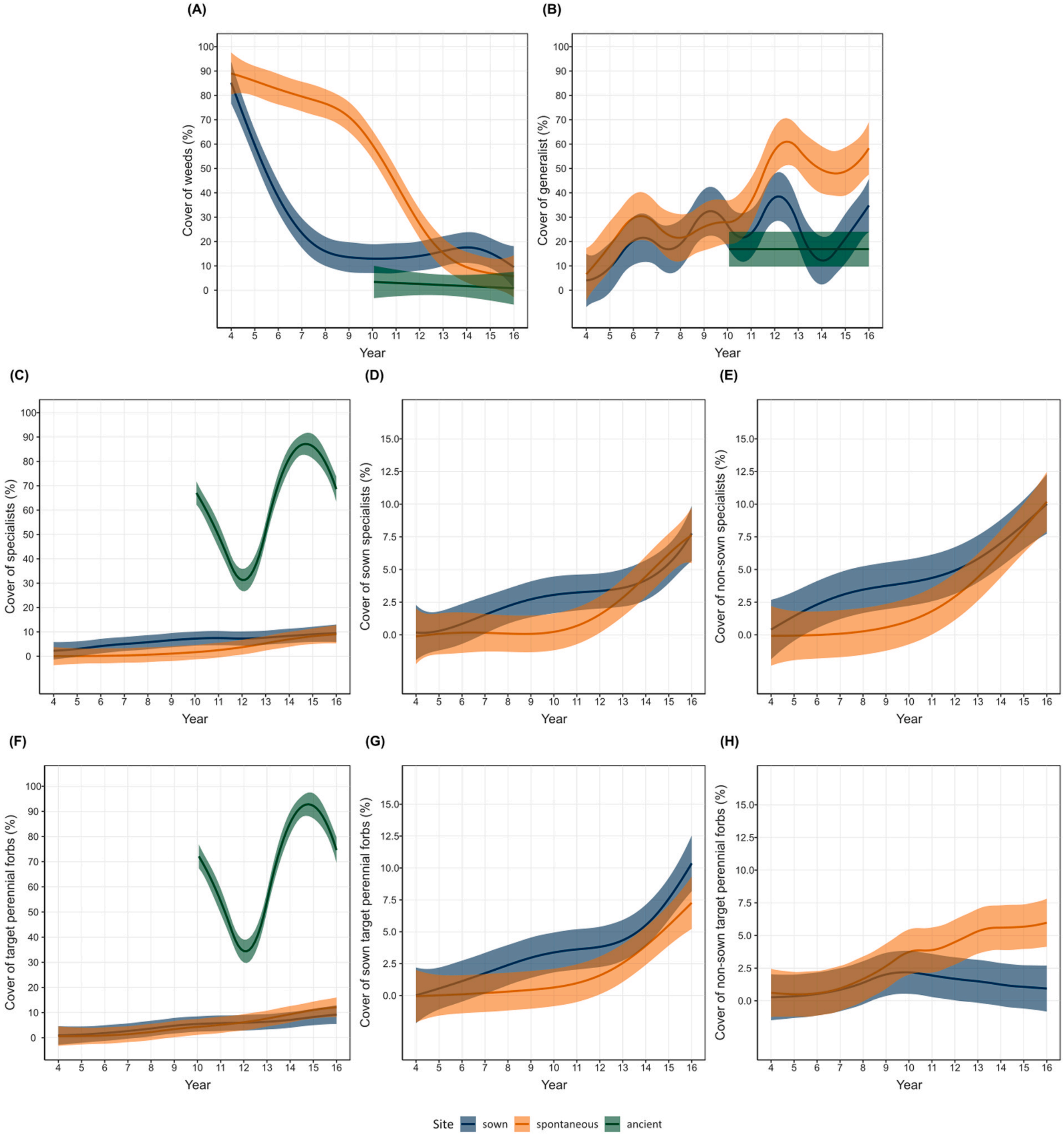

Fig. 2. Changes in the cover of weeds (A), generalists (B), specialists without *Festuca valesiaca* (C), sown specialists (D), non-sown specialists (E), target perennial forbs (F), sown target perennial forbs (G) and non-sown target perennial forbs (H) on 16 m^2 at the three study sites. Model lines were calculated using generalized additive mixed-effects models (GAMMs), where time was treated as a smooth term interacting with site, and plot ID included as a random effect. Year refers to years after abandonment. Shaded bands show the 95 % confidence interval.

spontaneous site, species number increased gradually at first but then declined from year 12 onward. In contrast, species richness in the ancient grassland was consistently higher than in both restored sites (GAMM main effect: spontaneous: $\beta = 8.23$, $SE = 1.48$, $p < 0.0001$; ancient: $\beta = 19.86$, $SE = 1.57$, $p < 0.0001$; adjusted $R^2 = 0.67$; see Table S1 for full model results).

There were no invasive herbaceous species in the ancient grassland, and only a few in the restored sites, where none reached high cover. Several woody invasive species (*Celtis occidentalis*, *Gleditsia triacanthos*, *Morus alba*, *Prunus cerasifera* and *Ulmus pumila*) occurred in the sown and the spontaneous sites, but their cover remained low due to regular vegetation management.

The sown site showed notable changes in species composition and cover. Between years 4 and 6, the dominant species changed from year to year. In year 4, two years after sowing, the most abundant species was *Cirsium arvense*, followed by *Bromus sterilis* in year 5. From year 6 after abandonment (four years after sowing) onwards, the sown grass, *Festuca valesiaca*, became the dominant species. Its cover increased steeply until peaking in year 8 (six years after sowing) at a mean cover of 66.2 %, and remained high thereafter with only small variation (Fig. 1B). The spontaneous site showed a delayed increase: early years were dominated first by *Cirsium arvense* (year 4) and *Bromus sterilis* (year 5–10), followed by *Alopecurus pratensis* (year 11 and 13) and *Trifolium arvense* (year 12) before *Festuca valesiaca* became dominant by year 14, stabilizing around 44 %. In contrast, *Festuca* cover in the ancient grassland was moderate, with substantial fluctuations. Despite this late, but rapid increase, *Festuca* cover was significantly higher throughout the study than in both the spontaneous site and the ancient grassland, where cover was moderate and highly fluctuating (GAMM main effect: spontaneous: $\beta = -36.02$, $SE = 4.35$, $p < 0.0001$; ancient: $\beta = -24.86$, $SE = 4.76$, $p < 0.0001$; adjusted $R^2 = 0.52$; see Table S2).

Altogether 11 of the 14 sown forb species occurred at least once, and all of them flowered and produced seeds. In the final year, eight were present in the sown grassland (for yearly frequencies, see Table S13) and five in the spontaneous site. Although their cover increased more in the sown site, these species remained relatively scarce in the restored sites, not exceeding 12 % on average (Fig. 1C) (GAMM main effect: spontaneous: $\beta = -1.60$, $SE = 0.93$, $p = 0.0871$; adjusted $R^2 = 0.33$; see Table S3).

Weed cover declined rapidly in the sown site, reaching small cumulative cover within just six years after sowing (by year 8). In comparison, in the spontaneous site, decline was slower until year 10, after which it dropped sharply and by year 14 approached the low levels observed in the ancient grassland (Fig. 2A; Table S4). Cover of generalist species increased in the early years but fluctuated strongly in both restored sites over time. In the spontaneous site, cover continued to rise from year 11 onward and, despite high variability, remained high through year 16. In the ancient grassland, generalist cover remained low throughout the study period (Fig. 2B; Table S5). Specialists had the highest species richness and cover in the ancient grassland, with consistently high but variable values. In contrast, the restored sites supported fewer species and lower cover (Fig. 2C) (GAMM main effect: spontaneous: $\beta = -3.22$, $SE = 1.57$, $p = 0.0416$; ancient: $\beta = 61.76$, $SE = 16.11$, $p = 0.0002$; adjusted $R^2 = 0.92$; see Table S6). In year 16, there were altogether 26 specialist species in the ancient grassland, compared to only ten in the sown site and nine in the spontaneous site. During the first two-thirds of the study, both sown and non-sown specialists reached higher cover in the sown site (Fig. 2DE; Table S7, S8). From year 12 onward, their cover in the spontaneous site rose steeply, surpassing the sown site between years 13–15. In the final study year, sown and non-sown specialists had only slightly higher average cover in the sown site (by 0.22 % and 0.18 %, respectively).

Despite considerable variation in abundance, the ancient grassland was dominated by perennial forbs, in both species richness and cover (Fig. 2F). Of the 118 recorded species, 55 were perennial forbs, which formed the most abundant group in the grassland across all

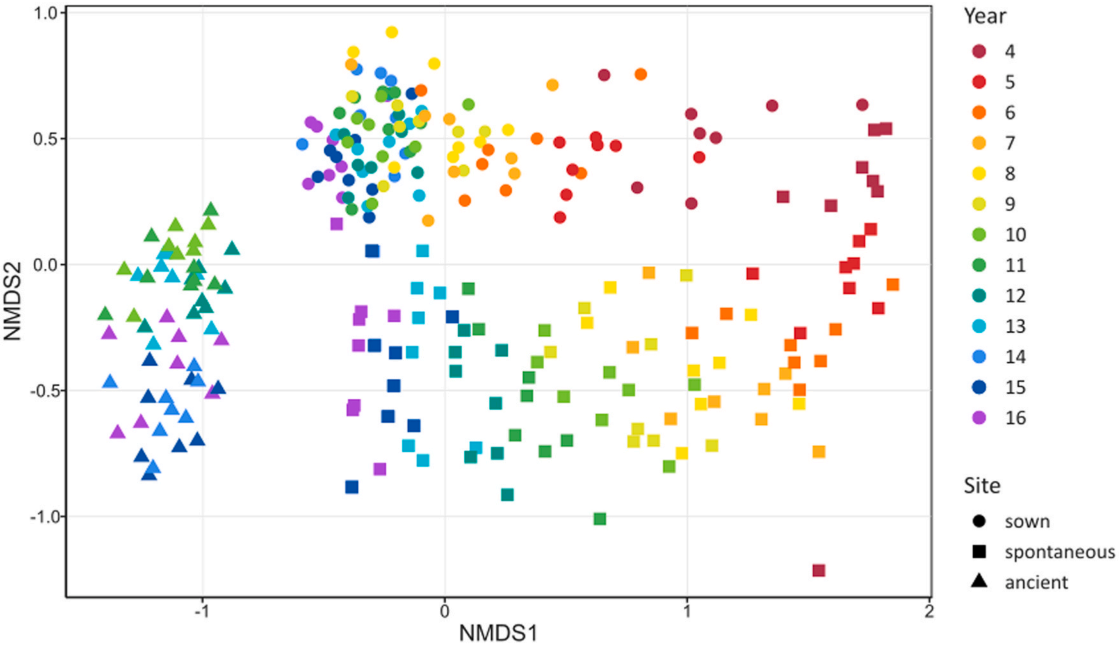

Fig. 3. NMDS ordination showing the differences in vegetation development of the restored sites over the thirteen study years. The ancient grassland was surveyed in only seven years. Year refers to years after abandonment. Stress: 0.170, solution converged after 30 iterations.

years. In contrast, only 38 among these target perennial forbs were recorded in the sown grassland and 35 in the spontaneous site, with their cover remaining substantially lower than in the ancient grassland. Nonetheless, cover of target perennial forbs increased steadily in the spontaneous site, exceeding the sown site by year 12 (see Table S9). Distinguishing between sown and non-sown target perennial forbs, cover of sown species was higher in the sown site throughout the study, but increased over time in both sites (Fig. 2G) (GAMM main effect: spontaneous: $\beta = -1.85$, SE = 0.85, $p = 0.0318$; adjusted $R^2 = 0.36$; see Table S10). Non-sown species expanded more strongly in the spontaneous site, reaching 11.9 times higher cover in the final year, whereas their cover declined in the sown site after year 10 (Fig. 2H) (GAMM main effect: spontaneous: $\beta = 1.98$, SE = 1.08, $p = 0.0690$; adjusted $R^2 = 0.28$; see Table S11).

Over the thirteen years, the vegetation of the two differently restored sites clearly progressed towards but still differed from the ancient grassland (Fig. 3).

Although the sown site started with a smaller successional distance from the ancient grassland, its compositional development slowed down markedly from year 8 (six years after sowing) onward and stagnated between years 11–14 (Fig. 4). In contrast, the spontaneous site recovered at a nearly constant rate throughout the study and even surpassed the sown site in successional distance after year 13 (see Table S12). From year 14 onward, both sites advanced at a similar pace of regeneration, with a slight deceleration in the spontaneous site and a modest renewed recovery in the sown site.

4. Discussion

4.1. Summary of key findings

Sowing the dominant grass of the reference grassland in the neighbouring abandoned field resulted in extremely high grass abundance, which persisted even more than a decade later. The sown grass successfully suppressed weeds within a few years, but in the longer term, it limited the establishment and expansion of several other target species. Notably, the sown vegetation initially developed promisingly towards the ancient grassland, but after a transition point around year six, regeneration substantially slowed in the subsequent years and showed only small further progress within this timescale. In contrast, spontaneous succession, despite starting further from the target, achieved more consistent progress with higher establishment of non-sown target perennial forbs. Even thirteen years after sowing, the sown grassland differed from the ancient grassland in several aspects, mainly in species richness, species composition, and relative abundances. The differences between short- and long-term outcomes in the sown grassland highlight the importance of time series studies to evaluate restoration methods beyond short-term results (Herrick et al., 2006).

4.2. Sown grass cover and its effects on species establishment and weed cover

In the first two study years, two species typical of newly abandoned croplands (*Cirsium arvense* and *Bromus sterilis*) were the most abundant in the sown field. Then, four years after being sown, *Festuca valesiaca* became dominant. Although the grass was sown two years after abandonment, this result is consistent with previous studies, which reported that related *Festuca* species sown right after

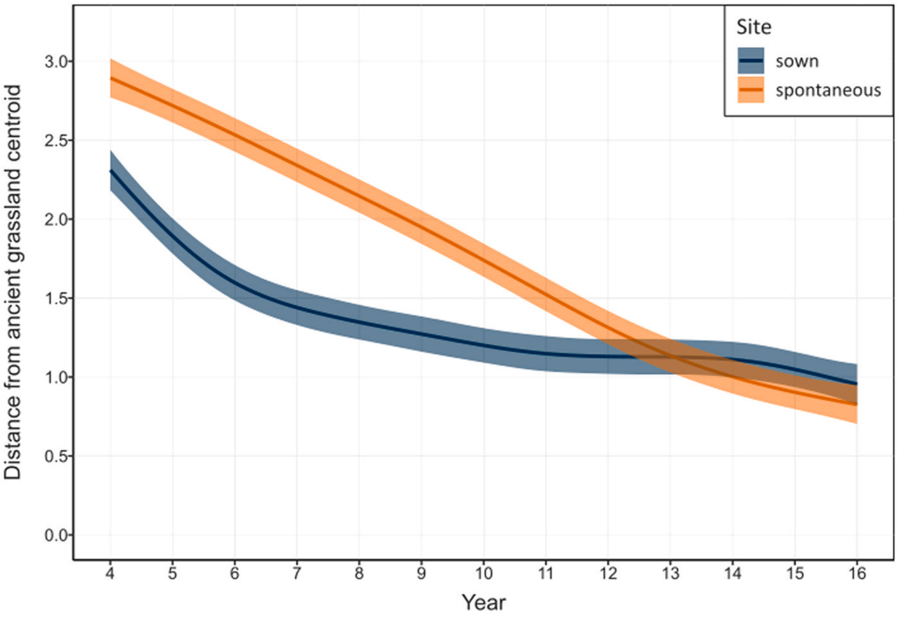

Fig. 4. Change in successional distance of sown and spontaneous sites from the seven-year mean centroid of the ancient grassland. Model lines were calculated using generalized additive mixed-effects models (GAMMs), where time was treated as a smooth term interacting with site, and plot ID included as a random effect. Year refers to years after abandonment. Shaded bands show the 95 % confidence interval.

abandonment became dominant by already the fourth year (Török et al., 2010; Vida et al., 2010). This suggests that sowing timing within the first few years after abandonment may not substantially affect the development of sown grass cover, especially on well-prepared, open soil surface. Subsequently, the abundance of the sown grass peaked six years after sowing and stabilized at an extremely high level thereafter.

Although most of the 14 sown forb species established in our study, their cumulative cover increased slowly and remained small more than a decade, suggesting that the sown competitive grass may hinder the expansion of sown forbs for a longer period than previously documented (McCain et al., 2010; Meissen et al., 2020). In contrast, non-sown target perennial forbs achieved substantially higher cover in the spontaneous site than in the sown site, and both sown and non-sown specialists initially attained higher cover in the sown site. Over time, however, specialist cover increased at the spontaneous site and in some years even exceeded levels observed at the sown site, suggesting that initial seeding advantages decreased in relation to the increasing abundance of *F. valesiaca*. Together, these patterns indicate competitive suppression by the sown grass species which ultimately constrained the long-term expansion of target perennial forbs and specialists in the sown site. Similarly, Grman et al. (2021) found that in the tallgrass prairies of the U.S., sown native (particularly C_4) grasses, suppressed non-target non-sown species, including weeds and invasives, but this benefit does not outweigh the negative impact on the establishment of forbs.

The extreme *F. valesiaca* abundance observed from year 4 was likely rather due to the high seeding density of the grass compared to forbs, than to the order of species arrival during restoration. Grasses often develop strong priority effect opposed to other species soon after the seedings, especially to forbs, when sown earlier than other species (Delory et al., 2019; Weidlich et al., 2021; Wilsey, 2010). In this experiment, however, although the grass was sown prior to forbs, in the early years, when priority effect can establish, it grew slowly initially. Even with three years after being sown, its cover was still under 25 %, thus other sown species did not face considerable grass suppression in this period.

In the spontaneously recovering field, *F. valesiaca* became dominant 14 years after abandonment, eight years later than in the sown site. This is consistent with Molnár and Botta-Dukát (1998), who found that in secondary loess meadow steppes of the region, the dominant grass of the reference sites appeared in old-fields after four years on average and became dominant by year 25. Together, the comparable or stronger expansion of other target species in the spontaneous site and the slower colonization of the dominant grass indicate that delayed grass dominance may allow a longer period for spontaneous establishment. However, it is also important to note that even if species-rich donor sites are nearby, spontaneous succession can take more time than active restoration and may follow unpredictable trajectories (Foster et al., 2007; Prach et al., 2007). In our study, the spontaneous site progressed from weed-dominated to generalist-dominated stage before the expansion of *F. valesiaca* began. As the cover of generalists and, in later years, the cover of *F. valesiaca* began to increase, weeds declined rapidly, eventually approaching the natural level observed in the ancient grassland.

During this trajectory, vegetation progressed steadily toward the target state without the marked slowdown observed in the sown grassland. However, from approximately year 14 onward, the rate of spontaneous regeneration also began to slow as *F. valesiaca* cover increased. It is important to note that the reference ancient grassland was not static during the study period. A substantial decline in *F. valesiaca* cover in the ancient grassland between year 13 and 15 shifted its compositional centroid somewhat closer to the spontaneous site, potentially contributing to the observed convergence between the two sites. Moreover, *F. valesiaca* appears to have reached a plateau in the spontaneous site from year 14 to 15, unlike in the sown site where it remained consistently dominant, suggesting potentially different long-term dynamics between the actively and passively restored old-fields. To test whether these patterns persist, further monitoring is necessary.

4.3. Suppression mechanisms of competitive grasses at high abundance

In the natural dry grasslands of the region, the dominance of grass species is primarily driven by the prevailing climatic conditions, as well as by the competition with stress-tolerant perennial forbs, which are naturally abundant in steppic grasslands (Illyés et al., 2007a). These interactions regulate grass abundance and enhance the overall complexity of the ecosystem. As a result of these processes, the cover of dominant *Festuca* species in the region can fluctuate greatly from year to year in response to climatic variations (Bartha et al., 2022; Orbán et al., 2023), as was the case at our reference site. In contrast to ancient grasslands, long-lived forbs were either missing from or were scarce in the sown site, allowing the competitive grass to become excessively abundant. Tussock grasses, such as *Festuca* species, gain their strong competitive ability primarily through dense belowground biomass and litter accumulation, inhibiting germination and establishment of other species (Ruprecht and Szabó, 2012; Titlyanova et al., 1999), which further reinforces the dominance of grasses. Presumably, with sufficient establishment of target perennial forbs, may reduce grass cover and advance recovery (Sluis, 2020). However, restoring target species cover is often the most challenging aspect of recovery due to weak dispersal abilities of climax species (Baur, 2014; Öster et al., 2009; Pywell et al., 2003).

High grass cover has been widely recognised as a barrier to the establishment and expansion of forbs and other target species (e.g., Dickson and Busby, 2009; Tölgyesi et al., 2019). In response to these strong suppressive effects, some restoration studies have applied small-scale disturbance interventions that create establishment gaps within dense grass swards, followed by the reseeding of diverse forb mixtures to temporarily reduce competition and provide microsites for germination (e.g., Valkó et al., 2016b).

4.4. Importance of long-term time series in ecological studies

Finishing vegetation sampling earlier or missing years could have led to different conclusions. Thus, we underline the benefits of long-term studies and annual monitoring in analysing dynamically changing ecological processes, such as succession and habitat restorations (e.g., Stadler et al., 2025; 36-year annual study). We are aware that the time scale of complete regeneration is much greater than what was surveyed in this study (cf., Prach et al., 2015; Nerlekar and Veldman, 2020). Still, longer monitoring periods might expand our understanding on the effects of treatments, which could contribute to more successful future grassland restoration, and thus, to the preservation of endangered grassland types.

4.5. Implications for practice

The presented results support previous recommendations for low seeding rates for grasses, which promotes restoration efforts more effectively (Barr et al., 2017; Meissen et al., 2020; Tischew et al., 2010), especially in the case of diverse and forb-rich grassland types (Grman et al., 2021), such as North American tallgrass prairies and European meadow steppe grasslands (Dengler et al., 2014; Polley et al., 2007). If grasses are sown at lower densities, introduced later during succession, or even not sown at all, the high cover of competitive grasses could be potentially avoided for a longer period, which could be thus open to dispersal and establishment of target species (Dickson and Busby, 2009; Kindscher and Faser, 2000; Tölgyesi et al., 2019). Where species-rich donor sites are nearby, our results support the use of passive restoration over high-density grass seeding, potentially avoiding prolonged competitive suppression while achieving similar or better outcomes at lower costs. This adds to the growing evidence that spontaneous succession can be effective across a broader range of conditions than commonly assumed (Prach et al., 2025). However, when the risk of alien plant invasion is high, sowing native competitive species in high densities can be an effective tool in reducing invasive species during restoration (Gornish and dos Santos, 2016).

5. Conclusions

Sowing competitive grass species is a common practice in grassland restoration, aimed at promoting succession. However, this treatment, even when supplemented with forb seed mixtures, may hinder key ecological processes. While the early dominance of the sown grass can be considered a short-term success compared to spontaneous succession, later it constrains vegetation development and the expansion of non-sown target species. This state sets in due to the extremely high abundance of the sown grass, which slows down rather than accelerating regeneration trajectories. Thus, despite its economic appeal, it seems that the widespread use of this method can lead to unintended negative consequences, hampering long-term restoration efforts.

CRediT authorship contribution statement

András István Csathó: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Sándor Bartha:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Gábor Szabó:** Writing – review & editing, Investigation. **Sándor Csete:** Writing – review & editing, Investigation. **Csaba Tölgyesi:** Writing – review & editing, Supervision, Methodology. **Zita Zimmermann:** Writing – review & editing, Investigation. **Csaba Molnár:** Writing – review & editing, Investigation. **Zsófia Eszter Guller:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Dragica Purger:** Writing – review & editing, Investigation. **Judit Házi:** Writing – review & editing, Investigation.

Ethics statement

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04110.

Data Availability

Data will be made available on request.

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