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The long-term effect of initial restoration intervention, landscape composition, and time on the progress of Pannonic sand grassland restoration

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Abstract

To help upscale ecological restoration of degraded lands, landscape factors and longer time scales should be considered when assessing restoration efforts. We evaluated the impact of initial restoration intervention, landscape composition, and elapsed time since the restoration began on the long-term progress of Pannonic sand grassland restoration. Treatments (seeding, mowing, and carbon amendment) were implemented for 6–7 years and monitoring lasted up to 23 years after the first treatment applications in eight experimental blocks belonging to three field experiments. The abundance of target/neophyte species, and distance from primary grasslands and plantations (as major source of target/neophyte species) were estimated in 500 m landscape buffers around each block to characterize landscape composition. Restoration progress was calculated as the difference between the relative cover of target/neophyte species in treatment and control plots. Restoration intervention and neophyte abundance in the landscape had a significant effect on the restoration progress, but time did not. Seeding had the highest positive effect on target species and also prevented invasion by neophyte species. Higher abundance of neophytes in the landscape and the proximity to plantations increased the cover of neophytes in treatment plots. We conclude that restoration interventions may have a greater impact on restoration progress in the longer term than landscape factors or elapsed time. Seeding proved to be the best method in restoring sand grasslands by both favoring target species and controlling invasion. From the landscape factors, the abundance of neophyte species and distance to plantations should be considered when prioritizing areas and efforts for restoration.

Keywords Long-term monitoring · Seeding · Mowing · Carbon amendment · Invasion · Vegetation recovery

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Introduction

To counteract land degradation, besides the conservation of remaining natural ecosystems, ecological restoration of degraded lands is considered crucial (Strassburg et al. 2020). Many initiatives to restore degraded lands have been launched around the word (e.g., Bohn Challenge, United Nations Decade on Ecosystem Restoration). To achieve these global targets, larger landscapes need to be restored and ecological restoration needs to be enhanced, which includes taking into account landscape features when prioritizing restoration actions in the world, and generally considering larger spatial and temporal scales in restoration (Waldén et al. 2017; Gann et al. 2019; Strassburg et al. 2020).

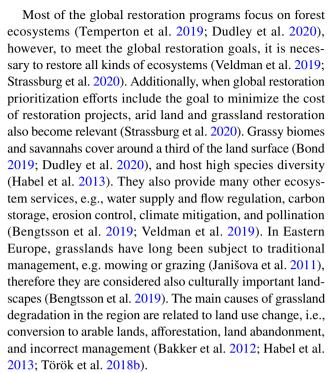
Although the need for landscape-scale restoration is evident by now and the importance of landscape factors in the restoration outcome is widely recognized (Holl et al.



2003; Helsen et al. 2013; Prach et al. 2015), the number of publications on terrestrial restoration studies that consider restoration sites as part of a larger surrounding landscape is still limited (Holl et al. 2003; Brudvig 2011; Waldén et al. 2017). This can be explained by the difficulty of investigating landscape-level patterns and processes, the large spatial and temporal scales that require non-traditional statistics, and also the poor documentation and lack of monitoring after restoration projects (Holl et al. 2003).

When the surrounding landscape is taken into account, patch area, perimeter, and proximity to propagules sources are the most common landscape factors to be quantified (e.g. Holl and Crone 2004; Alsfeld et al. 2010; Helsen et al. 2013; Guido et al. 2016). The species present in a landscape is another important factor that affects the restoration outcome (Zobel et al. 1998; Waldén et al. 2017), but it is not often evaluated due to laborious data collection (Prach et al. 2015). The dispersal from the surrounding landscape can influence the restoration process both positively and negatively, the former factor comprises the colonization by target species (Prach et al. 2015), the latter can be due to the lack of natural fragments in the landscape (Waldén et al. 2017; Török et al. 2018a) coupled with the low dispersal ability of species (Deák et al. 2018) and also to the spread of invasive alien species (Holl and Aide 2011; Vilà and Ibáñez 2011; Guido et al. 2016). Invasive species can transform community structure and function, and ecosystem processes (Vilà and Ibáñez 2011), harming the development of native vegetation (Von Holle et al. 2013; Yelenik and D'Antonio 2013), consequently threatening ecosystem integrity (Corbin and D'Antonio 2012).

Several authors highlight the importance of considering also the time scale in restoration projects and demonstrate that there is a positive relationship between the time elapsed since the start of restoration and the richness of target species of experimental sites (Prach et al. 2015; Waldén et al. 2017). A longer time scale in monitoring would be essential to better understand the restoration process (Reis et al. 2021). Several years may be necessary before the management impacts can be visible in a restored system, and early success might be proven false in the longer term (Herrick et al. 2006). The long-term monitoring allows us to evaluate the restoration success properly and to correct restoration trajectory through adaptive management, if necessary (Zahawi et al. 2015). Previously, the monitoring of most restoration projects lasted less than 5 years (Ruiz-Jaen and Aide 2005), more recently, the timescale of monitoring has generally increased (Wortley et al. 2013), but it depends on the restored ecosystem types and the studied organisms, with the longest time span found for forests (11 years) and 6.5 year on average for plants in general (Kollmann et al. 2016), but studies exceeding 20 years is still scarce.



It is acknowledged that, in some cases, grassland restoration of abandoned lands can rely on spontaneous recovery (Török et al. 2011; Valkó et al. 2016). Studies on the natural regeneration after land abandonment in Eastern Europe revealed that vegetation composition can approach the historical state in terms of generalist species already after one decade of abandonment (Csecserits et al. 2011; Valkó et al. 2016). However, some specialist species might not be able to establish and invasion often occurs hampering the succession process, therefore (Csecserits et al. 2011), calling for active restoration interventions (Török et al. 2011). One of the main constraints in grassland restoration is dispersal limitation (Halassy et al. 2016; Török et al. 2018a) that can be overcome by the introduction of seeds of target species (Kiehl et al. 2010; Kövendi-Jakó et al. 2019). Other limitations lie in the local abiotic conditions. For example, carbon addition or top-soil removal can be applied to reduce the availability of nitrogen to plants—a major limit in old-field restoration (Perry et al. 2010; Török et al. 2014). The third group of limiting factors is biotic, i.e. competitive relationships are often managed by mowing to control competitive dominants and to increase species diversity through the creation of establishment gaps (Valkó et al. 2012).

Standards for evaluating restoration success is rare, but there are some generalities that can be followed (Suding 2011). For example, structure, diversity and composition, and ecological functions (Ruiz-Jaen and Aide 2005; Wortley et al. 2013) are the most common ecological criterions in restoration ecology, since the overall goal is to restore the main features of an ecosystem that has been degraded, damaged, or destroyed (Benayas et al. 2009). Vegetation



development is either assessed based on trajectory analysis (Suding 2011) or the direct comparison of certain indicators between treatment and a no action baseline or the selected reference (Benayas et al. 2009). Indicators for biodiversity generally include the abundance, species richness, diversity, growth, or biomass of organisms present (Benayas et al. 2009). In case of grasslands, the presence, frequency and amount of specialist species are good indicators for restoration progress (Prach et al. 2015; Waldén et al. 2017), whereas the presence of invasive species can harm the development of native vegetation and threaten restoration aims (Yelenik and D'Antonio 2013; Corbin and D'Antonio 2012).

The present study aimed to evaluate the impact of the initial restoration intervention, the landscape composition, and the elapsed time since restoration has started on the long-term progress of Pannonic sand grasslands restoration. Restoration treatments were implemented for 6-7 years and monitoring lasted up to 23 years after the first treatment applications. Our main question was: What is the importance of restoration intervention, the landscape composition, and elapsed time on the restoration progress in terms of target species and invasive species? More specific questions related to the three factors were: (i) which of the studied restoration treatments (seeding, carbon amendment, mowing) was the most effective in restoring Pannonic sand grasslands? (ii) What is the impact of the abundance of target/neophyte species in the landscape and the distance from nearby propagule sources on the restoration progress? (iii) How does the time elapsed since restoration began affect the restoration progress?

Methods

Study area

The study was carried out in Fülöpháza (46° 53′ N, 19° 24′ E), in Bugac (46° 39′ 53.1″ N, 19° 36′ 11.7″ E) and Izsák (46° 45′ 23.2″ N, 19° 19′ 53.3″ E), KIskunság National Park, Central Hungary, Pannonian biogeographic region, Europe (Fig. 1). The climate of the region is continental with a sub-Mediterranean influence, characterized by warm and dry summers. The mean annual temperature is 10.5 °C and the mean annual precipitation is varying from 520 to 550 mm (Kovács-Láng et al. 2008). The typical soil is the Calcaric Arenosol with more than 90% of sand and less than 1% humus content (Lellei-Kovács et al. 2011).

The region presents a lowland landscape with inland scattered sand dunes. The potential natural vegetation is open forest steppe composed of open oak forests and juniper–poplar woodland sparsely scattered in a sand grassland matrix (Erdős et al. 2018). These sand grasslands present high endemism and therefore are considered as priority habitats

at the EU level (Pannonic sand steppes 6260) (EC 2013). From the various types of Pannonic sand steppes, open sand grasslands occupy the driest locations, and as such they are considered more of edaphic origin rather than a result of human management as general in Europe (Šefferová Stanová et al. 2008). However, their extent became much larger in history due to extensive grazing throughout the region, and this management can be important to sustain a desired conservation status in certain areas (Török et a. 2018b). Open sand grasslands are mainly dominated by perennial tussock grasses, such as *Festuca vaginata* and *Stipa borysthenica* (nomenclature follows Király 2009). The average vascular plant cover is around 40–70% with bare soil and cryptogams covering the remaining surface (Erdős et al. 2018).

Currently, 98% of the Pannonic sand steppes are already degraded (Biró et al. 2018). The main causes of degradation are land use change, i.e., conversion to arable lands, afforestation, land abandonment and incorrect management (Török et al. 2018b). The rate of land abandonment has increased with the fall of the socialist regime in the early 1990s (Mihók et al. 2017), and cessation of agricultural practices provides opportunity for grassland restoration and conservation (Valkó et al. 2016). The current landscape is composed of agricultural fields, old-fields, forest plantations, and fragments of semi-natural grasslands and semi-natural forests.

Description of the experiments

For this purpose, we studied eight experimental blocks belonging to three field experiments that aimed to restore Pannonic sand grasslands on the most common degraded areas in the studied region (old-fields and plantations). In the first experiment (Block 1-3), mowing was applied together with hay removal twice a year between 1995 and 2001 to control weeds and shrub encroachment where black locust (Robinia pseudoacacia) plantations were eliminated. In the second experiment, we applied carbon amendment (C-amendment) in the form of sucrose and sawdust, with different rates (further details see: Török et al. 2014), to induce microbial nitrogen immobilization on three abandoned agricultural fields (Block 4-6) between 1998 and 2003. In the third experiment, three treatments were applied (mowing, C-amendment, seeding) alone or in combinations on two abandoned agricultural fields (Block 7 and 8) differing in the time of abandonment. Seeding was carried out by hand in September 2002 and contained a mixture with five species including: two dominant grass species, F. vaginata (1.55 g/m^2) and S. borysthenica (1.05 g/m^2) , a subordinate grass, Koeleria glauca (1.00 g/m²), plus two forb species Dianthus serotinus and Euphorbia seguieriana (together: 0.20 g/m²). Mowing plus hay removal was applied twice in 2003 and once a year in September from 2004 until 2008.



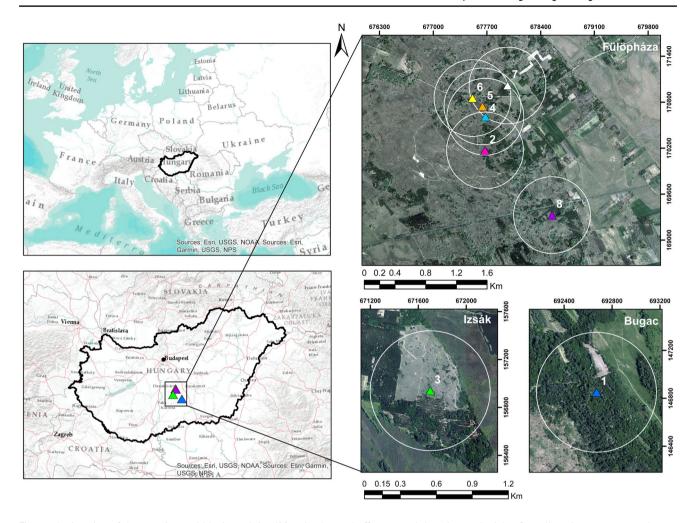


Fig. 1 The location of the experimental blocks and the 500 m landscape buffers around them in **a** Fülöpháza, **b** Izsák and **c** Bugac, central Hungary, Europe. Experiment 1: 1–3. Experiment 2: 4–6. Experiment 3: 7–8. Datum: D-hungarian-1972, Projected coordinate system: EOV-1972

C-amendment was applied in the form of sucrose addition at a rate of 45 g/m² four times per year from 2003 to 2008. Only the main treatments (no combinations) were included

in the present analysis. Table 1 demonstrates a summary of the three experiments: the number of blocks involved, the degradation status before restoration, pre-treatment activities

Table 1 Summary of studied experiments

Exp	Block number	Size	Degradation status	Pre-treatment	Restoration treatment		Blocks		Monitoring
					When?	What?	Design	Monitoring	years
1	1–3	30 × 40 m	Plantation of Robinia pseu- doacaia	Clear cut+chemi- cal applica- tion	1995–2001	Mowing + hay removal	6 Mowed 6 Control	$n = 2*18/\text{site}$ $(2 \times 2 \text{ m})$	1995–1999 yearly, six times 2002–2017
2	4–6	30 × 40 m	Abandoned crop fields (1991–1995)	-	1998–2003	Carbon amendment (sucrose + saw- dust)	6 Carbon 6 Control	$n = 2*18/\text{site}$ $(2 \times 2 \text{ m})$	1998–2006 yearly, 2008, 2010, 2018
3	7–8	20 × 20 m	Abandoned crop fields (1987, 1999)	Plough- ing + harrow- ing	2002–2008	Seeding, mow- ing, carbon amendment and combinations	8 Control 8 Seeded 8 Mowed 8 Carbon	$n = 8*8/\text{site}$ $(1 \times 1 \text{ m})$	2003–2008 yearly, 2019



if relevant, the types and timing of treatments applied, design and monitoring. For further details about the design of each experiment see the supplement material (Figs. S1, S2 and S3) and Halassy et al. (2016, 2019, 2021) and Reis et al. (2021).

Assessment of long-term vegetation development

The vegetation monitoring protocol was similar for all blocks, but the size and number of plots varied slightly (Table 1). We estimated the cover of each vascular plant species in permanent plots twice a year (in June and August) from the start till the end of experimental manipulations, and later re-sampled the blocks at less frequent intervals. Of the two estimations within year, we used the maximum estimated cover value for each species per plot per year for further analysis.

We classified the species according to their role in restoration as desirable (target), undesirable (neophyte species that represent current or future threat of invasion) and neutral species (non-target species, e.g. common weeds), not included in the present analysis. The selection of target species was based on Csecserits et al.'s (2011) classification of characteristic species of sand grasslands in the Kiskunság region. Neophyte species were identified according to Balogh et al. (2004). We calculated the relative cover (%) of target and neophyte species for all plots and treatments for each sampling year.

Assessment of landscape variables

We set a buffer of 500 m surrounding the center of each experimental block to consider as landscape with possible impact on the restoration progress. The selection of 0.5 km radius is based on the propagule pressure being the strongest within a few hundred meters from the source (Rouget and Richardson 2003). We created a habitat map for all the buffers based on previous vegetation maps for the locations updated according to recent aerial photos (2019) and field validation. We classified the vegetation into seven broad habitat categories following Csecserits et al. (2011): agricultural fields, secondary grasslands, tree plantations, semi-natural grasslands, semi-natural forest, wetlands and settlements. We calculated the area (ha and %) of all habitat categories per buffer (Fig. S4) with ArcGIS 10.5 (ESRI 2016).

To estimate the abundance of target and neophyte species in the landscape, we combined the GIS analyses above mentioned with field sampling. We estimated the percentage cover of target and neophyte species in six randomly allocated samples $(2 \times 2 \text{ m})$ in each habitat category per buffer in the field, except for wetlands and settlement. In case the buffers were overlapping (Fig. 1), we streamlined the sample collection resulting in 14 samples per habitat category

for the aggregated buffer. The field work was carried out in the summer of 2019 and 2020. Finally, to obtain a proxy of the abundance of target and neophyte species per buffer, we multiplied the average cover per indicator per habitat by the area of the given habitat (ha) and summed it for all habitats within the 500 buffer (hereafter called as weighted abundance, used as a proxy for propagule availability) (Fig. S5).

We also calculated the distance of the experimental blocks from semi-natural grasslands, the main source of target species and from tree plantations, the main source of invasion according to Csecserits et al. (2016) using the software ArcGIS 10.5 (ESRI 2016).

Data analysis

Statistical analyses were performed using R v 3.6.1 (R Core Team 2019). Two separate linear mixed effects models (LME) were constructed to investigate the effect of restoration intervention, landscape variables and time on the restoration progress using the package "lme4" (Bates et al. 2015). Restoration progress was analyzed based on a metaanalysis approach (Gómez-Aparicio et al. 2004), using the effect sizes of target and neophyte species as response variables in the models. The effect size for target species was calculated as the relative cover in treatment plots minus the relative cover in control plots, whereas the effect size for neophyte species was calculated as the relative cover in control plots minus the relative cover in treatment plots to obtain positive values for better restoration progress. The effect size and variances of target and neophyte species were calculated by Hedges' g (i.e. unbiased standardized mean difference between treatment and control) (Hedges and Olkin 1985), based on the mean, standard deviation and sample size (n)of the relative cover of target species and neophyte species for each block per monitoring year. The calculations were performed using "metafor" package (Viechtbauer 2010) in R v 3.6.1 (R Core Team 2019).

Time, restoration intervention and landscape variables were considered as fixed explanatory variables. For comparability of data, we considered the time as the number of years (from 1 up to 23) passed since the start of treatment applications. Time and restoration intervention were categorical variables including 15 levels for time (1–9, 11, 13, 15, 17, 21, 23 years passed since the first treatment) and three levels for restoration intervention (seeding, mowing, C-amendment; combinations, if any, were excluded). Landscape variables were the following: (1) the weighted abundance of target species and (2) the weighted abundance of neophytes, (3) the distance to the nearest semi-natural grassland and (4) the distance to the nearest plantation. Landscape variables were considered continuous. The monitoring year (1995–2019) and plot identity nested within block were



considered random variables to incorporate weather and geographic dependencies.

Multicollinearity between fixed variables was measured by variance inflation factor (VIF) from "car" package (Fox and Weisberg 2019). If VIF value was above 5.0 (Hair et al. 2010) the predictors were considered correlated, therefore, the weighted abundance of target and neophyte species in the landscape were not included in the same model. The model used for neophyte species included the elapsed time, the treatment, the weighted abundance of neophyte species in the landscape and the distance from plantations as fixed factors. In case of target species, we have built a parallel model to help the comparison between the two indicators that included the time, the treatment, the weighted abundance of target species in the landscape and the distance from semi-natural grasslands as fixed factors. Normality and variance homogeneity of residuals was checked by "Dharma" package (Hartig 2020). The significance of fixed factors was based on Type II Wald chi-square tests. Finally, for post hoc comparison of significant (p < 0.05) fixed categorical variables Tukey HSD test was applied, using the "multcomp" package (Hothorn et al. 2008).

Table 2 Results of Type II Wald chi-square test of fixed effects from linear mixed effects models (LME) on the effect size of target species and neophyte species

Response variable	Explanatory variable	Chisq	df	p-value
Effect size of target species	Time	9.8326	14	0.7743
	Restoration intervention	25.3812	2	0.0001
	Weighted abundance of target species	0.4573	1	0.4989
	Distance from semi-natural grasslands	1.6089	1	0.2046
Effect size of neophyte species	Time	14.0346	14	0.4471
	Restoration intervention	11.7992	2	0.0027
	Weighted abundance of neophyte species	4.6372	1	0.0313
	Distance from plantations	3.7442	1	0.053

Significant results (p < 0.05) are shown in bold

Fig. 2 The impact of mowing, C-amendment and seeding on the effect size of target species based on Tukey HSD multiple comparison post hoc test. Positive values of effect size indicate higher cover of target species in treatment than in control, i.e. a better progress toward successful restoration, while negative values indicate lower cover of target species in treatment than in control. Significant differences between treatments are indicated by lower case letters

effect size of target species b comparison of target species mowing C-amendment seeding

Results

Effect of restoration intervention, landscape variables and time on the effect size of target species

Restoration intervention was the only explanatory variable which had a significant impact on the restoration progress based on the effect size of target species (Table 2). All the restoration treatments affected positively the relative cover of target species compared to control. Based on the multiple comparison test, seeding resulted in significantly higher effect size of target species compared to the other treatments (seeding—mowing: Z=4.304, p-value < 0.001; seeding—C-amendment; Z=4.950, p-value < 0.001) (Fig. 2, Table S1).

None of the studied landscape factors had a significant effect on the effect size of target species (Table 2, Table S2).



Time did not have any significant effect on the effect size of target species (Table 2) (for the estimated coefficients and error range of the explanatory variables see Table S2).

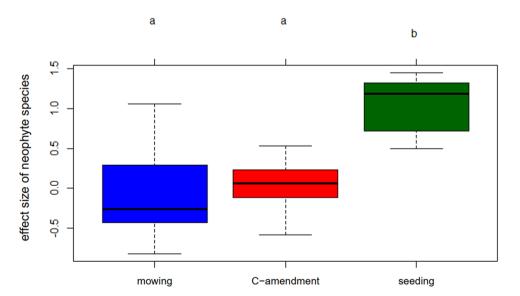
Time did not present a significant effect on the effect size of neophyte species (Table 2) (for the estimated coefficients and error range of the explanatory variables see Table S2).

Effect of restoration intervention, landscape variables and time on the effect size of neophyte species

Restoration intervention had a significant impact also on the effect size of neophyte species (Table 2). According to the multiple comparison, seeding significantly accelerated the restoration progress via decreasing the cover of neophyte species compared to the other treatments (seeding—mowing: Z=2.686, p-value = 0.0196; seeding—C-amendment; Z=3.407, p-value = 0.0018) (Fig. 3; Table S1). C-amendment and mowing were not statistically different, resulting in mean effect sizes of neophyte species around zero. While C-amendment presented a slightly positive mean effect size and a lower range of values, mean effect size in case of mowing was negative with a high range of variation between values.

The weighted abundance of neophyte species also had a significant impact on the effect size of neophyte species (Table 2). The higher the presence of neophyte species in the landscape, the smaller the effect size of neophyte species, indicating a higher relative cover of neophyte species in treatment plots compared to control plots (Table S2). Even though the distance from plantations did not present a significant impact at the p < 0.05 level (Table 2), there was a positive relationship between distance and the effect size of neophyte species (Table S2). A higher effect size, so a lower relative cover of neophyte species in treatment plots compared to control plots was observed further away from plantations.

Fig. 3 The impact of mowing, C-amendment and seeding on the effect size of neophyte species based on Tukey HSD multiple comparison post hoc test. Positive values of effect size indicate lower cover of neophyte species in treatment than in control, i.e. a better progress toward successful restoration, while negative values indicate higher cover of neophyte species in treatment than in control. Significant differences between treatments are indicated by lower case letters



Discussion

Long-term impact of restoration intervention on the restoration progress

Initial restoration intervention had significant long-term impact on restoration progress both in terms of target and neophyte species. Long-term monitoring revealed that from the three treatments, low rate seeding of a low diversity seed mixture (dominant grasses and subordinate species) was the most effective for restoring degraded areas of Pannonic sand grasslands. Seeding resulted in the highest increase in the relative cover of target species and the highest decrease in the relative cover of neophyte species. Seeding mixtures of target species is a widely used restoration method in grasslands restoration (Török et al. 2011), and it is highly recommended where dispersal limitation is an important constrain (Halassy et al. 2016; Török et al. 2018a). In our study area, the absence of seeds of specialist species and the high presence of undesired species in the seed bank have been reported (Halassy 2004). However, the spatial dispersal limitation is less evident, since there are still semi-natural grasslands remnants in the surroundings (Biró et al. 2013) that are excellent sources of propagules, and secondary grasslands that can also provide sources for regeneration depending on their age since abandonment (20–40 years) (Csecserits et al. 2011, 2016). Our results confirmed that active introduction of target species was necessary to facilitate the dispersal of target species and accelerate the restoration process of degraded



lands. Seed introduction can also be an alternative to suppress invasive species development (Bucharova and Krahulec 2020). Our results highlighted the importance of early seeding in halting the spread of neophyte species in the long term.

Mowing and C-amendment had a similar, somewhat lower impact on the restoration progress based on the relative cover of target and neophyte species. Mowing is a widely used management for maintaining the diversity of natural grasslands, frequently used also to speed up the restoration of degraded lands in terms of species diversity (Kelemen et al. 2014). Mowing can modify biotic interactions, i.e. competition among species, but there are some cases where it can also create conditions that hamper the restoration process (Török et al. 2011). Our previous findings in the same area, showed that initial mowing increased the cover of target species, however it was insufficient to control neophyte species development on the long run (Reis et al. 2021). Mowing is a disturbance that opens up the sward creating establishment gaps, and invasive species might be the first to colonize after disturbance if present in the landscape (Holl and Aide 2011). The presence of neophytes can prevent or slow down the colonization of native species (Von Holle et al. 2013; Yelenik and D'Antonio 2013; Reis et al. 2021). Therefore, if there is a threat of possible invasion, mowing should be applied in combination with other restoration techniques, especially seeding to accelerate the recovery of target species. Grazing can be applied as an alternative to mowing since it is considered a better management for nature conservation purposes (Tälle et al. 2016). Grazing can facilitate the dispersal and establishment of target species in longer distances (Labadessa et al. 2020), however the gaps opened by, e.g. animal trampling, can also favor invasion.

C-amendment is generally applied to reduce the availability of nitrogen in the soil, an existing abiotic constraint to natural vegetation recovery of low productive grasslands on abandoned arable fields that represent high availability of soil nutrients (Török et al. 2014), and consequently to manipulate competitive hierarchies (Perry et al. 2010; Török et al. 2014). Our previous results in the same area confirm the slightly positive impact of C-amendment on grassland restoration in terms of target species development, but its effect on neophyte species could not be proven (Halassy et al. 2021; Reis et al. 2022). C-amendment studies usually show contradictory impact on target and neophyte species in restoration projects (Perry et al. 2010), suggesting that often, but not always, its addition decreases invasive species and favors target species (Eschen et al. 2007). Also, this technique is reported to mainly affect annual invasive species (Davis et al. 2000), however in some of our study blocks perennial neophyte species (e.g. Asclepias syriaca) were also dominant. Based on our results, C-amendment can be a useful technique when applied in combination with other treatments, e.g. seeding, in nutrient rich environments (Halassy et al. 2016).

The impact of the landscape composition on the restoration progress

Our results confirm the studies where the progress of restoration was found to be influenced by the surrounding landscape (Holl and Aide 2011; Helsen et al. 2013; Prach et al. 2015; Waldén et al. 2017), principally because of the significant negative impact of the abundance of neophyte species in the landscape on the restoration progress. Higher relative cover of neophyte species was found in treated plots compared to control plots if higher amount of neophyte species were present in the landscape. Several studies have already proved that fragmented and intensively used landscapes have higher level of invasion, and consequently can present more risk to native fragments (Vilà and Ibáñez 2011; Csecserits et al. 2016; Guido et al. 2016) and recovery (Borgmann and Rodewald 2005), but our study is the first to confirm the negative role of neophyte pressure on the progress of grassland restoration. Furthermore, we found a positive relationship between distance from plantations and the progress of restoration, suggesting that a lower invasion of restoration sites is expected with increasing distance from plantations. In the region, tree plantations are hot spots of invasive propagules (Csecserits et al. 2016), also confirmed by our results where neophyte abundance was the highest in plantations, that threaten the remnants of semi-natural vegetation and hamper the restoration process.

Contrary to our expectations, the abundance of target species in the surrounding landscape and the distance from semi-natural grasslands had no significant impact on the effect size of target species. Other studies in grassland restoration have proved that the number of target and specialist species at a site is positively influenced by the target species present within the landscape (Prach et al. 2015; Waldén et al. 2017) and also by the proximity to natural fragments (Helsen et al. 2013). In addition to the fact that the presence of semi-natural remnants in the surroundings is an excellent source of propagation for the target species, it can also act as a physical barrier to invaders (Vilà and Ibáñez 2011; Guido et al. 2016). In our study, the two experimental blocks that presented the highest average effect size of target species included seeding as treatment that affected these results. Also, secondary grasslands in the region have considerable cover of sand grassland generalists 20-40 years after abandonment (Csecserits et al. 2011, 2016) that can represent a source for colonization of restoration sites irrespective of distance to primary grasslands. The low differences in the landscape matrix where blocks were located due to the proximity of our buffers and, the small number of blocks (n=8)considered in the analyses could also explain the lack of



landscape factors effects associated to target species, indicating the needs of further research considering more blocks located scattered in the landscape.

The impact of elapsed time on the restoration progress

Contrary to our expectations and to other restoration studies in semi-natural grasslands, where they found a positive relation between the elapsed time and the richness of target species at experimental sites (Prach et al. 2015; Waldén et al. 2017), time did not have a significant effect on the restoration progress in our case. When the long-term datasets were analyzed separately for each experiment (Reis et al. 2021; Halassy et al. 2021), there was an interaction between treatments and time, generally resulting an increasing cover of target species with time and treatments. The lack of response to time in the present study can be explained by the fact that the experiments were not monitored in the same years and for the same time length, and the sample size was very small (n=2) for certain years, not being enough to represent the population. Further research is needed with the involvement of a higher number of blocks with longer term data to confirm time-related results. Despite the lack of confirming data in our special case, we think that long-term monitoring is crucial in restoration projects to confirm or reject results of short-term analyses (Herrick et al. 2006).

Conclusions

We conclude that restoration intervention can successfully overcome landscape constrains and shorten the time required for recovery. From the three treatments applied, early seeding with low diversity seed mixture of target species can successfully overcome dispersal limitations (Halassy et al. 2016; Török et al. 2018a) and can also prevent the spread of invasive species. The manipulation of abiotic and biotic limiting factors is of secondary importance in Pannonic dry grasslands. Initial application of C-amendment and mowing have similar, low effects on the establishment of target and neophyte species. However, the establishment gaps created by mowing can be quickly occupied by invasive species if present in the landscape. We suggest the use of multiple treatments to restore the native vegetation, e.g. C-amendment in combination with seeding and/or mowing plus invasive species control.

Our research also emphasizes the importance of considering landscape factors in prioritizing areas and efforts for restoration to support scaling up restoration of degraded dry grasslands. For example, in areas with a high level of invasive species in the surroundings, where invasion is a possible threat to restoration success more active restoration

measures should be applied, primarily based on seed introduction. This significantly increases the cost of restoration and consequently reduces the area that can be restored. On the other hand, restoration costs can be minimized and larger areas can be restored by prioritizing efforts in areas where unwanted invasive species are absent (Török et al. 2018a). Contrary to our expectations, our results did not show any effect of the presence of dispersal sources of target species in the surroundings on the restoration success, in this regard, further studies in different landscape matrices are needed.

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