Biol Invasions (2025) 27:154
https://doi.org/10.1007/s10530-025-03613-5

ORIGINAL PAPER

Restorative seeding controls annual invasive species, but perennials can thrive in the long term despite treatments in sand grassland restoration

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Received: 17 May 2024 / Accepted: 22 May 2025

Abstract Biodiversity loss caused by invasive alien species is a major problem in planetary perspective. Ecological restoration can play a critical role in mitigating the impact of invasive species, but the presence of invasive plants in the landscape may simultaneously pose challenges to restoration success, and these processes are influenced by the life history of invasive species. We investigated long-term changes in annual and perennial invasive plant abundance as a function of restoration intervention, invasive species propagule pressure from the surrounding landscape and time since intervention in three sand grassland restoration experiments. Restoration interventions (native low diversity seeding, mowing and carbon amendment) were conducted at a total of eight sites in the Kiskunság region of Hungary. The interventions took place between 1995 and 2003 and were monitored for 17–25 years. To assess invasive propagule pressure around the experimental sites, total shoot numbers in adjacent 1 m by 1 m plots along 100-m-long transects were counted in 2020–2021 from the center of the eight experimental sites. Invasive propagule pressure within a 100-m buffer did not explain changes in the abundance of annual and perennial invasive species. The cover of annual invasive species has mostly decreased over time, and treatment (mainly seeding) accelerated this process. The cover of perennial invasive species increased over time irrespective of applied treatments and landscape invasive propagule pressure. Our research showed that seeding with native species is an effective tool for restoring

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-025-03613-5.

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Published online: 15 June 2025

sandy grasslands and preventing the spread of annual invasive species, but our toolbox for preventing perennial invasion in grassland restoration is limited.

Keywords Dry grassland restoration · Invasive alien plant species · Invasive propagule pressure · Landscape impact · Long-term monitoring

Introduction

Ecological restoration aims to restore degraded, damaged or destroyed ecosystems and has proven to be suitable for improving the ecological integrity of degraded habitats (Gann et al. 2019). Invasion control as part of ecological restoration involves several techniques, including eradication, grazing, mowing, fire, or topsoil removal (Hobbs et al. 2007; Flory and Clay 2009; Papanastasis 2009; Weidlich et al. 2020; Lyons et al. 2023). However, the persistence of the legacy effects of invaders after their removal (Wardle and Peltzer 2017) and restorative interventions that cause disturbances might promote re-invasion or secondary invasions (Hobbs and Huenneke 1992), especially when acquisitive, disturbance-adapted invasive species with good dispersal capacities are present (Funk et al. 2020). Reconstruction of pre-invasion state and revegetation efforts through ecological restoration can generally effectively suppress the possibility of re-invasion by increasing invasion resistance of the community (Wardle and Peltzer 2017; Halassy et al. 2023; Lyons et al. 2023). In search of best restoration practices, we need to understand how invasive species respond to restorative treatments in the long term and how the presence of invasive species in the surrounding landscape influences the progress of restoration.

Grasslands are one of the most vulnerable habitats as they are subject to the highest levels of plant invasion worldwide (Catford and Jones 2019; Zhang et al. 2024). Land-use change in general fosters plant invasions, and grasslands were found to become more prone to invasion when traditional human interventions (e.g. grazing or mowing) are abandoned (Foxcroft et al. 2010, Seastedt and Pysek 2011, Axmanová et al. 2021). Once an invasive species has established in a habitat, it can cause irreversible damage, due to their often long-term legacies (Corbin and D'Antonio 2012), especially in soil properties (Nsikani et al. 2018), soil seed bank (Gioira et al. 2012) or altering natural cycles (Kelly et al. 2020). This does not only lead to the loss of the original native diversity, but can also facilitate the establishment for additional invasive species (Simberloff and Von Holle 1999).

This is especially true for fragmented landscapes where the landscape matrix itself hosts several invasive species, and high propagule pressure implies higher risk of invasion (Rodewald and Arcese 2016). Assessing and understanding landscape-scale impacts is essential for planning successful restoration interventions from the target species' point of view (Török et al. 2020), but it also has implications for assessing invasion threat (Coutts et al. 2011). Landscape metrics include the size and shape (area and perimeter) of semi-natural habitat patches in the landscape, as well as their proximity to propagule sources (Helsen et al. 2013; Guido et al. 2016). Barriers to native dispersal combined with high invasive propagule pressure is one of the main factors determining the degree of invasion (Catford et al. 2011; Kröel-Dulay et al. 2019). In an anthropogenically modified landscape, many habitats are sources of invasive species that can undermine restoration efforts (Holl and Aide 2011; Vilà and Ibáñez 2011; Csecserits et al. 2016; Guido et al. 2016).

Although coincidence and timing play an important role in the establishment and spread of invasive species (Crawley 1989), this process is not solely due to a series of random events (Crawley et al. 1996), and several hypotheses exist for explaining the success of invasive species. In general, species that are able to colonize an area efficiently are those that grow rapidly and are able to convert available nutrients into biomass more quickly (Van Kleunen et al. 2010; Mächler and Altermatt 2012). Several studies have shown that plant life forms have implications for invasion spread and success (e.g. Fenesi & Botta-Dukát 2010; Coutts et al. 2011; Catford et al. 2019) and therefore might respond differently to restorative interventions that should also be taken into consideration in management planning (Nyamai et al. 2011; Funk et al. 2020; Halassy et al. 2021). Annual invasive species have a special set of traits that help them successfully colonize new areas: these species are characterized by efficient reproduction and dispersal (i.e. a wide variety of mixed dispersal vectors), and an appropriate germination strategy (e.g. biotic conditions are sensed by the seeds) can ensure their quick establishment in a new habitat (Fenesi and

Botta-Dukát 2010). In contrast, for perennial invasive species, population expansion and adaptive evolution to new habitats can be much slower and more difficult, but longer residence times allow perennial invasive species to spread to more places, increasing the scale of invasion (Ni et al. 2021). Consequently, the two life forms might require different land management approaches and restoration of the native habitat. For example, Ramula et al. (2008) found that manipulation of growth and reproductive mechanisms in annual invasive plants always resulted in population declines. However, in the case of perennial invasive species, a combined approach targeting survival with either growth or reproduction mechanisms were sufficient to reduce the population.

While the management of invasive species focuses on the characteristics of the invasive species, the primary goal of restoration efforts is to help restore the biotic characteristics of the area, partly by manipulating abiotic conditions and partly by manipulating biotic conditions (Weidlich et al. 2020). For example, overseeding with native forb species has also been shown to be effective in reducing annual invasive species (Urza et al. 2019) as well as productivity of perennial invasive species (Reinhardt and Galatowitsch 2008). Mowing, one of the widely used restoration interventions has been shown to be efficient in reducing the density of perennial invasive plants even in the short term (Nagy et al. 2022), and it also strongly hinders the reproductive success of annual invasive species (Milakovic et al. 2014). Nevertheless, mowing and grazing can open up spatial and temporal windows for colonization, which invasive species with good dispersal capacity can exploit first (Reis et al. 2021). Likewise, indirect methods, such as soil nitrogen immobilization using carbon sources, have been less successful in controlling invasive species (Perry et al. 2010; Halassy et al. 2021) and have been reported to affect mainly annual invasive species (Davis et al. 2000).

Methods for the restoration of Pannonian sandy grasslands have been studied for more than 20 years (Kiskun Restoration Experiments, KISKUN LTER—kiskun.lter.hu). We applied mowing, carbon amendment and seeding after the cessation of arable cultivation or the clear-cutting of non-native plantations and monitored the outcome of restorative interventions in the long term (17–25 years) (Reis et al. 2023). Results so far show that the outcome of restoration interventions depends not only on the restorative intervention itself, but also on the elapsed time and the surrounding landscape (Reis et al. 2022). Although a landscape impact is visible, there is a lack of knowledge about the distances from which the pressure of invasive alien species may pose a threat to the restoration efforts as well as the behavior of annual versus perennial invasive species. Building on our previous research (Reis et al. 2022), in which we described the impact of landscape habitat composition on the long-term success of restoration, we used a finer scale transect method to study the impact of invasive propagule pressure from the neighborhoods surrounding the restoration sites on invasive species abundance and separately analyzed the response of annual and perennial invasive species at the restoration sites.

Our research questions are: (1) How does the level of annual and perennial invasion change with time in three sand grassland restoration experiments in the long term? (2) To what extent does the degree of invasion within the restoration experiments depend on the type of restoration intervention, the time since the intervention, and the invasive propagule pressure from the landscape?

Materials and methods

Study area

We collected long-term datasets from three different experiments, which were carried out at the Kiskun LTER site (Kiskun LTER 2005–2024), Hungary. The experiments are near three settlements (Bugac: 46°39’N, 19°36’E; Fülöpháza: 46°52’N, 19°24’E; Izsák: 46°45’N, 19°19’E) in the Kiskunság Sand Ridge (Fig. 1). The area lies in a harsh temperature, moisture, wind and soil environment (Borhidi 1993; Kovács-Láng et al. 2008). The average annual temperature is 10.5 °C with large daily and annual fluctuations. The yearly precipitation is 520–540 mm, and drought events have become more frequent (especially during the summer). The predominant wind direction is NW to SE (Bagi 1990). The soils are Calcaric Arenosol with more than 90% sand and less than 1% humus content (Zólyomi et al. 1997; Kovács-Láng et al. 2000; Buzási et al. 2021).

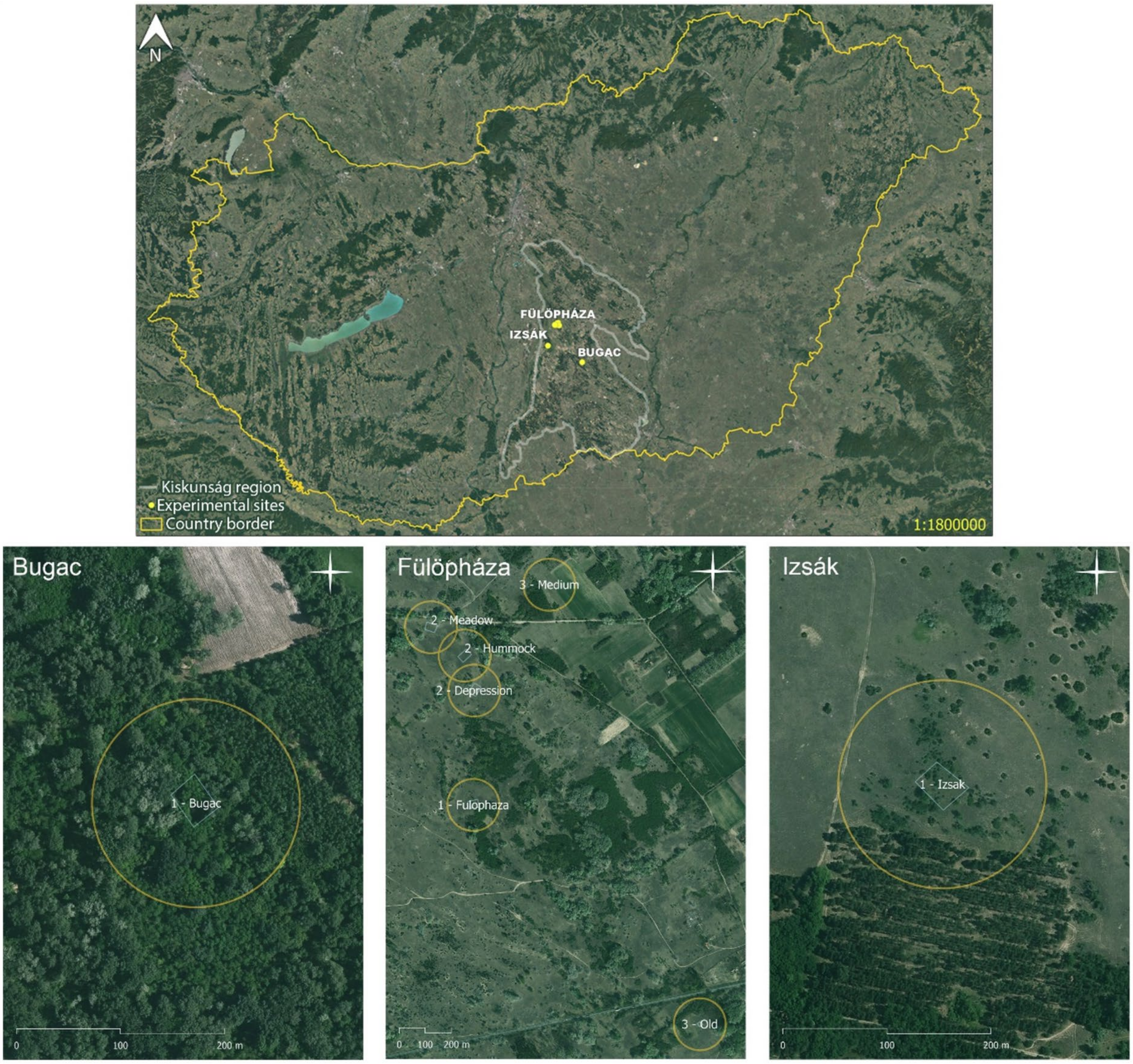

Fig. 1 The location of the studied experiments (EXP 1, EXP 2, EXP 3) and their 100 m radius buffer in Bugac, Fülöpháza and Izsák in the Kiskunság region, Hungary, Europe. Projected coordinate system: EOV-1972. Maps made in QGIS, orthophotos by the Lechner Knowledge Center, Budapest, 2019

The area is situated in the forest-steppe zone (Erdős et al. 2022) with a mosaic of different types of communities depending on topography and the parent material. Among the grassland types in Hungary, Pannonian sandy grasslands hold exceptional value due to their limited global distribution, with the majority of their extent located within the country (European Commission's Red List 2016). One of its most typical components at the driest locations is the open sandy grassland (*Festucetum vaginatae 'danubiale'* community). The *Festucetum vaginatae 'danubiale'* is semi-desert-like, rich in endemic species and dominated by the tussock grasses *Festuca vaginata* Waldst. & Kit. ex Willd. and *Stipa borysthenica* Klokov ex Prokudin. This grassland community is found primarily on the tops and Southern slopes of nutrient-poor and coarse-textured calcareous sand dunes (Kovács-Láng et al. 2000). Other typical natural habitat types found in the area include closed sand steppe, poplar-juniper shrubland, open and closed natural forest, and wetlands (mesotrophic wet meadows, *Molinia*-dominated meadows, and marshes) (Biró et al. 2013). Due to historical human land transformation, most of the present landscape is covered by agricultural areas (57%), forests—mostly non-native plantations—(19%), and settlements (6%) (CORINE 2000). Agricultural cultivation reached its peak during the socialist regime, in the 1960s. Afforestation by the non-native black and scots pine (*Pinus nigra* J.F.Arnold*, Pinus sylvestris* L.), black locust (*Robinia pseudoacacia* L.*)* and native white poplar (*Popolus alba* L.) was carried out during the 19—twentieth centuries to hold the sand. Land-use changes have led to the preservation of only approximately 19% of semi-natural habitats in the region. This includes not only remnants of primary habitats but also disturbed meadows and dry grasslands, some of which have been encroached by non-native trees (Biró et al. 2013).

During the post-socialist transformation (1987–1999), the abandonment of agricultural land reached a significant level (Valkó et al. 2016), especially in low productivity areas, such as the Kiskunság. While there was some spontaneous recovery of the native vegetation, invasive alien species began to spread to these abandoned areas (Török et al. 2003; Csecserits et al. 2011, 2016). According to a Hungarian countrywide survey (called MÉTA), 5.5% of the territory of Hungary is covered by invasive perennial herbaceous plants, and sand grasslands of the Kiskunság are among the most invaded habitats (Botta-Dukát 2008).

Restoration experiments

We analyze results from three experiments from the region with the aim to assist the recovery of sandy grassland habitats in degraded areas with long-term data (min. 17 years) to assess trends over time.

The first experiment (EXP1) was conducted across three sites (Bugac, Fülöpháza, Izsák) that had been afforested with black locust. In order to restore grasslands, the trees were clear-cut winter 1994–1995 and trunks were treated with the Garlon® 4E chemical to avoid re-sprouting. Mowing and hay removal were applied twice a year afterwards to help recovery of the sandy grassland between 1995 and 2001. The experimental design consisted of six treatment and six control plots (10 m × 10 m each adjacent plot, Fig. 2a). The monitoring of the vegetation took place yearly in 1995–1999 and less frequently between 2002 and 2019 (Bugac: 2019; Fülöpháza and Izsák: 2002, 2003, 2005, 2007, 2009, 2017) in 2 m by 2 m permanent sampling units (n = 18 per experimental unit; Reis et al. 2021).

The other two experiments focused on the restoration of abandoned croplands in Fülöpháza. In the second experiment (EXP2), we manipulated soil nitrogen availability on three fields (Depression, Hummock, Meadow), abandoned 3–7 years prior to the experiment, in order to facilitate the establishment of the species of low-productivity sandy grasslands. Carbon amendment (700 kg carbon·ha^{-1}· yr^{-1} was spread by hand on treatment plots as sucrose [1300 kg·ha^{-1}·yr^{-1}] and sawdust [300 kg·ha^{-1}·yr^{-1}]) was applied between 1998 and 2003 (Halassy et al. 2016). The design of the experimental plots was the same as in the previous experiment (six treatment and six control plots, 10 m × 10 m each, Fig. 2b). We monitored the changes in the vegetation yearly between 1998 and 2004, and later in 2006, 2008, 2010 and 2018 (n = 18 sampling per experimental unit) (Török et al. 2014; Halassy et al. 2021).

In the third experiment (EXP3), we combined mowing and carbon amendment with sowing on two arable fields (Medium and Old) abandoned in different years. Plowing and harrowing were used as a pretreatment to disrupt existing vegetation in the study area (20 m by 20 m), followed by sowing, mowing or carbon amendment between 2002 and 2008. The experimental design consisted of eight replicates of 1 m × 1 m for each of the eight types of treatments originally (single treatments, pairwise combinations, all three treatments and a control), separated by 1 m paths between the plots (Fig. 2c). In the present analysis we only focus on single treatments (1: Mowing, 2: Seeding, 3: C-amendment) and control per site that are comparable with the other two studies. Mowing was similar as in EXP1, but as carbon source, only sugar was applied (initial dosage of 45 g sucrose/m2 plot in September 2002 followed by the application of the same dosage every 3 weeks from April to October). As for seeding, five hand-collected open sandy grassland species were sown together (two grass species: *Festuca vaginata* [1.55 g/m^2]; *Stipa borysthenica* [1.05 g/m^2 – later 1.31 g/m^2]; and three forb species: *Koeleria glauca* (Schrad.) DC. [1.00 g/m^2]; *Dianthus serotinus* Waldst. & Kit., *Euphorbia*

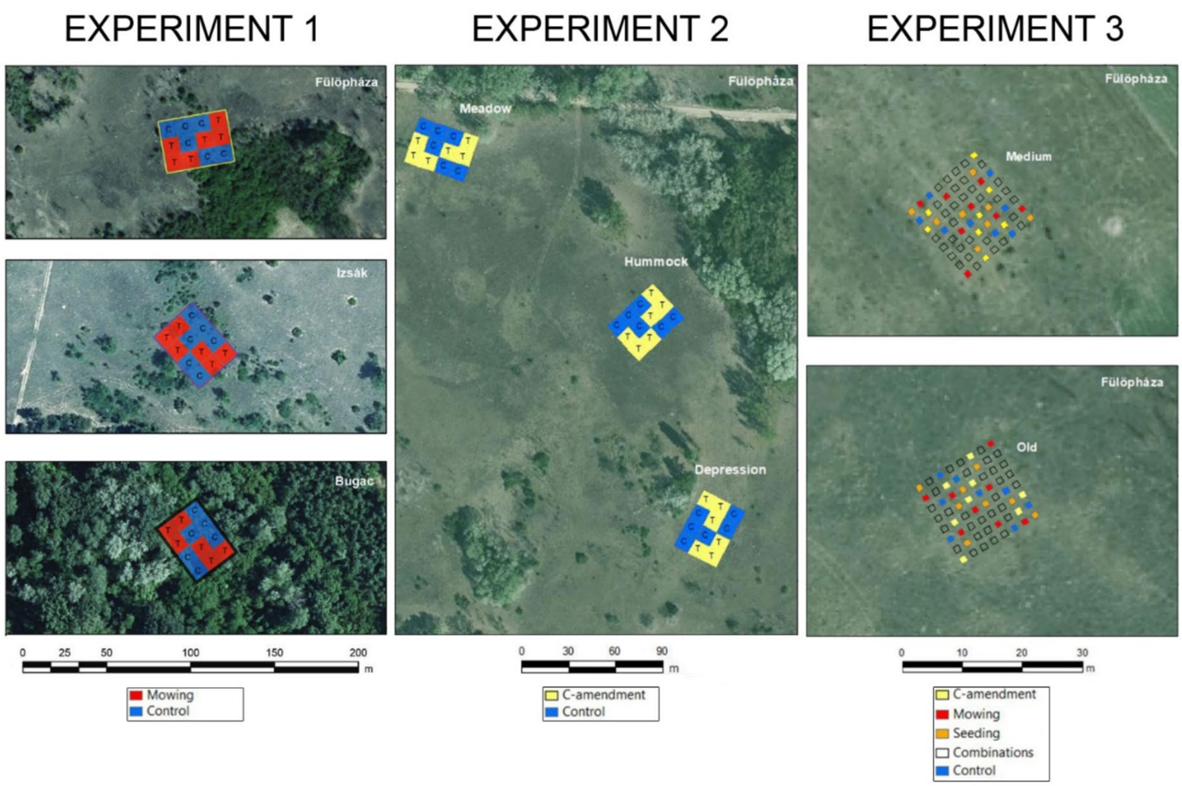

Fig. 2 Schematic figure showing the experimental setups of the three experiments. The figure is based on the work of Reis (2021). Projected coordinate system: EOV-1972. Maps made in QGIS, orthophotos by the Lechner Knowledge Center, Budapest, 2019

seguieriana Neck. [the two latter 0.20 g/m^2]) (Reis 2021). Monitoring took place yearly between 2003 and 2008 in all treatment plots, and the experiment was resampled in 2019 (Halassy et al. 2016, 2019; Llumiquinga et al. 2021; Reis et al. 2022).

A schematic figure showing the distribution of treatment and control plots in each of the three experiments is shown on Fig. 2.

Monitoring of invasive species in the experimental sites

Vascular plant cover was estimated twice a year in early and late summer, and in this paper, we focus on invasive alien species only. From these, we considered neophyte species (taxa that were introduced to a new region after 1500 AD; Preston et al. 2004) in the analysis, as archaeophytes (taxa that settled in an area before 1500 AD; Preston et al. 2004) cannot be clearly distinguished from native species in the region. Neophyte species were categorized based on the work of Balogh et al. (2004) and subdivided into annual and perennial life form groups (the latter also including woody species that did not have enough occurrence to be analyzed separately). We calculated the maximum relative cover of each neophyte species and the two life form groups within each plot per year for further analyses. The summary of all neophyte species and life form groups sampled in the experiments are shown in Table S1.

Monitoring of invasive species in the surroundings of the experiments

To evaluate the invasive propagule pressure in the surroundings of the experimental sites, we established eight 100-m-long transects from the center of each experimental site towards the eight cardinal directions (N, S, E, W, NE, NW, SE, SW) in 2020–2021 (Figure S1). We recorded the number of shoots of each neophyte species in 100 adjacent 1 × 1 m plots along each transect (n = 100 per transect, the neophyte shoot sampling also took place in 2020–2021). An example of the resulting heat maps can be found in Figure S2. We used the cumulative sum of the number of shoots of invasive species within 100 m buffer as a proxy for the landscape invasive propagule pressure.

Data analysis

The statistical analyses were carried out using R Studio 2022.12.0.353 (R core team 2022). We developed two groups of models for our two main questions applying Generalized Linear Mixed Models using Template Model Builder using the "*glmmTMB*" package (Brooks et al. 2017). We first analyzed the changes in the relative cover of annual and perennial neophyte species according to treatments and time for the three experiments separately. Treatment was used as fixed effects with two levels (1 = treatment, 0 = control), time since the start of intervention was included as a continuous variable (also fixed effect), and plot ID nested in sites was treated as random effects in the models. The cover of annual and perennial neophyte species was used as dependent variables in separate models, both of them were square root-transformed and centered to meet assumptions of normality and homoscedasticity of residuals checked by the "*DHARMa*" package (Hartig 2020).

To investigate the impact of treatment, time elapsed since treatment, and landscape invasive propagule pressure on the neophyte cover in the experimental areas, the three experiments were analyzed together. The dependent variables were also the two life form groups (annual and perennial), but we calculated their effect sizes by subtracting the relative neophyte cover of the treated plots from the relative neophyte cover of the control plots as a measure of restoration success. We applied the Hedges'g procedure to calculate the effect size (i.e. unbiased standardized mean difference between control and treatment) (Hedges and Olkin 1985). For the fixed effects, treatment (with three levels: carbon amendment, mowing, seeding) was a categorical variable, while landscape invasive propagule pressure were continuous variables. Since the three experiments were implemented in different years, instead of monitoring year as fixed factor, we included how many years passed since the start of restoration as a continuous time factors, and accounted for repeated measures in permanent plots by including plot nested in site as a random effect. Our data met the assumption of normality, and the homogeneity of residual variance was also verified using the "*DHARMa*" package (Hartig 2020). In case of significant ($p < 0.05$) treatment impacts, as a post hoc test, we used Estimated marginal means (Least-squares means) "*emmeans*" package's Tukey pairwise comparison analysis function (Lenth 2023).

Results

Changes in annual and perennial neophyte cover over the years in the restoration experiments

In case of the first experiment where treatment involved mowing at clear-cut black locust sites, only treatment (mowing) had a significant positive impact ($\chi^2 = 8.8411$; Df = 1; $p = 0.0029$) on annual neophyte cover, and we found no significant impact of time or their interaction (Table S2). The relative cover of annual neophyte species increased in the first three years of treatment applications with the highest value found in the 3rd year since management (1997) in treatment plots (an average relative cover of 34.8%), but decreased later with some fluctuations to 0.9% in the last monitoring year (Fig. 3a). In the case of perennial neophyte cover, only the elapsed time since the start of restoration intervention had a significant ($\chi^2 = 64.3666$; Df = 1; $p = < 0.001$) impact, treatment and the interaction did not (Table S2). The relative cover of perennial neophyte species increased with time (Fig. 3b). The highest average relative cover was in last monitored year (2019) in control plots (48.7%), while the lowest was observed in the initial year in the control plots with 0.5%. Treatment plots had generally higher cover of perennial neophyte species than control plots, except in the last monitoring year, but these differences were not confirmed statistically.

In the second experiment where carbon amendment was applied to accelerate grassland recovery on abandoned croplands, neither time nor treatment had a significant impact on the annual neophyte cover (Table S2). The relative cover of annual neophyte species showed some fluctuations: decreased initially during the treatment period, but returned to previous values by the 9th monitoring year (2006) and decreased again by the last survey (Fig. 3c). The highest average annual relative cover was observed in

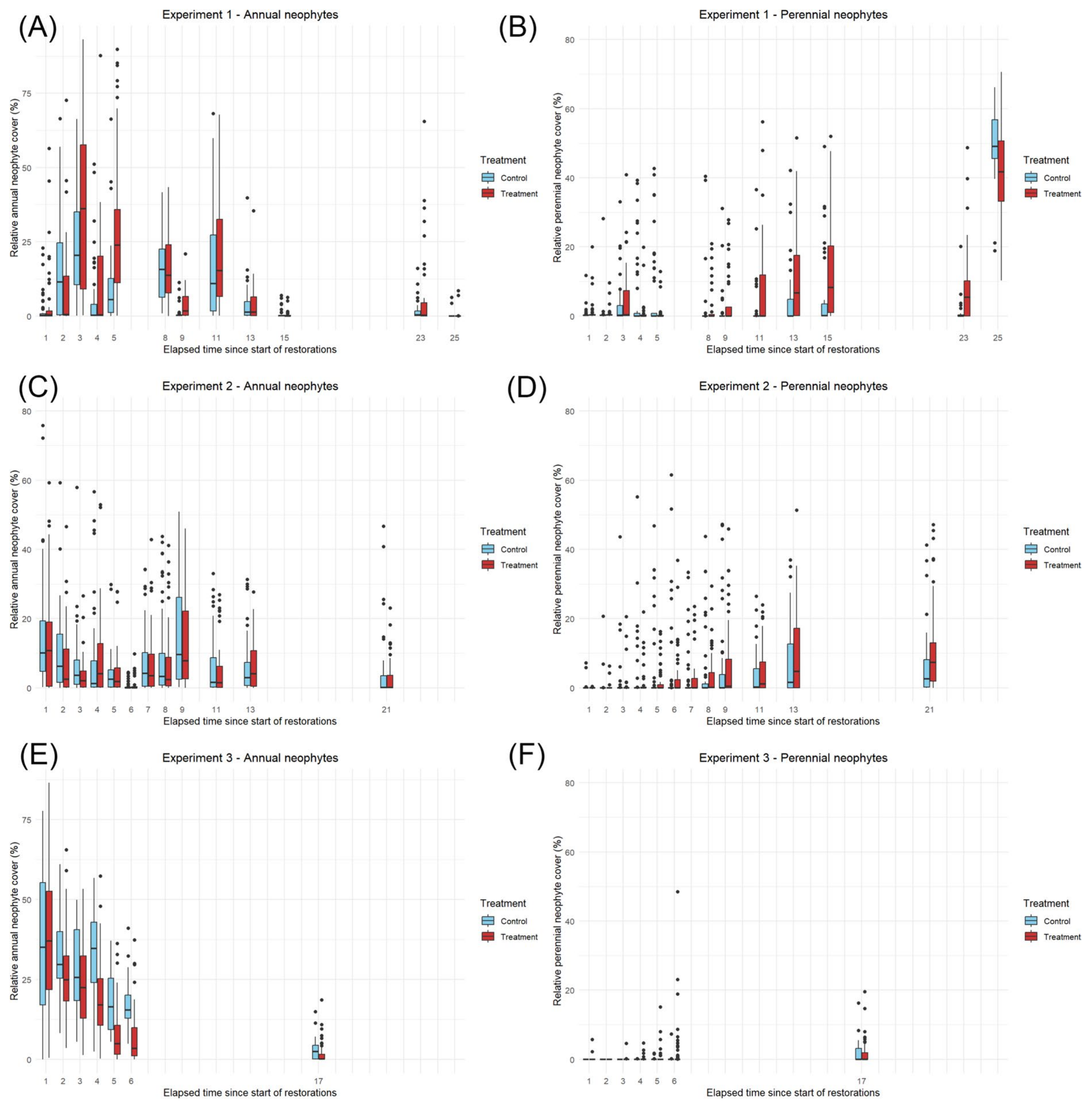

Fig. 3 Relative cover of annual (**a**, **c**, **e**) and perennial (**b**, **d**, **f**) neophyte life form groups in treatment (*red*) and control (*blue*) plots within the three studied restoration experiments (boxplots are made in R Studio)

the first year (1998) (in the control plots), which was 15.5%, while the lowest was observed in the 6th monitoring year (2003) in the treatment plots with only 0.7%. In the case of perennial neophyte cover, time and treatment did not have a significant impact, but their interaction did ($\chi^2 = 11.8595$; Df = 1; $p = 0.0005$, Table S2). The average cover of perennial neophyte species increased with time, and reached 11% in the last year since management (2018) in treatment plots, while the lowest value was observed in the initial year in the treatment plots with 0.01% (Fig. 3d).

In the third experiment that included carbon amendment, mowing, and seeding on abandoned cropland, both treatment ($\chi^2 = 3.991$; Df = 1; $p = 0.0457$) and time ($\chi^2 = 75.114$; Df = 1; $p = < 0.001$) had a significant effect on annual neophytes without interaction (Table S2). In this case, the relative cover of annual neophytes was higher in the control plots. The relative cover of annual neophyte species clearly decreased with time (Fig. 3e). The highest average relative cover of annual neophyte species was observed in the initial year (2003) in treatment plots (37.3%). We found the lowest average relative annual neophyte cover in the last monitoring year (2019) with only 1.32% in treatment plots. In the case of perennial neophyte species, neither treatment nor time or their interaction showed significant impact. The relative cover for perennial neophyte species was very low during the monitored years. Basically, they were absent in control plots and were insignificant in treatment plots in the beginning, and then increased in cover up to 2.4% in the control plots by the last year (2019) since the start of the management (Fig. 3f).

Effect of treatment, time and surrounding invasive propagule pressure on within site invasion

We analyzed all experiments together and found a significant impact of only the treatment in the case of annual species ($\chi2 = 30.8648$; $Df = 2$; $p = < 0.001$), but no effect of time or invasive propagule pressure (Table S3). Tukey pairwise comparisons showed that of the three treatments, seeding resulted in a significantly higher effect size than carbon amendment or mowing (Table S4) that shows a high positive impact on the progress of restoration indicated by a lower cover of annual neophytes in treated plots compared to control (Fig. 4). Carbon amendment and mowing were not statistically different from each other, and the effect sizes were around zero showing that the cover of annual neophyte species in treatment plots did not differ from control plots. In the case of perennial neophytes, neither treatment nor invasive propagule pressure affected the cover of perennial neophytes, but the elapsed time since interventions was significant (Table S3). Effect sizes started around zero at the beginning of treatments showing that treatment and control plots had similar cover of perennial neophytes initially (Figure S3). However, as the succession proceeded, effect sizes became negative, indicating that treatment plots harbored higher cover of perennial neophyte species than control plots with time with a few exceptions. All the effect size values can be found in Supplementary Information 2.

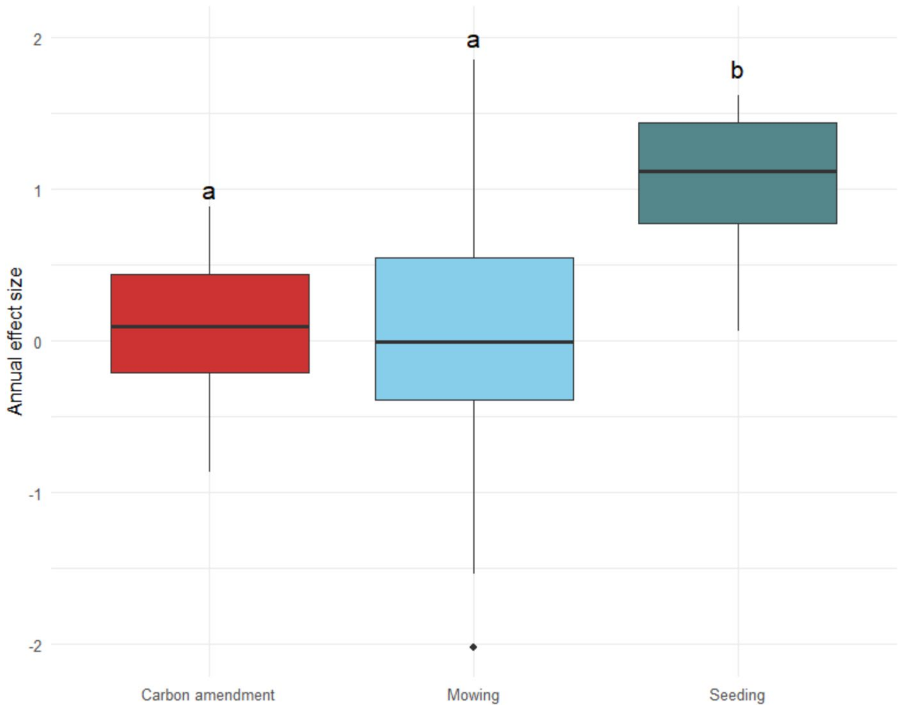

Fig. 4 The impact of carbon amendment, mowing and seeding on the effect size of annual neophyte species based on "*emmeans*" Tukey pairwise comparison post hoc test. Positive values of effect size indicate lower cover of annual neophyte species in treatment than in control. Significant differences between treatments are indicated by lower case letters (boxplots are made in R Studio)

Discussion

Long-term trends of annual and perennial invasive species in sand grassland restoration

Our research suggests that the amount of annual invasive species can fluctuate greatly during restoration, but can show a downward trend over time depending on the pre-restoration state and the treatments applied. However, the cover of perennial invasive species tends to increase over time, regardless of treatments. Short-lived species are generally successful in early successional or disturbed habitats, where they can rapidly colonize and exploit resources, while long-lived species are more competitive than annuals in undisturbed habitats (Fenesi and Botta-Dukát 2010), and therefore replace short-lived species during succession (Grime 2006; Csecserits et al. 2022). A short-lived strategy also involves the persistence of seeds, which allows the use of resources that change over time and raises the issue of managing invaded soil seed banks in order to ensure long-term viability of restoration efforts (Gioira et al. 2012). Disturbances that lead to the disruption of vegetation and open soil surfaces such as drought, vegetation or soil disturbance can lead to the re-emergence of invasive alien species either from the soil seed bank or from the surrounding landscape (Enders et al. 2020; Meyer et al. 2021; Orbán et al. 2021; Krpán 2023). Among the dominant annual invasive alien species in our research, *Ambrosia artemisiifolia* L. was one of the most dominant species that is known to decrease as succession progresses and can be suppressed by dominant native species from the above-ground vegetation, but survives in the seed bank (Kröel-Dulay et al. 2019; Zhao et al 2023). The other dominant annual species was *Conyza canadensis* (L.) Cronq. that produces high number of seeds capable of longer-distance dispersal (Liu et al 2022).

Community-level analyses were conducted for the three experiments prior to this study to assess community compositional trajectories (Török et al. 2014; Halassy et al. 2019; Reis et al. 2021).

The soil legacy left by the N_2-fixing black locust (Nsikani et al. 2018) further complicates the picture, as although N leaching has lowered the levels of N in the upper soil layers in our case (Reis et al. 2021), the potential impact of changes in the soil microbiome on the invasion process is unknown and requires further research. Soil legacy is also important when restoring low productive grasslands on croplands. The increased resource availability in the form of nutrients from agricultural practices and a seed bank poor in grassland species but rich in weeds favors the establishment and survival of invasive species (Cramer et al. 2008; Öster et al. 2009).

Unlike annual invaders, once established, perennial species are expected to persist and spread over longer periods (Fenesi and Botta-Dukát 2010; Ramula et al. 2008). Among plants, the most important invasive species worldwide are long-lived species (Global Invasive Species Database 2023). Moreover, the dominant invasive species in our case has a special set of traits that do not occur in the native system (ideal weapon or novel weapon hypothesis in Enders et al. 2020). *Asclepias syriaca* L. has intensive vegetative spread, abundant fruit set and viable seed production and its roots can penetrate up to 1 to 1.5 m deep in the soil that helps the long-term survival of clones (Bakacsy and Bagi 2020; Follak et al. 2021).

Effect of elapsed time, restoration intervention and invasive propagule pressure on restoration success

When analyzing the three experiments together, treatment and time both showed a significant effect on invasive species, but we failed to prove the direct impact of invasive propagule pressure in the neighboring landscape. The degree of invasion depends on the inherent properties of habitats (invasibility), the invasive potential of the alien species (invasiveness), the actual propagule pressure and the landscape structure (Catford et al. 2011). In anthropogenic landscapes, the landscape matrix can host several invasive species (Vilà and Ibáñez 2011; Csecserits et al. 2016), and obstruct the dispersal of native species (Török et al. 2018). This coupled with high invasive propagule pressure threaten the success of restoration efforts (Holl and Aide 2011). Although our previous research (Reis et al. 2022) has shown that habitat-level invasion in a 500 m buffer has a significant effect on the invasion of restoration sites, we failed to detect the direct effect of invasive propagule pressure at a shorter distance of 100 m. The lack of effect may be interpreted as a sign of saturation at the investigated scale, when a higher abundance of invasive species does not increase their cover in the restored plots (Vilá et al. 2011). Our contradicting results on the landscape effects at the two scales are also in line with findings that habitat type that reflects the combination of local abiotic conditions, current and historical land use and disturbances is the most important determinant of the level of invasion in the region (Csecserits et al. 2016).

The success of the restoration in terms of invasion control depended largely on the treatment used. From the treatments applied, only seeding had a significant negative effect on annual invasive species. Invasive plant control is often unsuccessful, because the removal of the invasive plant is not followed by active reintroduction of native plants (Kettenring and Adams 2011; Weidlich et al. 2020). Dispersal barriers are a major problem in the restoration of degraded habitats, which often need to be overcome by species introductions and assisted dispersal (Öster et al. 2009; Török et al. 2018). Moreover, providing priority to native species by sowing before the establishment of invasive alien species was found to be an important mechanism for increasing invasion resistance (Halassy et al. 2023; Byun 2023; Urza et al. 2019). Dispersal barriers partly explain why mowing as a treatment favored annual invasive species. Mowing kept the vegetation open after black locust elimination, while the encroachment of shrubs in the control plots prevented the establishment of invasive alien species (Reis et al. 2021). The timing and frequency of mowing should be carefully chosen to avoid secondary invasion by species of high dispersal capacity or permanent seed bank (Song et al. 2018). The lack of native species dispersal also accounted for the failure of carbon modification in our case, where the temporal limitation of nitrogen availability failed to provide negative impact on invasive plant species (Halassy et al. 2021), similar to other studies (Perry et al. 2010).

We found that perennial invasive species were not significantly affected by restoration treatments and tended to increase over time during the succession process. This suggests that these species have inherent advantages (see e.g., Enders et al. 2020), such as resilience to conventional management practices, making them a persistent challenge in restoration efforts. Promising approaches, such as repeated mowing or grazing, may offer better control, but there is limited knowledge about their long-term efficacy and the outcomes of discontinuing treatments (Berki et al. 2023). Furthermore, these repeated interventions can be costly and, in some cases, may even exacerbate secondary invasions (Valliere et al. 2019). Effective management of clonal perennial invasive species, like in our case *A. syriaca,* requires an integrated, long-term approach that combines repeated interventions with efforts to mitigate costs and risks of further invasion. Additional research is needed to develop innovative, sustainable strategies for controlling perennial invasive species, particularly in restoration contexts.

Conclusions

Our research highlights challenges in managing invasive species during sand grassland restoration, emphasizing the behavior of annual versus perennial invaders. Annual invasive species may decline over time with restoration in sand grassland ecosystems, but recurrent outbreaks may occur if disturbance and climatic conditions favor re-invasion. Our current treatment approaches fail to control perennial invasive species that become more dominant in the long-term threatening restoration success. Of the treatments applied, seeding proved to be the best at controlling invasive species, but only for annual invaders, and neither mowing nor carbon amendment was able to sufficiently control invasive species in sand grasslands. While mowing can aid restoration, it may inadvertently create "establishment windows" for invasive species if present in the landscape. Our study indicates that the pressure of invasive alien species on restoration success is more strongly influenced by their presence in the broader landscape beyond 100 m, rather than in the immediate vicinity. Our results highlight the importance of a comprehensive approach to habitat restoration that considers not only the specific features of the area to be restored, but also the dispersal potential of native and potential invader species, as well as the life history of problematic invaders in order to find best practices for restoration. Further research should focus in particular on developing proactive strategies to prevent the encroachment of perennial invasive species in sand grasslands, since after establishment, adequate eradication methods are often lacking.

Author's contribution KT and MH designed the experiments. MH and NS conceived the study. MH, NS, BPR, EC, CAC, MV, and KNV participated in field work and data sampling. NS analyzed the data with inputs from BPR and MV. MH and NS wrote the article. All authors reviewed and commented on the manuscript.

Funding Open access funding provided by HUN-REN Centre for Ecological Research. This work was supported by the National Research, Development and Innovation Office (NKFIH FK127996, K138060) and National Laboratory of Health Security (RRF-2.3.1–21-2022–00006) in Hungary. BPR was supported by FCT—Fundação para a Ciência e a Tecnologia (UIDB/00329/2020; PTDC/ASP-SIL/7743/2020) and both BPR and MV were financed by ELKH – Eötvös Loránd Research Network (ELKH SA-66/2021). EC was supported by the Ministry of Culture and Innovation (NTP-NFTÖ-22-B-0056 grants). MH was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences [grant number Bo/00145/23/8].

Data availability Long-term vegetation data is available at B2SHARE data repository under LTER, KISKUN Restoration Experiments, Hungary—Vegetation data 1995–2019. Any other relevant data are available from the corresponding author upon reasonable request.

Declarations

Competing interests The author declares that they have no conflict of interest.

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