Received: 21 July 2023 | Revised: 19 April 2024 | Accepted: 2 June 2024

DOI: 10.1002/ldr.5208

RESEARCH ARTICLE

WILEY

Accumulated soil seed bank of the invasive sand dropseed (*Sporobolus cryptandrus*) poses a challenge for its suppression

Péter Török[1,2,3] | Francis David Espinoza Ami[1] | Katalin Szél-Tóth[1,2] | Patrícia Díaz Cando[1] | Luis Roberto Guallichico Suntaxi[1] | Andrea McIntosh-Buday[1,2] | Alida Anna Hábenczyus[4] | Viktória Törő-Szijgyártó[1] | Gergely Kovacsics-Vári[1] | Csaba Tölgyesi[4,5] | Béla Tóthmérész[1,6] | Judit Sonkoly[1,2]

[1]Department of Ecology, University of Debrecen, Debrecen, Hungary

[2]ELKH-DE Functional and Restoration Ecology Research Group, Debrecen, Hungary

[3]Polish Academy of Sciences, Botanical Garden - Center for Biological Diversity Conservation in Powsin, Warszawa, Poland

[4]Department of Ecology, University of Szeged, Szeged, Hungary

[5]MTA-SZTE Lendület Applied Ecology Research Group, University of Szeged, Szeged, Hungary

[6]ELKH-DE Biodiversity and Ecosystem Services Research Group, Debrecen, Hungary

Correspondence
Péter Török, Department of Ecology, University of Debrecen, Egyetem sqr. 1, 4032 Debrecen, Hungary.
Email: molinia@gmail.com

Funding information
Bolyai János Scholarship of the Hungarian Academy of Sciences, Grant/Award Number: BO/00587/23/8; Nemzeti Kutatási Fejlesztési és Innovációs Hivatal, Grant/Award Numbers: K 137573, KKP 144068

Abstract

Global warming, elevated atmospheric CO_2 concentrations and increased likeliness of extreme drought and wildfires in many regions will likely favour C4 grass species. To support future management actions, we explored the effect of the encroachment of an invasive perennial C4 grass, *Sporobolus cryptandrus* on the composition of soil seed banks in dry sand grasslands in Central Europe. In five mass-locality sites of the species we assessed the composition and vertical segmentation of the soil seed bank in 12 1-m^2 plots along an increasing cover of the invasive species. We found that the seed bank diversity and density decreased with increasing sampling depth; the decrease in density was affected by the increasing *S. cryptandrus* cover. Neither the diversity nor the seed bank density of other species were affected by increasing *S. cryptandrus* cover but both were affected by the sampling site. Most of the studied seed bank characteristics were affected by the sampling depth, but none of them were affected by the increasing cover of *S. cryptandrus*. Increasing cover of *S. cryptandrus* in the vegetation was associated with an increasing proportion of *S. cryptandrus* seeds in the seed bank, and we found a low-density soil seed bank of the species even in plots with no *S. cryptandrus* cover. Our finding that *S. cryptandrus* forms a massive soil seed bank, together with the predicted decrease in the precipitation of the summer months and increase in the frequency of droughts in the region, projects further rapid spread of the species.

KEYWORDS
C4 grass, dispersal, germination, plant invasion, prairie, restoration, *Sporobolus*

1 | INTRODUCTION

Studying the relationship between climate change and the spread of invasive species has been at the forefront of research in the last decades (Hulme, 2017; Ravi et al., 2022). It has been reported that climate change affects the phenology of species (Parmesan & Hanley, 2015; Piao et al., 2019), it shifts the distribution range of many species and causes changes in the composition of communities

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Author(s). *Land Degradation & Development* published by John Wiley & Sons Ltd.

(Esquivel-Muelbert et al., 2019; Feeley et al., 2020), which also favours plant invasions and results in the formation of hybrid and novel ecosystems (Hobbs et al., 2006; Richardson & Gaertner, 2013). The C4 photosynthetic pathway has several advantages over the C3 pathway in drier and warmer climates; the most important advantages being the higher temperature optimum of carbon fixation, the lack of photorespiration and also the more effective water usage, which enables a higher drought tolerance (Johnston, 1996). Consequently, global warming, elevated atmospheric CO_2 concentrations and the associated increased likelihood of weather extremities including prolonged droughts and wildfires in many terrestrial regions are expected to benefit species with a C4 photosynthetic pathway (Chuine et al., 2012; Dukes & Mooney, 1999).

According to the predicted scenarios of climate change, wide regions of Europe will become drier and hotter in the summer months in the forthcoming decades. Precipitation in the summer months is expected to decrease in Southern and Central Europe, and extreme weather events such as heatwaves and droughts will become more frequent throughout Europe (Kovats et al., 2014). The duration and intensity of droughts are projected to increase especially in Southern and Central Europe. However, due to increasing evapotranspiration, soil moisture can decrease even in regions where an increase in summer precipitation is expected (Kovats et al., 2014). The predicted changes can support the spread of invasive plant species better adapted to these conditions, not only in the Mediterranean region but also in areas of Central, Western and Northern Europe (Thuiller et al., 2005; Walther et al., 2009). While European grasslands are characterised by the dominance of C3 grasses, with the ongoing climate change, C4 grasses might gain momentum for their spread and establishment in many regions (de Deus Vidal et al., 2021). As serious droughts and associated wildfires will occur more frequently in the future, the resulting dieback of C3 grasses (Orbán et al., 2023) can also facilitate the establishment and spread of C4 grasses, especially those with an effective dispersal.

Soil seed banks, that is, viable seeds accumulated in the upper soil layers, help to bridge unfavourable conditions and form a 'backup' storage of the plant community (Thompson et al., 1997). Species accumulating a persistent soil seed bank have the possibility to easily re-establish in the community after serious diebacks caused, for example, by drought or wildfire events (Kiss et al., 2018; Måren & Vandvik, 2009). These species can rapidly establish in spontaneously or disturbance created gaps speeding up their expansion (Kalamees & Zobel, 2002). Dynamic processes in the soil seed bank, including the changes in its composition and density can have crucial importance in community resilience (Miao et al., 2020; Török et al., 2020).

The impact of invasive species on the soil seed banks and the subsequent consequences for plant communities can be analysed from two perspectives. First, the encroachment of invasive species affect the native species' soil seed banks. Previous studies have indicated a negative correlation between plant invasion and the density and/or diversity of native species' soil seed banks; however, the magnitude of the effect is strongly species-specific, and also depends on the duration of the invasion (Dairel & Fidelis, 2020; Hager et al., 2015; Jia et al., 2024; Wang et al., 2022). A meta-analysis of the effects of plant invasions on the seed bank of the invaded communities showed that invasions by large, perennial herbs had a remarkably strong negative effect on the species richness and density of the native seed banks (Gioria et al., 2014). Second, understanding how invasive species' seeds accumulate in soil seed banks is of great importance for conservation efforts. The success of invasive species in colonising a particular habitat and then persisting there for a long time is largely driven by the formation of soil seed banks (Gioria et al., 2012, 2021; Pyšek et al., 2015). This knowledge is crucial not only for managing invasive species but also for effective suppression strategies. Several successful invasive species have been found to form persistent seed banks in the soil, highlighting the significance of soil seed bank formation for their long-term survival (Fletcher et al., 2015; Gioria et al., 2012; Moravcová et al., 2018). However, comprehensive information on soil seed bank formation for individual species remains limited (Skálová et al., 2019).

Invasions by C4 grasses can result in decreasing species richness of the invaded habitats (see, e.g. Olsson et al., 2012; Reed et al., 2005; Török et al., 2021), generating great concern for nature conservation. One notable example among C4 grasses is the global spread of *Sporobolus* species, which has been reported in the last few decades from many continents including South America and Australia (Bortolus et al., 2015; Brooks et al., 2010; Rayment et al., 2022; Williams & Baruch, 2000). Taxonomically, the *Sporobolus* genus comprises 160 to 220 species, with variations arising from the inclusion of certain *Crypsis* or *Spartina* species into the genus (Peterson et al., 2014). In Europe, most *Sporobolus* species are non-native, with the exception of *Sporobolus pungens* (Bauer & Verloove, 2023).

Central Europe has recently observed the establishment and spread of three *Sporobolus* species native to temperate regions of North America (*Sporobolus vaginiflorus*, *Sporobolus neglectus* and *Sporobolus cryptandrus*), along with the establishment of a single tropical species, *Sporobolus indicus* (Bauer & Verloove, 2023). Notably, *S. neglectus*, *S. indicus* and *S. vaginiflorus* have been documented in the Mediterranean region and eastern central Europe (Englmaier & Wilhalm, 2018; Király, 2016; Király & Hohla, 2015). These species predominantly proliferate and rapidly spread on frequently mowed roadsides along highways, or in lawns characterised by frequent trampling (*S. indicus*, Bauer & Verloove, 2023). Due to the disturbed character of the habitats they invade, their establishment currently poses a relatively low threat to natural vegetation. In contrast, the current spread of *S. cryptandrus* in sandy areas affects not only disturbed grasslands and the verges of dirt roads but also large areas of semi-natural grasslands and forest steppes. In Hungary alone, over 620 distinct locations of the species have been detected, and its spread continues to expand (Török et al., 2021; Török & Aradi, 2017).

Most studies so far analysed only the effect of invasive species encroachment on the aboveground vegetation composition and diversity, while belowground processes including the effects of invasive species on the soil seed banks have only started to receive increasing attention in the past few years (See e.g. Gioria et al., 2019; Gioria & Pyšek, 2016). *S. cryptandrus* produces very small seeds in large

numbers (Brown, 1943) and it has been shown to form a soil seed bank in its native range (Clements et al., 2007). In the current study, we aimed to explore the effect of the encroachment of *S. cryptandrus* on the composition and diversity of soil seed banks in dry sand grasslands in Central Europe. We also intended to quantify the vertical distribution of the soil seed bank and to explore how dense the soil seed bank of this invasive perennial grass species is. We focused particularly on testing the following hypotheses: (i) The density and diversity of the soil seed bank of other species decreases with increasing cover of *S. cryptandrus*. (ii) The soil seed bank density of *S. cryptandrus* is highly affected by its cover: the soil seed bank density of the species increases with its increasing cover. (iii) Soil seed bank diversity and density decrease with increasing sampling depth, and this decrease in density is influenced by the cover of *S. cryptandrus*.

2 | MATERIALS AND METHODS

2.1 | Vegetation and soil seed bank sampling

Five mass-localities of *S. cryptandrus* were chosen for the study: one in the Nyírség region, Hungary (the Debrecen site), and four in the Kiskunság region, Hungary (the sites Kiskunhalas North, Kiskunhalas East, Kecskemét Airport and Kecskemét Katonatelep) (Table 1 and Figure 1). The climate of the two regions is fairly similar: the climate of both regions is continental with a sub-mediterranean influence in the Kiskunság. In the Nyírség region, the mean annual temperature is 9.4–9.8°C and the annual rainfall is between 530 and 680 mm (Dövényi, 2010). In the Kiskunság region, the mean annual temperature is 10.4°C and the yearly average precipitation is between 500 and 550 mm (Kovács-Láng et al., 2000).

In each site, we selected a sampling area of approximately 1 ha. In each sampling area, we sampled the vegetation in 1-m^2 plots in four cover categories of the species. The four cover categories were as follows: no *S. cryptandrus cover* (1), cover of *S. cryptandrus* is between 1% and 25% (2), 26%–50% (3) and 51%–75% (4). In total, in 200 plots (five sites × four cover categories × 10 plots), we visually estimated the percentage cover of all vascular plant species in the summer of 2019 (Hábenczyus et al., 2022). Vegetation data were used only (i) to assess the similarity between vegetation and soil seed banks in ordination and similarity calculations and (ii) to provide reference species lists for the seedling emergence study (for detailed vegetation data see the appendix of Török et al., 2021).

The composition and density of soil seed banks were assessed with intact soil coring and thin-layer seedling emergence method by Ter Heerdt et al. (1996). For each cover category, in three stratified but randomly selected 1 × 1 m plots, 10 soil cores (10 cm depth and 4 cm diameter, separated into four 2.5-cm-long vertical segments of 0–2.5, 2.5–5, 5–7.5 and 7.5–10 cm) were collected from late March to early April 2022. We opted for spring sampling to maximise the comparability of our results and the results of other soil seed bank studies conducted in the region. Matching vertical segments originating from a 1 m × 1 m plot were pooled and treated together during sample processing, resulting in four pooled samples for each 1 m^2 plot. We processed altogether 240 pooled soil samples (five sites × four cover categories × four vertical segments × three replications). Soil samples were concentrated by washing using two sieves with different mesh sizes (2.8 and 0.2 mm, Retsch GmbH). To ensure the effective separation of soil particles, we used a rough mesh for removing large organic and inorganic matter (e.g. root fragments or small stones). Subsequently, a fine sieve was applied to retain soil samples containing all the seeds while reducing bulk by washing out

TABLE 1 Environmental characteristics of the study sites.

Site characteristics	Study sites				
	Debrecen	Kiskunhalas North	Kecskemét Katonatelep	Kecskemét Airport	Kiskunhalas East
Coordinates	47.55422 N	46.48243 N	46.95044 N	46.92774 N	46.40935 N
	21.61537 E	19.47987 E	19.76217 E	19.72590 E	19.56305 E
Subjected habitat type	Degraded urban sand grassland	Natural sand steppe surrounded with pine plantations	Meadow steppes managed by grazing	Sandy old-field (>30 years abandoned)	Sandy forest steppe
Soil characteristics					
Physical soil type	Loam/clay-loam	Sand/sandy loam	Loam/clay-loam	Sandy loam/loam	sandy loam/loam
pH	5.99–6.42	6.67–7.24	6.98–7.35	7.46–7.48	7.31–7.53
$CaCO_3$ (m/m%)	0.10–0.21	1.19–2.59	0.10–2.45	1.19–3.57	1.82–3.26
Nitrogen (NO_2-NO_3, mg/kg)	1.25–8.38	2.15–3.25	1.32–5.35	1.30–2.32	1.25–3.78
Phosphorous (P_2O_5, mg/kg)	246–523	29–60	65–179	41–104	23–54
Potassium (K_2O, mg/kg)	244–430	40–87	132–192	114–123	42–68
Humus (m/m%)	2.33–4.44	0.87–1.95	1.79–2.96	1.61–2.38	0.52–1.89

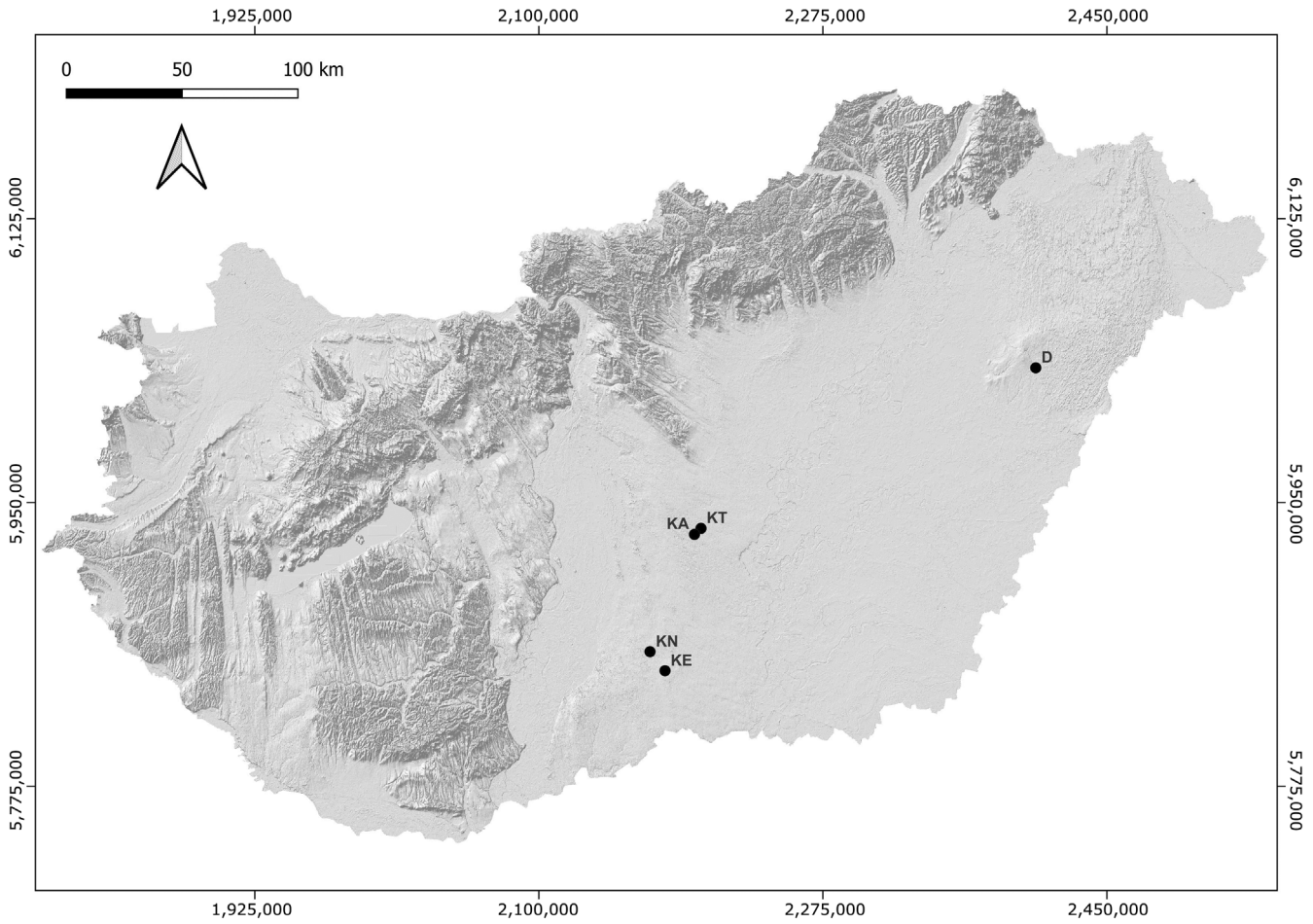


FIGURE 1 The sampled *Sporobolus cryptandrus* sites in Hungary, Central Europe. The dots show the study sites within the country, abbreviated as: D, Debrecen; KA, Kecskemét Airport; KE, Kiskunhalas East; KN, Kiskunhalas North; KT, Kecskemét Katonatelep.

fine clayey particles. After soil concentration, the samples were spread in a few millimetres in thickness, onto flowerpots (60 cm × 15 cm) filled with steam-sterilised potting soil. These flowerpots were placed in an unheated greenhouse located in the Botanical Garden of the University of Debrecen. The pots were regularly watered and checked for emerged seedlings. Seedlings were regularly counted and removed or transplanted into separate pots for later identification. The germination period extended from early April to mid-November (altogether, 32 weeks). We also included a watering break from late June until to end of August (altogether 8 weeks). During this time, we let the sample surface get dry to mimic the natural heat and drought conditions of the summer period (see also Török et al., 2018 and Valkó et al., 2021), as this heat stratification may be needed to break the dormancy of the seeds of some species (Baskin & Baskin, 1998; Finch-Savage & Leubner-Metzger, 2006). During this interval, no seedlings emerged. Following the watering break, regular watering resumed and the germination process continued until mid-November, at which point the conditions became unfavourable for further germination.

At the end of the germination period, we identified all seedlings at the lowest possible taxonomic level, most individuals to the species level. Based on a former small-scale germination experiment with autumn-collected samples (Török et al., 2021) we were able to identify *S. cryptandrus* seedlings at a very early stage, which enabled us to count and remove them from the flowerpots. In case of graminoids, we pooled vegetative individuals of *Carex stenophylla* with *Carex liparicarpos* and *Typha latifolia* with *Typha angustifolia* as we were not able to grow them until identification at the species level was possible. In case of dicots, we pooled the seedlings of *Arenaria leptoclados* with *Arenaria serpyllifolia*, *Artemisia scoparia* with *Artemisia campestris* and *Polygonum aviculare* with *Polygonum arenarium*.

We also monitored the airborne seed contamination (especially crucial in the autumn period of germination) by including sample-free control flowerpots filled with steam-sterilised potting soil only. Seed contamination was primarily detected in the autumn period. Seedlings of wind-dispersed short-lived weeds or trees (*Sonchus oleraceus*—three seedlings, *Conyza canadensis*—10 seedlings, *Senecio vulgaris*—one seedling, *Populus* spp.—four seedlings) and other short-lived weedy species occurring in the close vicinity of the greenhouse (*Geranium molle*—two seedlings, *Oxalis* ***corniculata***—seven seedlings) were established in the control pots. We considered these and decreased the number of the germinated seedlings of these species in the

flowerpots accordingly or totally excluded them when it was deemed necessary.

Only a very small fraction of the seedlings was unidentified at the species level, either because they perished before identification, or because they did not develop diagnostic features even after 1 year (a few dicots, and *Carex* specimens; 16 individuals in total, less than 0.1% of all emerged seedlings, these were omitted from analyses). For the comparisons of species composition of vegetation and soil seed banks, we applied the same pooling also for the vegetation data.

2.2 | Data analyses

Two-way ANOVAs were calculated to compare the diversity and density of soil seedbanks of different sites. In these calculations, the four vertical segments of the soil seed bank samples were pooled and *S. cryptandrus* cover categories (ordinal variable) and site (nominal variable) were included as fixed factors. Dependent variables were soil seed bank density, species richness, Shannon diversity and Pielou's evenness calculated with the exclusion of *S. cryptandrus*. We also included the soil seed bank density of *S. cryptandrus* and the proportion of *S. cryptandrus* seeds in the soil seed banks as dependent variables. Two-way GLMMs were calculated to analyse the effect of sampling depth (ordinal variable), *S. cryptandrus* cover (ordinal variable) and their interactions on soil seed bank characteristics like soil seed bank density, species richness, Shannon diversity and Pielou's evenness calculated with the exclusion of *S. cryptandrus*. We also included the soil seed bank density of *S. cryptandrus* and the proportion of *S. cryptandrus* seeds in the total soil seed banks as dependent variables. Site identity was included as random factor in the latter calculations. Seed density scores were square root transformed to improve normality before the analyses. For the calculation of GLMs and GLMMs we used SPSS 26.0 (IBM Corp., 2019). We calculated Sørensen similarity index (Sørensen, 1948) between vegetation and soil seed banks with the following equation: $2a/(A + B)$, where 'a' is the number of species present both in vegetation and soil seed banks, 'A' and 'B' are the total number of species in the vegetation or soil seed banks respectively. We prepared two separate DCA ordinations for revealing compositional patterns. The first ordination was based on germinated seedling numbers of species, and the soil seed bank composition of different sites was compared. In the second ordination, we compared presence–absence datasets of vegetation and soil seed banks of different sites. Both ordinations were calculated using CANOCO 5.0 program package (Šmilauer & Lepš, 2014).

3 | RESULTS

3.1 | Composition and density of soil seed bank

Besides *S. cryptandrus*, we found 92 species in the soil seed banks. Only 30 species comprised more than 90% of all viable seeds of the total soil seed bank density (Appendix A). Species with over 100 viable seeds included *C. canadensis* (847 seeds), *Portulaca oleracea* (774), *A. serpyllifolia* (700), *Cerastium semidecandrum* (126), *C. stenophylla* (112) and *Potentilla argentea* (105). Altogether 19,313 seedlings emerged from the soil samples, out of these 15,149 were the seedlings of *S. cryptandrus*.

There were high differences both in the total soil seed bank densities and in the *S. cryptandrus* soil seed bank densities between the study sites (Table 2). The lowest soil seed bank densities were detected in the Kiskunhalas North site and almost 10 times higher values were found in the Debrecen site. The highest density of *S. cryptandrus* soil seed banks was detected in the Kecskemét Katonatelep site, the highest mean seed densities of the species were detected at cover category 4 and reached 95,000 seeds per m^2 (Table 2). We found that increasing the cover of *S. cryptandrus* did not affect most of the studied soil seed bank characteristics. However, the soil seed bank density and the proportion of *S. cryptandrus* seeds in the soil seed bank were affected by *S. cryptandrus* cover and the highest soil seed bank densities of the species were found in plots with the highest cover of the species. All the studied soil seed bank characteristics were, however, affected by the study site, and in case of the density and proportion of *S. cryptandrus* soil seed bank, Shannon diversity and Pielou's evenness, the effect of the interaction between *S. cryptandrus* cover and site identity was also significant (Table 3).

The similarity of the vegetation and the soil seed banks was the highest in the Debrecen site, where the Sørensen similarity ranged between 0.32 and 0.59. For the other sites in the Kiskunság region, much lower scores were typical (0.10–0.31). This is also clearly shown by the presence-absence DCA ordination in Figure 2. It is also clearly shown that the species composition of vegetation and soil seed banks were clearly separated. The point clouds representing the vegetation and soil seed bank composition of the Debrecen site were both clearly separated from that of the other four sites (Figure 2). The soil seed bank composition of the Debrecen site is clearly separated from the point clouds for the Kecskemét Airport and Kiskunhalas North sites, while the other two sites were scaled in between these three sites (Figure 3).

3.2 | Vertical composition and density of the soil seed bank

Both total soil seed bank density and the density of *S. cryptandrus* seeds were the highest in the upper 2.5 cm of the soil. Most of the studied soil seed bank characteristics were affected by the sampling depth, and none of the studied characteristics were affected by the increasing cover of *S. cryptandrus*. According to the model of *S. cryptandrus* seed density, the interaction between *S. cryptandrus* cover and sampling depth was also significant (Table 4). It was found that the density of *S. cryptandrus* seeds in the upper 2.5 cm of the soil was much higher in the high cover plots (3rd and 4th cover category) than in the case of lower cover plots (Figure 4). A similar but less pronounced pattern was found for the seed density of the species in the deeper soil layers: the seed density of *S. cryptandrus* was much higher in the deeper soil layers of the high cover plots than in that of the low cover plots.

TABLE 2 Most important characteristics of the soil seed banks of the different study sites.

	Cover category of *Sporobolus cryptandrus*			
	1	2	3	4
Debrecen				
Seed bank density[a]	8727 ± 3000	10,425 ± 46	8223 ± 1960	12,228 ± 2488
Sporobolus cryptandrus seed density	318 ± 183	345 ± 148	2387 ± 452	3024 ± 443
Proportion of *Sporobolus cryptandrus* seeds (%)	5.2 ± 4.2	3.2 ± 1.3	23.3 ± 2.5	21.1 ± 5.5
Species richness[a]	17.3 ± 0.3	13.0 ± 1.7	7.7 ± 1.2	10.7 ± 1.5
Shannon diversity[a]	2.52 ± 0.08	1.52 ± 0.20	0.93 ± 0.16	1.00 ± 0.27
Pielou's evenness[a]	0.88 ± 0.02	0.59 ± 0.06	0.47 ± 0.09	0.42 ± 0.09
Kiskunhalas North				
Seed bank density[a]	716 ± 122	1034 ± 518	1406 ± 70	1088 ± 299
Sporobolus cryptandrus seed density	186 ± 116	1114 ± 301	6446 ± 2671	9921 ± 2128
Proportion of *Sporobolus cryptandrus* seeds (%)	18.8 ± 9.5	55.4 ± 16.4	78.4 ± 5.7	90.4 ± 0.8
Species richness[a]	2.3 ± 0.9	5.0 ± 0.6	5.7 ± 0.3	5.7 ± 0.9
Shannon diversity[a]	0.65 ± 0.37	1.35 ± 0.10	1.37 ± 0.07	1.47 ± 0.11
Pielou's evenness[a]	0.63 ± 0.31	0.86 ± 0.08	0.79 ± 0.02	0.86 ± 0.03
Kecskemét Katonatelep				
Seed bank density[a]	4775 ± 1143	5411 ± 1658	5968 ± 622	3395 ± 879
Sporobolus cryptandrus seed density	637 ± 184	33,555 ± 11,149	85,731 ± 42,584	95,413 ± 7470
Proportion of *Sporobolus cryptandrus* seeds (%)	13.8 ± 6.5	82.8 ± 6.8	90.8 ± 3.3	96.6 ± 0.78
Species richness[a]	16.0 ± 1.5	13.7 ± 3.9	12.3 ± 1.5	11.0 ± 1.5
Shannon diversity[a]	2.44 ± 0.08	1.88 ± 0.24	1.80 ± 0.14	1.90 ± 0.13
Pielou's evenness[a]	0.88 ± 0.03	0.76 ± 0.04	0.72 ± 0.06	0.80 ± 0.03
Kecskemét Airport				
Seed bank density[a]	4669 ± 853	3263 ± 279	3979 ± 858	6048 ± 4109
Sporobolus cryptandrus seed density	80 ± 46	32,786 ± 2529	60,028 ± 10,928	51,460 ± 4464
Proportion of *Sporobolus cryptandrus* seeds (%)	1.9 ± 1.0	90.9 ± 1.0	93.7 ± 1.1	90.9 ± 5.3
Species richness[a]	11.3 ± 1.5	9.3 ± 1.5	10.0 ± 1.7	9.3 ± 2.8
Shannon diversity[a]	1.81 ± 0.05	1.79 ± 0.10	1.68 ± 0.13	1.59 ± 0.07
Pielou's evenness[a]	0.76 ± 0.06	0.81 ± 0.01	0.74 ± 0.02	0.76 ± 0.06
Kiskunhalas East				
Seed bank density[a]	4801 ± 2193	13,608 ± 4728	6764 ± 1874	3925 ± 2654
Sporobolus cryptandrus seed density	106 ± 27	3183 ± 211	6923 ± 557	8196 ± 2087
Proportion of *Sporobolus cryptandrus* seeds (%)	3.4 ± 1.8	23.3 ± 7.5	52.2 ± 8.2	71.1 ± 15.1
Species richness[a]	14.0 ± 2.3	7.7 ± 1.5	10.0 ± 2.0	10.7 ± 4.3
Shannon diversity[a]	2.03 ± 0.17	0.66 ± 0.05	1.39 ± 0.36	1.91 ± 0.28
Pielou's evenness[a]	0.79 ± 0.09	0.34 ± 0.06	0.60 ± 0.11	0.87 ± 0.02

Note: Density scores are calculated as seeds/m^2 in the upper 10 cm soil layer (one-way ANOVA and Tukey test). Cover categories of *Sporobolus cryptandrus*: (1) no cover; (2) cover between 1% and 25%; (3) cover between 26% and 50%; (4) cover between 51% and 75%.
[a]Calculated with the exclusion of *Sporobolus cryptandrus* (Mean ± SE).

4 | DISCUSSION

4.1 | Composition and density of the soil seed bank

We hypothesised that the soil seed bank diversity and density of other species decrease with the increasing cover of *S. cryptandrus*. This hypothesis was not supported by the results as neither the diversity nor the density of the soil seed bank was affected by increasing *S. cryptandrus* cover. Former results indicated that the change in the composition of soil seed banks is much slower compared to the aboveground vegetation which is also the reason why soil seed banks can act as successional memory reflecting the past composition of the vegetation (Sun et al., 2013; Tóth et al., 2022). A meta-analysis

TABLE 3 Effect of *Sporobolus cryptandrus* cover, site and their interaction on soil seed bank characteristics.

	Sporobolus cryptandrus cover		Site		*Sporobolus cryptandrus* cover × site	
Seed bank characteristic	$F_{3,40}$	*p*	$F_{4,40}$	*p*	$F_{12,40}$	*p*
Seed bank density[a]	0.836	0.482	**15.944**	**<0.001**	1.180	0.329
Sporobolus seed density	**5.444**	**0.003**	**59.278**	**<0.001**	**6.955**	**<0.001**
Proportion of *Sporobolus cryptandrus* seeds (%)	**8.718**	**<0.001**	**52.353**	**<0.001**	**6.316**	**<0.001**
Species richness[a]	0.242	0.866	**11.600**	**<0.001**	1.427	0.194
Shannon diversity[a]	0.628	0.601	**10.533**	**<0.001**	**6.942**	**<0.001**
Pielou's evenness[a]	0.195	0.899	**4.053**	**0.008**	**2.982**	**0.005**

Note: Significant effects are denoted with bold face ($p < 0.05$), marginally significant effects ($p < 0.1$) with *italics* (two-way GLMs).
[a]Calculated with the exclusion of *S. cryptandrus*.

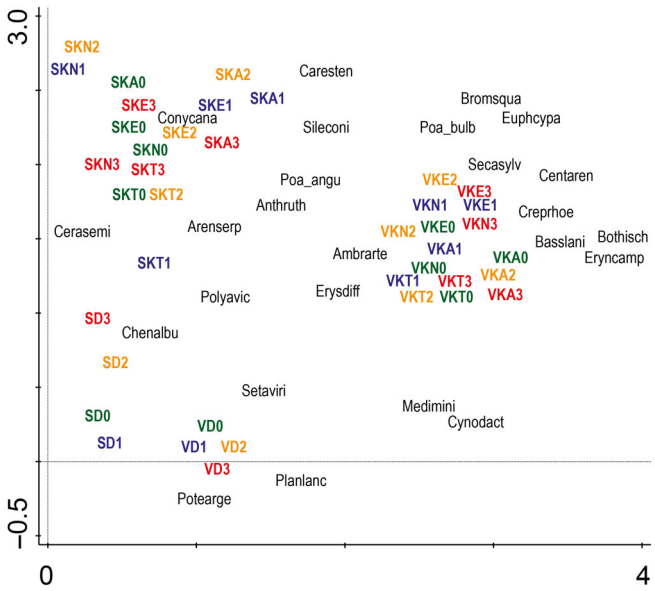


FIGURE 2 The similarity of vegetation and soil seed banks of the studied sites displayed by a DCA ordination based on presence–absence datasets of vegetation and soil seed banks. The gradient length of the first and second axis are 5.32 and 4.07 respectively. Notations: First letter of the site codes denotes with V—vegetation or S—soil seed bank, second one or two letters denote the sites D, Debrecen; KA, Kecskemét Airport; KE, Kiskunhalas East; KN, Kiskunhalas North; KT, Kecskemét Katonatelep. Different numbers and colours denote the cover categories of *Sporobolus cryptandrus*. 0 and green = 0% of *S. cryptandrus*, while 1 with blue = 1%–25%, 2 with orange = 26%–50%, 3 with red = 51%–75% respectively. The most frequent 30 species are shown with an abbreviation of four letters of the genus and four letters of species names as follows: Ambrarte, *Ambrosia artemisiifolia*; Anthruth, *Anthemis ruthenica*; Arenserp, *Arenaria serpyllifolia*; Basslani, *Bassia laniflora*; Botrisch, *Botriochloa ischaemum*; Bromsqua, *Bromus squarrosus*; Caresten, *Carex stenophylla*; Centaren, *Centaurea arenaria*; Cerasemi, *Cerastium semidecandrum*; Chenalbu, *Chenopodium album*; Conycana, *Conyza canadensis*; Creprhoe, *Crepis rhoeadifolia*; Cynodact, *Cynodon dactylon*; Eryncamp, *Eryngium campestre*; Erysdiff, *Erysimum diffusum*; Euphcypa, *Euphorbia cyparissias*; Medimini, *Medicago minima*; Planlanc, *Plantago lanceolata*; Poa_angu, *Poa angustifolia*; Poa_bulb, *Poa bulbosa*; Polyavic, *Polygonum aviculare*; Potearge, *Potentilla argentea*; Secasylv, *Secale sylvestre*; Setaviri, *Setaria viridis*; Sileconi, *Silene conica*. [Colour figure can be viewed at wileyonlinelibrary.com]

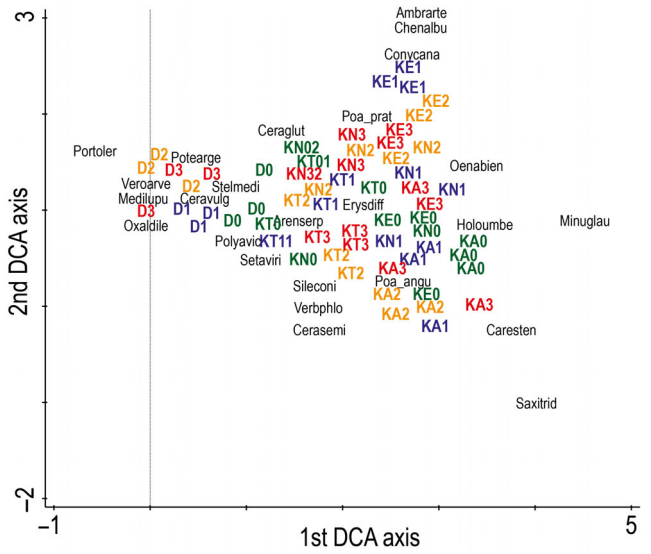


FIGURE 3 The similarity of seed banks of the studied sites displayed by a DCA ordination based on seedling numbers. The gradient length of the first and second axis are 3.57 and 3.01 respectively. Notations: The letters denote the sites D, Debrecen; KA, Kecskemét Airport; KE, Kiskunhalas East; KN, Kiskunhalas North; KT, Kecskemét Katonatelep. Different first numbers and colours denote the cover categories of *Sporobolus cryptandrus*. 0 and green = 0% of *S. cryptandrus*, 1 and blue = 1%–25%, 2 and orange = 26%–50%, 3 and red = 51%–75% respectively. The most abundant 30 species are shown with an abbreviation of four letters of the genus and four letters of species names as follows in order of decreasing number of seedlings: Ambrarte, *Ambrosia artemisiifolia*; Arenserp, *Arenaria serpyllifolia*; Caresten, *Carex stenophylla*; Ceraglut, *Cerastium glutinosum*; Cerasemi, *Cerastium semidecandrum*; Ceravulg, *Cerastium vulgare*; Chenalbu, *Chenopodium album*; Conycana, *Conyza canadensis*; Erysdiff, *Erysimum diffusum*; Holoumbe, *Holosteum umbellatum*; Medilupu, *Medicago lupulina*; Minuglau, *Minuartia glaucina*; Oenobien, *Oenothera biennis*; *Oxaldill*, *Oxalis dillenii*; Poa_angu, *Poa angustifolia*; Poa_prat, *Poa pratensis*; Polyavic, *Polygonum aviculare*; Portoler, *Portulaca oleracea*; Potearge, *Potentilla argentea*; Saxitrid, *Saxifraga tridactylites*; Setaviri, *Setaria viridis*; Sileconi, *Silene conica*; Stelmedi, *Stellaria media*; Verbphlo, *Verbascum phlomoides*; Veroarve, *Veronica arvensis*. [Colour figure can be viewed at wileyonlinelibrary.com]

by Gioria et al. (2014) indicated that plant invasions generally reduce the density and species richness of the soil seed banks of the subjected community. Hager et al. (2015) found a markedly negative

TABLE 4 Effect of *Sporobolus cryptandrus* cover, sampling depth and their interaction on soil seed bank characteristics.

Seed bank characteristic	*Sporobolus cryptandrus* cover		Sampling depth		*Sporobolus cryptandrus* cover × sampling depth	
	$F_{3,224}$	*p*	$F_{3,224}$	*p*	$F_{9,224}$	*P*
Seed bank density[a]	1.166	0.324	**74.465**	**<0.001**	0.403	0.933
Sporobolus cryptandrus seed density	0.657	0.579	**45.443**	**<0.001**	**4.481**	**<0.001**
Proportion of *Sporobolus cryptandrus* seeds (%)	1.878	0.134	**5.030**	**0.002**	0.592	0.803
Species richness[a]	0.084	0.969	**62.106**	**<0.001**	0.909	0.518
Shannon diversity[a]	0.069	0.976	**34.571**	**<0.001**	0.501	0.873
Pielou's evenness[a]	0.005	1.000	*2.455*	*0.064*	0.485	0.884

Note: Significant effects are denoted with bold face ($p < 0.05$), marginally significant effects ($p < 0.1$) with *italics* (two-way GLMMs). Site identity was included as a random factor to the calculations.
[a]Calculated with the exclusion of *S. cryptandrus*.

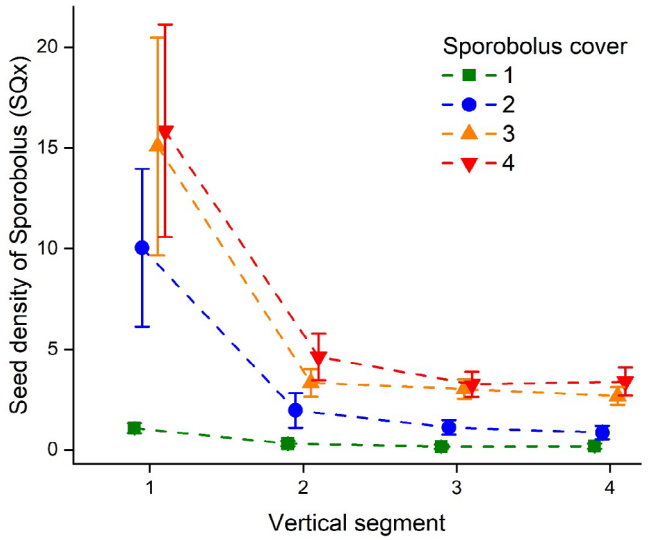


FIGURE 4 Density of *Sporobolus cryptandrus* seeds in different vertical segments of the soil seed bank in plots with different cover of the species (Square root/SQ transformed data). Cover categories: no *S. cryptandrus* cover (1), cover of *Sporobolus cryptandrus* is between 1% and 25% (2), 26%–50% (3) and 51%–75% (4) respectively. Vertical segments: 1 = 0–2.5 cm, 2 = 2.5–5 cm, 3 = 5–7.5 cm and 4 = 7.5–10 cm respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

effect of invasive species encroachment on soil seed bank diversity and a less marked negative effect on the density of the soil seed bank. Upon excluding the seed bank of the invasive species from the analyses, we observed that neither the density nor the diversity of the seed banks in the studied communities were affected by the invasive species. There may be several reasons for these contrasting results. First, the composition of the soil seed bank is highly conservative and changes rather slowly, thereby acting as a successional memory of the community. For evaluating the effects of an invasive species on the soil seed bank it is important to know the residence time of the invasive species, that is, the time elapsed since the invasive species was established in a particular site or community (Gioria & Pyšek, 2016). In our case, we assume, considering also the regular field works and monitoring activities of the national park rangers in the region, that in most of the study sites the establishment of the species is quite recent and its residence time should not be longer than a maximum of about 10–15 years (the first discovery of the species in Hungary was near the Debrecen site in 2016, Török et al., 2018). Second, as *S. cryptandrus* is a tussock-forming species (bunchgrass) with a very limited ability of clonal spreading, it does not form a very dense plant cover compared to some clonally spreading grasses like *Calamagrostis* or *Elymus* species (it was rare that its cover exceeded 60% in our study sites). Thus, it is also possible that its spread causes weaker dispersal and establishment limitation than some other invasive but clonally spreading species which form a dense and more even cover of the soil surface.

The density and diversity of soil seed banks (excluding *S. cryptandrus*) were highly affected by the site, but none of the studied characteristics were affected by the increasing cover of *S. cryptandrus* except for the proportion of the species' seeds in the soil seed bank. In former studies, it was found that the soil seed bank density of sand grasslands ranged from a few hundred to a couple of 10,000 seeds per square meter considering the upper 5 or 10 cm layer of the soil (see e.g. Godefroid et al., 2018; Symonides, 1979 and Török et al., 2018). Besides the study region, soil seed bank densities in our study sites were presumably also influenced by water availability and degradation status (Thompson et al., 1997). In our study, the highest density of soil seed banks not considering the seeds of the invasive species has been detected at the Debrecen site, which is a degraded grassland with many weedy species in the vegetation, which usually form persistent soil seed banks. The high site effect also points out that the density and composition of soil seed banks are highly conservative and, as also found in other studies, it reflects the past vegetation composition of the sites (Bossuyt & Honnay, 2008; Wellstein et al., 2007).

Hopfensperger (2007) stressed that in grasslands similarity between the standing vegetation and the soil seed bank is higher compared to wetland and forest ecosystems. Similarity between the standing vegetation and the soil seed bank can be variable even within

grasslands: low similarity is typical for sand grassland, for example (Godefroid et al., 2018; Török et al., 2018), but similarity is higher, for example, in fen meadows and alkali grasslands (Valkó et al., 2011, 2014). It was also shown that the similarity between the vegetation and the soil seed bank is strongly influenced by grassland management, disturbances, different conditions of stress and by dispersal and establishment limitations (Auestad et al., 2013; Valkó et al., 2014). We found the highest similarity between the vegetation and the soil seed bank in the Debrecen site; the similarities for the other four sites in the Kiskunság were rather low. These findings are also in line with our results on soil seed bank densities and suggest that the composition of the soil seed bank and its similarity to the composition of aboveground vegetation are both highly site-dependent.

4.2 | The soil seed bank density of *S. cryptandrus*

We hypothesised that the soil seed bank density of *S. cryptandrus* is highly affected by its cover and the soil seed bank density of the species increases with its increasing cover. This hypothesis was supported by our results. The soil seed bank formation ability of *S. cryptandrus* has been previously validated in its native range (Clements et al., 2007). In the present study, we demonstrated that it forms a massive soil seed bank in invaded grasslands as well. Gioria et al. (2012) listed only 36 species for which soil seed bank studies are available in their introduced ranges. Unfortunately, for perennial grasses, soil seed bank data was collected only for *Agropyron desertorum* invasion in North America in which only sporadic soil seed banks (up to 93 seeds/m^2) have been validated for the species in invaded sites (Gioria et al., 2012). In contrast, we found that in some of the sites, the seed density of *S. cryptandrus* exceeded several tens of thousands of seeds per square metre. We also found that the increasing cover of the species caused an increasing proportion of *S. cryptandrus* seeds in the total soil seed bank, and even in plots with no *S. cryptandrus* cover, we found some viable seeds of the species in the soil. This can be explained by the massive seed production and effective dispersal of the species (Ingimarsdóttir et al., 2012; Shmida & Wilson, 1985). Former studies indicated that the yearly seed production of the species can reach 10,000 seeds per individual; the seeds of the species are tiny (approx. 1 mm in diameter) and likely being incorporated in the soil seed banks. By a very small-scale autumn sampling in the Debrecen site in 2019, we also found that the species built up a persistent soil seed bank of 1114–3077 seeds/m^2 (Török et al., 2021). Comparing these results with our current findings for spring samples (637–3899 seeds/m^2), considering that the species germinates in the spring, we can assume that the species builds up a considerably dense persistent soil seed bank in all sites.

The detected soil seed bank density of *S. cryptandrus* in some sites is comparable to the seed density of small-seeded hygrophytic graminoids in some wet grassland habitats, and much higher than that of characteristic grass species in primary and secondary dry grasslands in the region. Many characteristic perennial C3 grass species of dry grasslands with relatively high cover in the vegetation (>20%) like *Festuca vaginata* (Török et al., 2018), *Festuca pseudovina* (Valkó et al., 2014), *Poa angustifolia* (Török et al., 2009, 2018), or some *Stipa* species (Török et al., 2018) possessed much lower density soil seed banks (up to 1200–1400 seeds/m^2 for the upper 10 cm of the soil) than *S. cryptandrus* in our study. Among the perennial grasses that have at least 5% cover in the vegetation in at least one of the study sites (reported in Török et al., 2021), we detected soil seed bank only for *Calamagrostis epigeios* (80 seeds/m^2), *Lolium perenne* (239 seeds/m^2), *F. pseudovina* (up to 318 seeds/m^2) and *P. angustifolia* (up to 2308 seeds/m^2). Large-seeded wetland graminoids such as *Elymus athericus* (Erfanzadeh et al., 2010) were found not forming a seed bank, but high soil seed bank density scores similar to what we found for *S. cryptandrus* are typical for small-seeded but hygrophytic perennial graminoids like *Scirpoides holoschoenus* (Török et al., 2018), *Agrostis stolonifera* and several *Juncus* species (found in many studies, see e.g. Schmiede et al., 2009; Valkó et al., 2011, 2014).

Although existing information on the residence time of *S. cryptandrus* in our sites is scarce and largely based on anecdotal evidence and estimations (up to 10–15 years), we can consider the plots with progressively increasing invasive species cover as a temporal scale to assess the invasion's progression (space-for-time substitution, Miao et al., 2018; Wang et al., 2022). In line with our findings, previous studies comparing stands invaded for different durations have demonstrated that long-term invaded stands have higher seed abundance and greater impact on vegetation compared to recently invaded stands (Gioria & Pyšek, 2016). Due to its quickly accumulating soil seed bank, spending more time trying to understand the characteristics of this invasive species will probably make its suppression more costly and difficult (Simberloff, 2003). Moreover, the droughts becoming more and more frequent and severe in several regions can cause the dieback of native plants (Miao et al., 2022, Orbán et al., 2023), creating further opportunities for *S. cryptandrus* to colonise natural grasslands. Thus, we emphasise the critical importance of initiating management actions aimed at suppressing *S. cryptandrus* as soon as possible, in the meantime conducting further studies on the ecology and population biology of the species.

4.3 | Vertical composition and density of the soil seed bank

We hypothesised that both soil seed bank diversity and density decrease with increasing sampling depth and that the decrease in density is affected by the increasing *S. cryptandrus* cover. This hypothesis was only partly supported: while the diversity and density of soil seed banks decreased with increasing soil depth, the decrease in its density was not affected by *S. cryptandrus* cover. Gioria and Pyšek (2016) suggested that future soil seed bank studies focusing on the effect of invasive species should consider the seed bank in different soil layers. This knowledge can help in the assessment of the persistence of the invasive species seed banks and also to assess the effect of possible accumulation of the seeds of invasive species on the persistent soil seed banks of the deeper soil layers (Gioria et al., 2011; Gioria &

Osborne, 2010; Gioria & Pyšek, 2016; Holmes, 2002). In our study, we analysed four 2.5 cm soil segments and analysed the seed bank composition of both the invasive species and the subjected community. All soil seed bank characteristics were affected by the increasing sampling depth; there was a decreasing richness, diversity and soil seed bank density detected with an increasing sampling depth. The same results were found in most soil seed bank studies in various types of grasslands and regions (Godefroid et al., 2006; Luzuriaga et al., 2005; Niknam et al., 2018; Qian et al., 2016). It is also stated that viable seeds detected in deeper soil layers are likely older than those detected in more shallow layers because getting incorporated into deeper soil layers takes more time (Bekker et al., 1998). It was found also by other studies that the density of soil seed banks is rapidly decreasing with increasing soil depth and in general the upper few centimetres of the soil contain a high proportion of the soil seed banks (Bekker et al., 1998; Ma et al., 2010; Tóth et al., 2022). This was also validated by the current study, as most of the seeds both for other species and the invasive species were located in the upper 5 cm of the soil.

In a former laboratory experiment, we found that 1 cm of soil covering was enough to significantly decrease the germination percentage of the seeds of *S. cryptandrus* (Török et al., 2021). This effect is even stronger when there is some litter covering the soil surface. This implies that the successful re-establishment of the species even in sites with its high-density soil seed banks needs at least shallow soil disturbance and the formation of gaps in the vegetation with bare soil. It was also found in the current study that the density of *S. cryptandrus* seeds in the upper 2.5 cm of the soil increased with higher magnitude in the soil of high cover plots than in plots with lower cover of the species and also distinct patterns for the deeper soil layers were found for the first two lower cover categories than for the last two higher ones (See Figure 4). This means that the massive seed production of *S. cryptandrus* in the two higher cover categories results in an increased density of the species' soil seed bank in the deeper layers as well.

5 | CONCLUSIONS

We found that *S. cryptandrus* forms a high-density soil seed bank, highly supporting its local establishment and persistence. These findings suggest that the suppression and/or eradication of this invasive species will be especially challenging. Our findings suggest that the eradication of the species can be the most successful in sites where the establishment of the species is very recent and its cover is still low because at those sites the species has a relatively low seed density at least in the deeper soil layers. This means that immediate actions would be necessary in sites where the species was established only recently to avoid the accumulation of its soil seed bank. Our result that the species generates a dense soil seed bank even at sites where it does not have a very high cover yet indicates that any intervention that would disturb the soil surface could result in the activation of this seed bank and thus in an even faster spread of the species. Therefore, control methods that generate soil disturbance and patches with bare soil surface should be avoided. If the physical removal of tussocks is necessary, it should be accompanied by soil covering by hay or grass litter, which was previously found to effectively prevent the germination of the seeds. The exceptionally long and dramatic drought to which our study region has been exposed in the past few years resulted in some dieback of the native perennial species. This dieback of native plants, together with the dense soil seed bank formation of *S. cryptandrus*, forecasts the further rapid spread of this invasive species in the region, which should be closely monitored in the forthcoming years.

ACKNOWLEDGEMENTS

The authors are thankful for the Botanical Garden, University of Debrecen (in particular, László Papp director) providing germination facilities and support. We are indebted to Evelin Károlyi, Szilvia Madar and Luca Di Vita for their help in taking care of the samples. PT was supported by the Hungarian Research Fund (NKFIH Grants: K 137573 and KKP 144068) during manuscript preparation. JS: PD 137747 and Bolyai János Scholarship of the Hungarian Academy of Sciences (BO/00587/23/8). The authors are thankful for the comments and suggestions of three anonymous reviewers and editor to a former version of the ms.

CONFLICT OF INTEREST STATEMENT

The authors declare that the published research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

Detailed underlying data summarised in the Appendix are available on request from the corresponding author.

ORCID

Péter Török https://orcid.org/0000-0002-4428-3327
Alida Anna Hábenczyus https://orcid.org/0000-0003-0905-6724
Gergely Kovacsics-Vári https://orcid.org/0000-0002-9995-5733
Csaba Tölgyesi https://orcid.org/0000-0002-0770-2107
Béla Tóthmérész https://orcid.org/0000-0002-4766-7668
Judit Sonkoly https://orcid.org/0000-0002-4301-5240

REFERENCES

Auestad, I., Rydgren, K., & Spindelböck, J. P. (2013). Management history affects grassland seed bank build-up. *Plant Ecology*, *214*, 1467–1477. https://doi.org/10.1007/s11258-013-0267-x

Baskin, C. C., & Baskin, J. M. (1998). *Seeds: Ecology, biogeography, and, evolution of dormancy and germination*. Elsevier.

Bauer, N., & Verloove, F. (2023). The accelerated spread of a neophyte introduced to Europe long ago - First occurrence of *Sporobolus indicus* (Poaceae) in Hungary. *Acta Botanica Croatica*, *82*, 20–26. https://doi.org/10.37427/botcro-2022-024

Bekker, R. M., Bakker, J. P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K., & Willems, J. H. (1998). Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. *Functional Ecology*, *12*, 834–842. https://doi.org/10.1046/j.1365-2435.1998.00252.x

Bortolus, A., Carlton, J. T., & Schwindt, E. (2015). Reimagining south American coasts: Unveiling the hidden invasion history of an iconic ecological engineer. *Diversity and Distributions*, *21*, 1267–1283.

Bossuyt, B., & Honnay, O. (2008). Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. *Journal of Vegetation Science*, *19*, 875–884. https://doi.org/10.3170/2008-8-18462

Brooks, K. J., Setterfield, S. A., & Douglas, M. M. (2010). Exotic grass invasions: Applying a conceptual framework to the dynamics of degradation and restoration in Australia's tropical savannas. *Restoration Ecology*, *18*, 188–197. https://doi.org/10.1111/j.1526-100X.2008.00470.x

Brown, H. R. (1943). Growth and seed yields of native prairie plants in various habitats of the mixed-prairie. *Transactions of the Kansas Academy of Science*, *46*, 87–99.

Chuine, I., Morin, X., Sonié, L., Collin, C., Fabreguettes, J., Degueldre, D., Salager, J.-L., & Roy, J. (2012). Climate change might increase the invasion potential of the alien C4 grass *Setaria parviflora* (Poaceae) in the Mediterranean Basin. *Diversity and Distributions*, *18*, 661–672. https://doi.org/10.1111/j.1472-4642.2011.00880.x

Clements, D. R., Krannitz, P. G., & Gillespie, S. M. (2007). Seed bank responses to grazing history by invasive and native plant species in a semi-desert shrub-steppe environment. *Northwest Science*, *81*, 37–49. https://doi.org/10.3955/0029-344X-81.1.37

Dairel, M., & Fidelis, A. (2020). The presence of invasive grasses affects the soil seed bank composition and dynamics of both invaded and non-invaded areas of open savannas. *Journal of Environmental Management*, *276*, 111291. https://doi.org/10.1016/j.jenvman.2020.111291

de Deus Vidal, J., Jr., le Roux, P. C., Johnson, S. D., te Beest, M., & Clark, V. R. (2021). Beyond the tree-line: The C3-C4 "grass-line" can track global change in the World's Grassy Mountain systems. *Frontiers in Ecology and Evolution*, *9*, 760118. https://doi.org/10.3389/fevo.2021.760118

Dövényi, Z. (Ed.). (2010). *Cadastral inventory of landscapes in Hungary (Hungarian)* (p. 876). MTA Földrajztudományi Kutatóintézet.

Dukes, J. S., & Mooney, H. A. (1999). Does global change increases the success of biological invaders? *Trends in Ecology and Evolution*, *14*, 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7

Englmaier, P., & Wilhalm, T. (2018). Alien grasses (Poaceae) in the flora of the eastern Alps: Contribution to an excursion flora of Austria and the eastern Alps. *Neilreichia*, *9*, 177–245. https://doi.org/10.5281/zenodo.1196285

Erfanzadeh, R., Hendrickx, F., Maelfait, J. P., & Hoffmann, M. (2010). The effect of successional stage and salinity on the vertical distribution of seeds in salt marsh soils. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *205*, 442–448.

Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J., Feldpausch, T. R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B. S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., … Phillips, O. L. (2019). Compositional response of Amazon forests to climate change. *Global Change Biology*, *25*, 39–56. https://doi.org/10.1111/gcb.14413

Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M., & Zuleta, D. (2020). Climate-driven changes in the composition of New World plant communities. *Nature Climate Change*, *10*, 965–970. https://doi.org/10.1038/s41558-020-0873-2

Finch-Savage, W. E., & Leubner-Metzger, G. (2006). Seed dormancy and the control of germination. *New Phytologist*, *171*, 501–523. https://doi.org/10.1111/j.1469-8137.2006.01787.x

Fletcher, C. S., Westcott, D. A., Murphy, H. T., Grice, A. C., & Clarkson, J. R. (2015). Managing breaches of containment and eradication of invasive plant populations. *Journal of Applied Ecology*, *52*, 59–68. https://doi.org/10.1111/1365-2664.12361

Gioria, M., Carta, A., Baskin, C. C., Dawson, W., Essl, F., Kreft, H., Pergl, J., van Kleunen, M., Weigelt, P., Winter, M., & Pyšek, P. (2021). Persistent soil seed banks promote naturalisation and invasiveness in flowering plants. *Ecology Letters*, *24*, 1655–1667. https://doi.org/10.1111/ele.13783

Gioria, M., Dietrich, B., & Osborne, B. A. (2011). Battle of the giants: Primary and secondary invasions by large herbaceous species. *Biology and Environment*, *3*, 177–193. https://www.jstor.org/stable/23188047

Gioria, M., Jarošík, V., & Pyšek, P. (2014). Impact of invasions by alien plants on soil seed bank communities: Emerging patterns. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*, 132–142. https://doi.org/10.1016/j.ppees.2014.03.003

Gioria, M., Le Roux, J. J., Hirsch, H., Moravcová, L., & Pyšek, P. (2019). Characteristics of the soil seed bank of invasive and non-invasive plants in their native and alien distribution range. *Biological Invasions*, *21*, 2313–2332. https://doi.org/10.1007/s10530-019-01978-y

Gioria, M., & Osborne, B. A. (2010). Similarities in the impact of three large invasive plant species on soil seed bank communities. *Biological Invasions*, *12*, 1671–1683. https://doi.org/10.1007/s10530-009-9580-7

Gioria, M., & Pyšek, P. (2016). The legacy of plant invasions: Changes in the soil seed bank of invaded plant communities. *Bioscience*, *66*, 40–53. https://doi.org/10.1093/biosci/biv165

Gioria, M., Pyšek, P., & Moravcová, L. (2012). Soil seed banks in plant invasions: Promoting species invasiveness and long-term impact on plant community dynamics. *Preslia*, *84*, 327–350.

Godefroid, S., Le Pajolec, S., Hechelski, M., & Van Rossum, F. (2018). Can we rely on the soil seed bank for restoring xeric sandy calcareous grasslands? *Restoration Ecology*, *26*, S123–S133. https://doi.org/10.1111/rec.12647

Godefroid, S., Phartyal, S. S., & Koedam, N. (2006). Depth distribution and composition of seed banks under different tree layers in a managed temperate forest ecosystem. *Acta Oecologica*, *29*, 283–292. https://doi.org/10.1016/j.actao.2005.11.005

Hábenczyus, A. A., Tölgyesi, C., Pál, R., Kelemen, A., Aradi, E., Bátori, Z., Sonkoly, J., Tóth, E., Balogh, N., & Török, P. (2022). Increasing abundance of an invasive C4 grass is associated with larger community changes away than at home. *Applied Vegetation Science*, *25*, e12659. https://doi.org/10.1111/avsc.12659

Hager, H. A., Rupert, R., Quinn, L. D., & Newman, J. A. (2015). Escaped *Miscanthus sacchariflorus* reduces the richness and diversity of vegetation and the soil seed bank. *Biological Invasions*, *17*, 1833–1847. https://doi.org/10.1007/s10530-014-0839-2

Hobbs, R. J., Arico, A., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. K., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R., & Zobel, M. (2006). Emerging ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, *15*, 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x

Holmes, P. M. (2002). Depth distribution and composition of soil seed banks in alien-invaded and uninvaded fynbos vegetation. *Austral Ecology*, *27*, 110–120. https://doi.org/10.1046/j.1442-9993.2002.01164.x

Hopfensperger, K. N. (2007). A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos*, *116*, 1438–1448. https://doi.org/10.1111/j.0030-1299.2007.15818.x

Hulme, P. E. (2017). Climate change and biological invasions: Evidence, expectations, and response options. *Biological Reviews*, *92*, 1297–1313.

IBM Corp. (2019). *IBM SPSS statistics for windows* (version 26.0) [Computer software]. IBM Corp.

Ingimarsdóttir, M., Caruso, T., Ripa, J., Magnúsdóttir, Ó. B., Migliorini, M., & Hedlund, K. (2012). Primary assembly of soil communities: Disentangling the effect of dispersal and local environment.

Oecologia, *170*, 745–754. https://doi.org/10.1007/s00442-012-2334-8

Jia, P., Qu, G., Jia, J., Li, D., Sun, Y., & Liu, L. (2024). Long-term *Spartina alterniflora* invasion simplified soil seed bank and regenerated community in a coastal marsh wetland. *Ecological Applications*, *34*, e2754.

Johnston, W. H. (1996). The place of C4 grasses in temperate pastures in Australia. *New Zealand Journal of Agricultural Research*, *39*, 527–540. https://doi.org/10.1080/00288233.1996.9513213

Kalamees, R., & Zobel, M. (2002). The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology*, *83*, 1017–1025.

Király, G. (2016). An invader at the edge of the world: *Sporobolus neglectus* (Poaceae) discovered at a remote locality in Hungary. *Studia Botanica Hungarica*, *47*, 335–344. https://doi.org/10.17110/StudBot.2016.47.2.335

Király, G., & Hohla, M. (2015). New stage of the invasion: *Sporobolus vaginiflorus* (Poaceae) reached Hungary. *Studia Botanica Hungarica*, *46*, 149–155. https://doi.org/10.17110/StudBot.2015.46.2.149

Kiss, R., Deák, B., Török, P., Tóthmérész, B., & Valkó, O. (2018). Grassland seed bank and community resilience in a changing climate. *Restoration Ecology*, *26*, S141–S150. https://doi.org/10.1111/rec.12694

Kovács-Láng, E., Kröel-Dulay, G., Kertész, M., Fekete, G., Bartha, S., Mika, J., Dobi-Wantuch, I., Rédei, T., Rajkai, K., & Hahn, I. (2000). Changes in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change. *Phytocoenologia*, *30*, 385–407.

Kovats, R. S., Valentini, R., Bouwer, L. M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., & Soussana, J.-F. (2014). Europe. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate Change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* (pp. 1267–1326). Cambridge University Press.

Luzuriaga, A. L., Escudero, A., Olano, J. M., & Loidi, J. (2005). Regenerative role of seed banks following an intense soil disturbance. *Acta Oecologica*, *27*, 57–66. https://doi.org/10.1016/j.actao.2004.09.003

Ma, M., Zhou, X., & Du, G. (2010). Role of soil seed bank along a disturbance gradient in an alpine meadow on the Tibet plateau. *Flora*, *205*, 128–134. https://doi.org/10.1016/j.flora.2009.02.006

Måren, I. E., & Vandvik, V. (2009). Fire and regeneration: The role of seed banks in the dynamics of northern heathlands. *Journal of Vegetation Science*, *20*, 871–888.

Miao, R., Guo, M., Ma, J., Gao, B., Miao, Y., Yang, Z., & Liu, Y. (2020). Shifts in soil seed bank and plant community under nitrogen addition and mowing in an inner Mongolian steppe. *Ecological Engineering*, *153*, 105900.

Miao, R., Miao, Y., Liu, Y., Guo, M., Fu, G., Xiao, R., Yang, Z., Li, G., Chen, Z., & Han, S. (2022). Late-season drought exerts more negative effects on plant diversity and cover than early-season drought through changing soil moisture in a semi-arid grassland. *Journal of Vegetation Science*, *33*, e13151.

Miao, R., Qiu, X., Guo, M., Musa, A., & Jiang, D. (2018). Accuracy of space-for-time substitution for vegetation state prediction following shrub restoration. *Journal of Plant Ecology*, *11*, 208–217.

Moravcová, L., Pyšek, P., Krinke, L., Müllerová, J., Perglová, I., & Pergl, J. (2018). Long-term survival in soil of seed of the invasive herbaceous plant *Heracleum mantegazzianum*. *Preslia*, *90*, 225–234. https://doi.org/10.23855/preslia.2018.225

Niknam, P., Erfanzadeh, R., Ghelichnia, H., & Cerdà, A. (2018). Spatial variation of soil seed bank under cushion plants in a subalpine degraded grassland. *Land Degradation & Development*, *29*, 4–14. https://doi.org/10.1002/ldr.2811

Olsson, A. D., Betancourt, J., McClaran, M. P., & Marsh, S. E. (2012). Sonoran Desert ecosystem transformation by a C4 grass without the grass/fire cycle. *Diversity and Distributions*, *18*, 10–21.

Orbán, I., Ónodi, G., & Kröel-Dulay, G. (2023). The role of drought, disturbance, and seed dispersal in dominance shifts in a temperate grassland. *Journal of Vegetation Science*, *34*, e13199. https://doi.org/10.1111/jvs.13199

Parmesan, C., & Hanley, M. E. (2015). Plants and climate change: Complexities and surprises. *Annals of Botany*, *116*, 849–864.

Peterson, P., Romaschenko, K., Arrieta, H., & Saarela, J. (2014). A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoideae: Sporobolinae). *Taxon*, *63*, 1212–1243. https://doi.org/10.12705/636.19

Piao, S., Liu, Q., Chen, A., Janssens, I. A., Fu, Y., Dai, J., Liu, L., Lian, X., Shen, M., & Zhu, X. (2019). Plant phenology and global climate change: Current progresses and challenges. *Global Change Biology*, *25*, 1922–1940. https://doi.org/10.1111/gcb.14619

Pyšek, P., Manceur, A. M., Alba, C., McGregor, K., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., Klimešová, J., Lučanová, M., Moravcová, L., Nishino, M., Sádlo, J., Suda, J., Tichý, L., & Kühn, I. (2015). Naturalization of central European plant species in North America: Species traits habitats propagule pressure residence time. *Ecology*, *96*, 145–157. https://doi.org/10.1890/14-1005.1

Qian, J., Liu, Z., Hatier, J. H. B., & Liu, B. (2016). The vertical distribution of soil seed bank and its restoration implication in an active sand dune of northeastern Inner Mongolia, China. *Land Degradation & Development*, *27*, 305–315. https://doi.org/10.1002/ldr.2428

Ravi, S., Law, D. J., Caplan, J. S., Barron-Gafford, G. A., Dontsova, K. M., Espeleta, J. F., Villegas, J. C., Okin, G. S., Breshears, D. D., & Huxman, T. E. (2022). Biological invasions and climate change amplify each other's effects on dryland degradation. *Global Change Biology*, *28*, 285–295. https://doi.org/10.1111/gcb.15919

Rayment, J., French, K., & Bedward, M. (2022). Understanding patterns and pathways of exotic perennial grass invasion in south-eastern Australian grassy communities. *Diversity and Distributions*, *28*, 1136–1150.

Reed, H. E., Seastedt, T. R., & Blair, J. M. (2005). Ecological consequences of C4 grass invasion of a C4 grassland: A dilemma for management. *Ecological Applications*, *15*, 1560–1569.

Richardson, D. M., & Gaertner, M. (2013). Plant invasions as builders and shapers of novel ecosystems. In R. J. Hobbs, E. S. Higgs, & C. M. Hall (Eds.), *Novel ecosystems*. Wiley. https://doi.org/10.1002/9781118354186.ch11

Schmiede, R., Donath, T. W., & Otte, A. (2009). Seed bank development after the restoration of alluvial grassland via transfer of seed-containing plant material. *Biological Conservation*, *142*, 404–413. https://doi.org/10.1016/j.biocon.2008.11.001

Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, *12*, 1–20. https://doi.org/10.2307/2845026

Simberloff, D. (2003). How much information on population biology is needed to manage introduced species? *Conservation Biology*, *17*, 83–92. https://doi.org/10.1046/j.1523-1739.2003.02028.x

Skálová, H., Moravcová, L., Čuda, J., & Pyšek, P. (2019). Seed-bank dynamics of native and invasive *impatiens* species during a five-year field experiment under various environmental conditions. *NeoBiota*, *50*, 75–95. https://doi.org/10.3897/neobiota.50.34827

Šmilauer, P., & Lepš, J. (2014). *Multivariate analysis of ecological data using Canoco 5*. Cambridge University Press.

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter. Kongelige Danske videnskabernes Selskab*, *5*, 1–34.

Sun, Z., Ren, H., Schaefer, V., Lu, H., Wang, J., Li, L., & Liu, N. (2013). Quantifying ecological memory during forest succession: A case study from lower subtropical forest ecosystems in South China. *Ecological Indicators*, *34*, 192–203. https://doi.org/10.1016/j.ecolind.2013.05.010

Symonides, E. (1979). The structure and population dynamics of psammophytes on inland dunes. IV. Population phenomena as a phytocenose-forming factor (a summing-up discussion). *Ekologia Polska*, *27*, 259–281.

Ter Heerdt, G. N. J., Verweij, G. L., Bekker, R. M., & Bakker, J. P. (1996). An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. *Functional Ecology*, *10*, 144–151. https://doi.org/10.2307/2390273

Thompson, K., Bakker, J. P., & Bekker, R. M. (1997). *Soil seed banks of NW Europe: Methodology, density and longevity*. Cambridge University Press.

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, *10*, 8245–8250. https://doi.org/10.1073/pnas.0409902102

Török, P., & Aradi, E. (2017). A new potentially invasive grass, sand dropseed (*Sporobolus cryptandrus*) discovered in sandy areas of Hungary – A call for information on new localities. *Bulletin of the Eurasian Dry Grassland Group*, *35*, 24–25.

Török, P., Bullock, J. M., Jiménez-Alfaro, B., & Sonkoly, J. (2020). The importance of dispersal and species establishment in vegetation dynamics and resilience. *Journal of Vegetation Science*, *31*, 935–942. https://doi.org/10.1111/jvs.12958

Török, P., Kelemen, A., Valkó, O., Miglécz, T., Tóth, K., Tóth, E., Sonkoly, J., Kiss, R., Csecserits, A., Rédei, T., Deák, B., Szűcs, P., Varga, N., & Tóthmérész, B. (2018). Succession in soil seed banks and its implications for restoration of calcareous sand grasslands. *Restoration Ecology*, *26*, S134–S140. https://doi.org/10.1111/rec.12611

Török, P., Matus, G., Papp, M., & Tóthmérész, B. (2009). Seed bank and vegetation development of sandy grasslands after goose breeding. *Folia Geobotanica*, *44*, 31–46. https://doi.org/10.1007/s12224-009-9027-z

Török, P., Schmidt, D., Bátori, Z., Aradi, E., Kelemen, A., Hábenczyus, A. A., Díaz-Cando, P., Tölgyesi, C., Pál, R. W., Balogh, N., Tóth, E., Matus, G., Táborská, J., Sramkó, G., Laczkó, L., Jordán, S., McIntosh-Buday, A., Kovacsics-Vári, G., & Sonkoly, J. (2021). Invasion of the north American sand dropseed (*Sporobolus cryptandrus*) – A new pest in Eurasian sand areas? *Global Ecology and Conservation*, *32*, e01942. https://doi.org/10.1016/j.gecco.2021.e01942

Tóth, Á., Deák, B., Tóth, K., Kiss, R., Lukács, K., Rádai, Z., Godó, L., Borza, S., Kelemen, A., Miglécz, T., Bátori, Z., Novák, T. J., & Valkó, O. (2022). Vertical distribution of soil seed bank and the ecological importance of deeply buried seeds in alkaline grasslands. *PeerJ*, *10*, e13226. https://doi.org/10.7717/peerj.13226

Valkó, O., Deák, B., Török, P., Tóth, K., Kiss, R., Kelemen, A., … Tóthmérész, B. (2021). Dynamics in vegetation and seed bank composition highlight the importance of post-restoration management in sown grasslands. *Restoration Ecology*, *29*, e13192.

Valkó, O., Török, P., Tóthmérész, B., & Matus, G. (2011). Restoration potential in seed banks of acidic fen and dry-msophilous meadows: Can restoration be based on local seed banks. *Restoration Ecology*, *19*, 9–15. https://doi.org/10.1111/j.1526-100X.2010.00679.x

Valkó, O., Tóthmérész, B., Kelemen, A., Simon, E., Miglécz, T., Lukács, B. A., & Török, P. (2014). Environmental factors driving seed bank diversity in alkali grasslands. *Agriculture, Ecosystems & Environment*, *182*, 80–87. https://doi.org/10.1016/j.agee.2013.06.012

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarošík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., … Settele, J. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution*, *24*, 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Wang, H., Liu, T., Dong, H., Zhao, W., Liu, X., Wang, R., & Xu, W. (2022). Changes in the composition of the soil seed bank of grassland after giant ragweed (*Ambrosia trifida* L.) invasion. *Journal of Environmental Management*, *317*, 115468.

Wellstein, C., Otte, A., & Waldhardt, R. (2007). Seed bank diversity in mesic grasslands in relation to vegetation type, management and site conditions. *Journal of Vegetation Science*, *18*, 153–162. https://doi.org/10.1111/j.1654-1103.2007.tb02527.x

Williams, D. G., & Baruch, Z. (2000). African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions*, *2*, 123–140. https://doi.org/10.1023/A:1010040524588

How to cite this article: Török, P., Espinoza Ami, F. D., Szél-Tóth, K., Díaz Cando, P., Guallichico Suntaxi, L. R., McIntosh-Buday, A., Hábenczyus, A. A., Törő-Szijgyártó, V., Kovacsics-Vári, G., Tölgyesi, C., Tóthmérész, B., & Sonkoly, J. (2024). Accumulated soil seed bank of the invasive sand dropseed (*Sporobolus cryptandrus*) poses a challenge for its suppression. *Land Degradation & Development*, *35*(13), 4105–4120. https://doi.org/10.1002/ldr.5208

APPENDIX A: Seed bank Composition of the Studied Sites

	Debrecen				Kiskunhalas North				Kecskemét Katonatelep				Kecskemét airport				Kiskunhalas east			
Cover categories	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Sporobolus cryptandrus	318	345	2387	3024	186	1114	6446	9921	637	33,555	85,731	95,413	80	32,786	60,028	51,460	106	3183	6923	8196
Achillea collina	27												27							
Agrostis stolonifera																			27	
Alyssum alyssoides																			53	
Ambrosia artemisiifolia									27	106								106	159	557
Anthemis ruthenica										53	292	27				80				27
Arabis recta																		27		
Arenaria serpyllifolia/ leptoclados	398	2334	398	1035	318	159	451	212	1061	1512	2626	1273	186	796	1645	477	1804	477	690	716
Artemisia campestris/ scoparia																				212
Bellis perennis	133																			
Bromus arvensis														80						
Bromus hordeaceus										27										
Bromus squarrosus														27	53				53	
Bromus tectorum										53	53									
Calamagrostis epigeios																		27		
Capsella bursa-pastoris	318			27													80			
Carex hirta									27											
Carex stenophylla/ liparicarpos									318		27	53	584	477	424	53	743		80	212
Centaurea arenaria																27				
Centaurium pulchellum									27		27	27	212						27	
Cerastium glutinosum	53			80					186	27	265		106							53
Cerastium semidecandrum	239	292	80	159				53	186	212	345	265	265	186	424	398	159		80	
Cerastium vulgare	875	53		133					27											
Chenopodium album	80		27						186	186						27	265	955	424	159
Convolvulus arvensis																27				
Conyza canadensis	875	27	27	186	106	424	424	451	106		27	292	80	584	106	2122	133	11,565	4271	663
Crepis capillaris																	27			
Crepis foetida ssp. *rhoeadifolia*																	27			

	Debrecen				Kiskunhalas North				Kecskemét Katonatelep				Kecskemét airport				Kiskunhalas east			
Cover categories	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Digitaria ciliaris		159						27												
Digitaria sanguinalis	424	27	27																	
Echium vulgare										27										
Erodium cicutarium		80	27	80																
Erophila verna					159	80	27		27	27					80	27	27			318
Erysimum diffusum									186	424	159	106								
Euphorbia cyparissias														27	27					
Euphorbia seguieriana								27												
Fallopia convolvulus																			27	
Festuca pratensis	80																			
Festuca pseudovina									133											
Holosteum umbellatum						239	53	27	80	27	451	27		80			318	27		
Juncus articulatus				27		27			53		27	27	53							27
Juncus bufonius									186			27	27					27		27
Juncus compressus									27				159		53		53			
Kochia laniflora											27		27		27					
Koeleria glauca														265	80	53				
Lamium purpureum	265																			
Linaria vulgaris														80			27			27
Medicago lupulina		212	212	265						27		106								
Minuartia glaucina													2096			133				
Myosotis stricta						27	53	53			27					345	27			
Oenothera biennis																1379				
Oxalis dilenii	1088	27	53																	
Panicum capillare																	53	106		159
Plantago indica														292	27	106				
Plantago lanceolata	451	27														53				
Plantago major	265																			
Poa angustifolia									318	1194	345	186	80	27	27					80
Poa annua	159																			
Poa bulbosa				53										27				27		
Poa pratensis									186	292	80	80	27						159	

(Continues)

	Debrecen				Kiskunhalas North				Kecskemét Katonatelep				Kecskemét airport				Kiskunhalas east			
Cover categories	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Polygonum aviculare/ arenarium	318	371	80	80	106	27	292	133		27				53	106		265		27	133
Portulaca oleracea		5464	5995	8674				27			27					53	27			265
Potentilla arenaria						27	27						186				80		27	
Potentilla argentea		318	822	796					424	186	239									
Rumex acetosella									292		27									
Saxifraga tridactylites													133	239	690	318	27			27
Scleranthus annuus		371		265																
Secale sylvestre								27												
Setaria viridis	531	106							80	371	159	106					80		27	
Silene alba			27	27					53	27								27		
Silene conica									265	318	477	186			80		80	53		
Sisymbrium orientale																27		159	504	27
Sonchus arvensis																	27			
Stellaria media	849	27								53		27	27							
Taraxacum officinale	53																			
Thymus glabrescens													53							
Tragus racemosus					27														27	
Trifolium campestre	106																			
Trifolium repens	610	53																		
Typha angustifolia/latifolia			27	27								27	53	27	27		53		27	
Urtica dioica															27					
Verbascum lychnitis																	27	27	27	80
Verbascum phlomoides									265	133	265	424								
Veronica arvensis	292	398	424	292					27	53										
Veronica hederifolia	27																			
Veronica polita	212																			
Veronica praecox							27						212	27	53	133	159		53	80
Veronica prostrata													80				53			
Veronica triphyllos										27		53								
Veronica verna																	53			
Vicia angustifolia		53		27																
Vicia lathyroides		27																		
Viola kitaibeliana						27	53	53	27	27		80				212	133			80