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Invasion of the North American sand dropseed (Sporobolus cryptandrus) – A new pest in Eurasian sand areas?

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ABSTRACT

For the effective control of an invasive species, gathering as much information as possible on its ecology, establishment and persistence in the affected communities is of utmost importance. We aimed to review the current distribution and characteristics of Sporobolus cryptandrus (sand dropseed), an invasive C4 grass species of North American origin recently discovered in Hungary. We aimed to provide information on (i) its current distribution paying special attention to its invasion in Eurasia; (ii) the characteristics of the invaded habitats in Central Europe; (iii) seed bank formation and germination characteristics, crucial factors in early establishment; and (iv) the effects of its increasing cover on vegetation composition. Finally, we aimed to (v) point out further research directions that could enable us to understand the invasion success of this potential invasive species. Field surveys uncovered large stands of the species in Central and Eastern Hungary with most of the locations in the former, especially in the Kiskunság region. The species invaded disturbed stands of dry and open sand grasslands, closed dune slack grasslands and it also penetrates natural open sand grasslands from neighboring disturbed habitats. Increasing cover of Sporobolus cryptandrus was associated with a decline in species richness and abundance of subordinate species both in the vegetation and seed banks, but a low density of Sporobolus cryptandrus can even have a weak positive effect on these characteristics. Viable seeds of Sporobolus were detected from all soil layers (2.5 cm layers measured from the surface to 10 cm in depth), which indicates that the species is able to form a persistent seed bank (1114 to 3077 seeds/m^2 with

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increasing scores towards higher abundance of the species in vegetation). Germination of *Sporobolus cryptandrus* was negatively affected by both litter cover and 1 cm deep soil burial. To sum up, *Sporobolus cryptandrus* can be considered as a transformer invasive species, whose spread forms a high risk for dry sand and steppe grasslands in Eurasia. We can conclude that for the effective suppression of the species it is necessary: (i) to clarify the origin of the detected populations; (ii) to assess its competitive ability including its potential allelopathic effects; (iii) to assess its seed bank formation potential in habitats with different abiotic conditions; and (iv) to assess the possibility of its suppression by natural enemies and management techniques such as mowing or livestock grazing.

1. Introduction

The distribution range and abundance of invasive plants have dramatically increased in recent decades providing a serious challenge for protection, conservation, and restoration of natural and semi-natural habitats worldwide (van Kleunen et al., 2019; Pyšek et al., 2020). While casual establishment of alien species in various natural ecosystems became a relatively frequent phenomenon as a consequence of increased human influence, transformer invasive species form one of the most serious threats for natural communities and ecosystems (Richardson et al., 2000). Transformer invasive species often reduce biodiversity, alter disturbance regimes, and affect ecosystem structure and functions in the subjected communities (Richardson et al., 2000; Byers et al., 2010; Catford et al., 2011).

For the effective control of an invasive species, it is crucial to collect as much information as possible on (i) their ecology, especially establishment and persistence characteristics, and on (ii) communities potentially threatened by its invasion. It is also crucial to detect the plant invasion in an early stage, when the distribution of the invasive species is still limited to one or a few isolated locations, where its eradication still might be possible. However, this is rather challenging for inconspicuous species (such as certain grasses), which are usually difficult to detect and to identify (Jarić et al., 2019). Members of the Poaceae and Asteraceae families contribute most of the aggressive invasive plant species across the globe (Pyšek et al., 2017). Invasions of many short-lived and perennial grasses present serious problems worldwide including grasses characterized either by C3 or C4 photosynthetic pathway (D'Antonio and Vitousek, 1992; Fusco et al., 2019; van Kleunen et al., 2019). The C4 photosynthetic pathway provides many advantages over the C3 one in arid and warm climate, such as carbon fixation with a lower water cost, higher temperature optimum for carbon fixation, lower sensitivity to water stress and high fire resistance (Johnston, 1996).

Thermophilic neophytes include numerous species of Poaceae with the C4 photosynthetic pathway, which have become constant elements of some warm ruderal communities in Eurasia (Leuschner and Ellenberg, 2017). Introduced C4 grasses have already caused dramatic losses of biodiversity in the Americas (e.g., savanna and forest ecosystems in central and South America or desert grasslands and dry woodlands in the North America, Williams and Brauch, 2000) or in Australia (e.g., tropical grasslands in Australia, Brooks et al., 2010). Similarly, the Eurasian steppe zone is characterized by the prevailing dominance of C3 grasses with only some notable exceptions of C4 species (e.g., *Bothriochloa ischaemum*, *Cynodon dactylon*), which are thought to have been introduced in historical times (Hurka et al., 2019). According to the projected climate change scenarios, global temperatures will increase in the future, likely resulting in an increased expansion of C4 grasses in plant communities of arid environments of Eurasia. Direct and indirect effects of climate change include the increase of minimum and maximum temperatures, the increasing frequency and magnitude of droughts in the vegetation period, and the changing annual distribution of precipitation shifting the peak of precipitation from the vegetation period to the dormant period (in Central Europe shifting from the summer period to winter, IPCC, 2013). This means that increased levels of aridity, increased likeliness of weather extremes, and the associated increased risk of extreme fire events favor the formation and spread of more drought-adapted communities and species. The decline of dominant native C3 grasses like *Festuca* species increases the risk of invasion via the colonization of drought-adapted non-native C4 species. The effects of climate change may be amplified at the regional scale by large-scale water regulation works and the increased demand for irrigation in agricultural areas, or by the high evapotranspiration rate of established non-native tree plantations (Tölgyesi et al., 2020). The water-stressed open sand grasslands are excellent targets for the establishment of non-native C4 plant species. The establishment and the effects of several invasive herbaceous species on the native communities have been studied and reported for sand regions (e.g., *Asclepias syriaca* – Kelemen et al., 2016 or *Conyza canadensis* – Mojzes et al., 2020).

In recent decades, spread of several non-native *Sporobolus* species was detected in Europe. The establishment and intensive spread of naturalized populations of *S. neglectus* and *S. vaginiflorus* was reported from the Mediterranean regions and from dry regions of the eastern part of Central Europe (Englmaier and Wilhalm, 2018; Hohla et al., 2015; Jogan, 2017; Király, 2016; Király and Hohla, 2015). Rapid spread and expansion in the last decade were detected for both species along regularly mown margins of roads and motorways, and because of the circumstances of their establishment, they constitute a relatively low threat to natural vegetation. In contrast to the other two species, the spread of the recently discovered stands of *S. cryptandrus* is not limited to road margins and to the close vicinity of ruderal sites, but affects large areas characterized by natural, semi-natural and degraded dry-grassland vegetation (Török and Aradi, 2017).

In the current paper, we aim to study the current distribution and characteristics of *Sporobolus cryptandrus* (sand dropseed), an invasive C4 grass species of North American origin, recently detected in Hungary (Török and Aradi, 2017). We aimed to evaluate its effects on the native sand grassland vegetation by analysing plots along an increasing *Sporobolus* abundance gradient. In particular, we aimed to provide information on (i) the current distribution of the species with special attention to its invasion in Eurasia by

summarizing published occurrence data, (ii) the characteristics of the invaded habitats in Central Europe, (iii) seed bank formation and germination characteristics, crucial in early establishment of the species, and on (iv) the effects of increasing cover of the species on vegetation composition. Finally, we aimed to (v) point out further research directions that would help to understand the invasion success of this species.
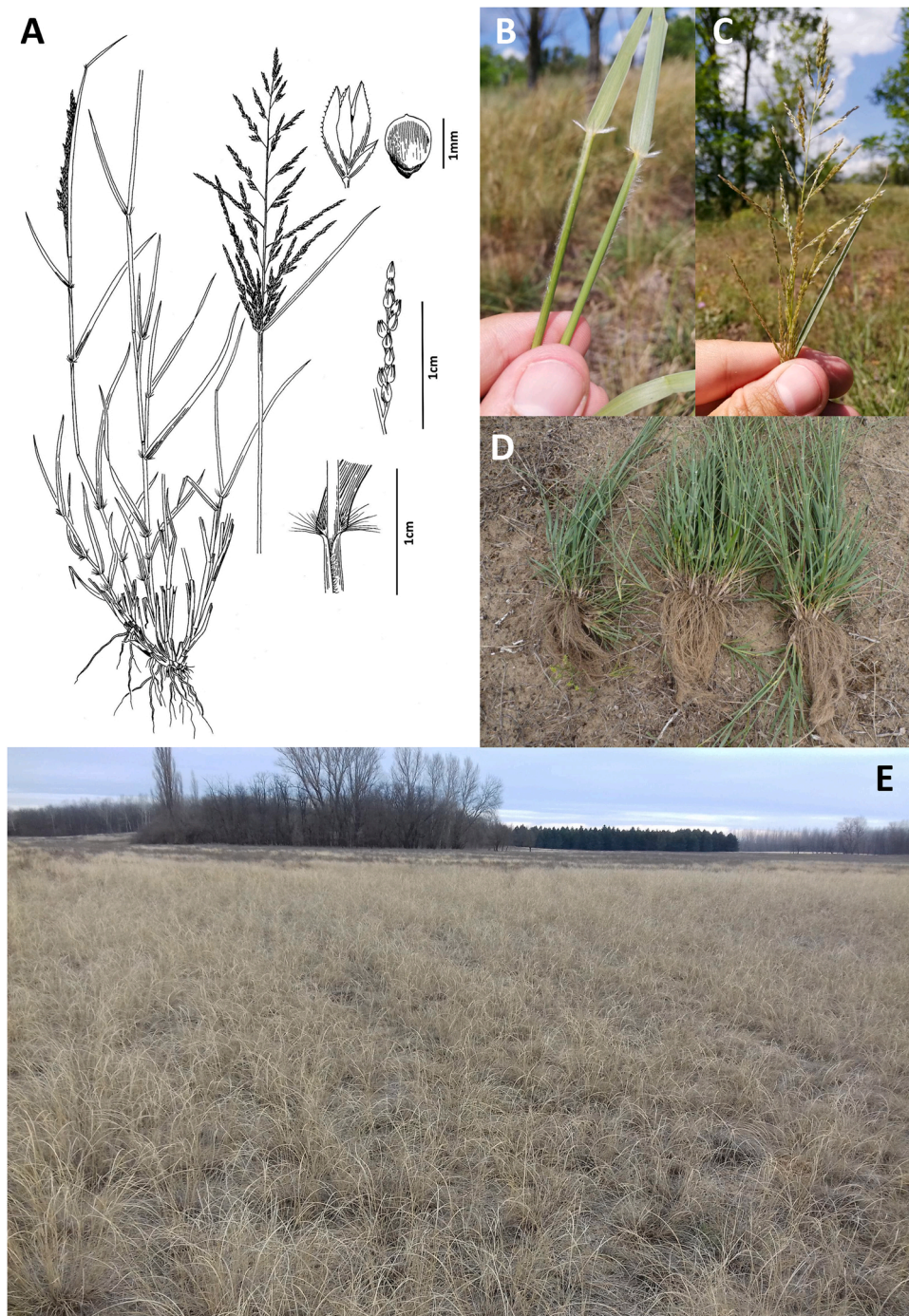
Fig. 1. The habitus and morphological characteristics of *Sporobolus cryptandrus*. Notations: A) habitus and morphological characteristics of the species (drawings by J. Táborská), B) Nodes with leaves and C) inflorescences (photos by Z. Bátori); D) root system of the species (photo by E. Aradi); and E) a site in the Kiskunság region with a mass invasion by *S. cryptandrus* (photo by C. Tölgyesi).

2. Materials and methods

2.1. Morphological characteristics and ecology of the species

The species is a member of the dropseed genus (*Sporobolus* R.Br.) consisting of more than 160 species with the highest number of endemic species in Africa, Australasia, North and South America (Simon and Jacobs, 1999; Király and Hohla, 2015). Species in the genus are typical in tropical and warm temperate climate, generally tolerate drought but can also be found in saline habitats from loose sandy soils to heavy floodplain soils (Simon and Jacobs, 1999). Sand dropseed (*Sporobolus cryptandrus* (Torr.) A.Gray) is a perennial bunchgrass with a height of 40–80 cm (up to 100 cm with inflorescences). Both the auricula and the ligula are very short and at the orifice of the sheaths, on the leaves' margin around the nodes there is a collar of dense white hairs, but scattered hairiness is typical also for the whole leaf edge. The edge of the 4–5 mm wide leaves is sharp, but the leaves are softer than the leaves of a *Calamagrostis*. The inflorescences are at least partly covered by the flag leaf but are very similar to those of an *Agrostis*, not surprisingly formerly the genus was classified together with the latter one (Fig. 1, Simon and Jacobs, 1999). The species is characterized by a C4 photosynthetic pathway. The species has limited ability for clonal reproduction, thus, seed production, seed dispersal and seed bank formation are of crucial importance in its establishment and spread. It produces very tiny propagules in high abundance (the caryopsis is approx. 1 mm in length); based on literature data, one individual is able to produce up to ten-thousand seeds (Brown, 1943). The thousand-seed weight of the species is 0.083 g (Török et al., unpublished). It was also reported that the epicarp of the seeds becomes sticky when wet, which, besides the small weight of the seeds, may contribute to its effective dispersal (Holub and Jehlík, 1987). Seeds have high viability but a high proportion of them can become dormant, which means that dormancy breaking in the form of stratification, moist conditions and/or scarification is necessary for successful germination (Holub and Jehlík, 1987; Sartor and Malone, 2010). The species is likely able to build up persistent seed banks in its native range (Clements et al., 2007) and might have an allelopathic effect on the germination of other species as extrapolated from *Sporobolus pyramidatus* (Lam.) Hitchc. (Rasmussen and Rice, 1971).

2.2. Distribution range of the species

The native range of *S. cryptandrus* lays in North America including the United States, Southern Canada, and the northern part of Mexico (Britton and Brown, 1970; Holub and Jehlík, 1987; Lackschewitz, 1991; Nobis et al., 2015). The species occurs typically in short-grass prairies, sagebrush deserts, and chaparral communities but sometimes it also enters the sagebrush steppe (Hitchcock et al., 1969; Tilley et al., 2009; Lesica, 2012). It is a member of the climax plant communities on deep sands; it grows at lower elevations on sandy soils (which explains the English colloquial name: sand dropseed), mainly on disturbed sites such as dry riverbeds, rocky slopes,
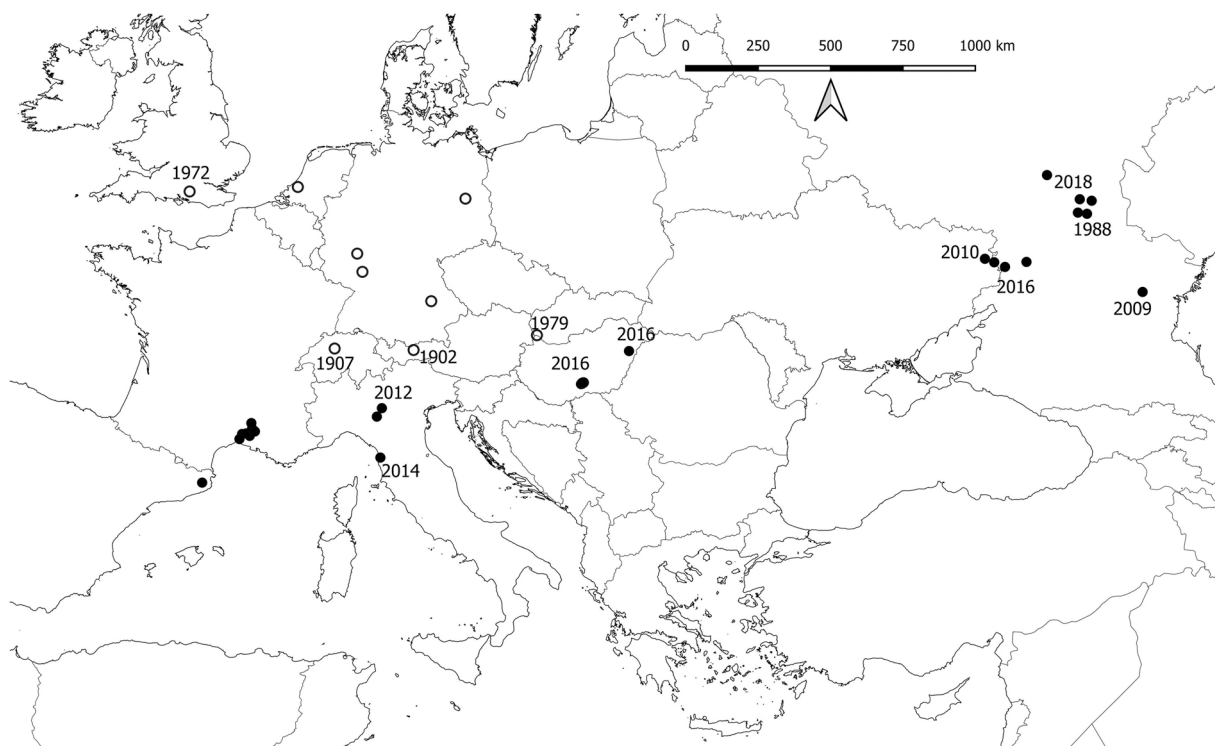
Fig. 2. The distribution of *Sporobolus cryptandrus* in Eurasia. The full symbols show naturalized populations, while the empty ones denote casual establishment. See more details on locations in Electronic Appendix 1.

and along roadsides. It can also be found at higher elevations and coarser soils and acts as an early successional colonizer. The plant is extremely drought-tolerant and it is highly competitive with co-occurring native species even in desert climates (Wan et al., 1993; Ogle et al., 2009; Tilley et al., 2009).

Outside of its native range, the species has been reported from Australia and Tasmania, Japan, New Zealand, and Argentina (Edgar and Connor, 2000; Curto, 2012; Randall, 2017). In Eurasia, the species was detected formerly in several locations (Fig. 2); *Sporobolus cryptandrus* is known from isolated locations from Austria, France, Germany, Italy, the Netherlands, Russia, Slovakia, Spain, Switzerland, Ukraine, and the United Kingdom (Ryves, 1988; Sani et al., 2015; Thellung, 1919; Dflor, 2021; Murr, 1902; NMBC, 2021; Sparrius et al., 2019; Romani et al. 2015, Electronic Appendix 1). As in the case of *S. neglectus and S. vaginiflorus*, the current distribution map of *S. cryptandrus* clearly shows that the naturalized populations of this species are confined to the European Mediterranean or to regions of Eastern Central and Eastern Europe characterized by semi-arid, at least moderately continental climate. Only occasional establishment of the species was detected in more humid regions of Central and Western Europe (Fig. 2).

Amongst the first naturalized populations was a riverbank near Bratislava, Slovakia (Holub and Jehlík, 1987). Large-scale spreading was reported also into steppe habitats in Western Russia and Ukraine (Alekseev et al., 1996; Kuvaev and Stepanova, 2014; Demina et al., 2016, 2018; Gouz and Timoshenkova, 2017; Maltsev and Sagalaev, 2018;). Historical data of the species were reported from the western part of Hungary, near to the city of Győr (= *Sporobolus subinclusus*, 1927 in Polgár, 1933; one specimen detected from the territory of an oil seed factory, and likely originated from Argentina), but the data cannot be validated and was not supported with a herbarium sheet. In 2016, the species was discovered in two sandy regions of Hungary, in the city of Debrecen (Nyírség region, acidic sand) and near the town Kiskunhalas (Kiskunság region, calcareous sand) in several small locations (Török and Aradi, 2017; Erdős et al., 2018; Molnár et al., 2020).

2.3. Vegetation and soil sampling

After its discovery in Eastern and Central Hungary (Debrecen, Nyírség region and Kiskunhalas, Kiskunság region, Török and Aradi, 2017) more detailed and systematic surveys were initiated. We started a large-scale data collection on the distribution of the species by visiting possible grassland sites including degraded stands and former old-fields in the Kiskunság region and also collected data on the distribution of the species in Debrecen city with the involvement of National Park rangers, university students and field botanists from Hungary. In the city of Debrecen we searched along roads and tramlines and in other public areas and parks covered with open, mostly grassy vegetation. In the Kiskunság region we started the field surveys first in the near vicinity of the first detected localities and increased the radius of search focusing on sites characterized by open vegetation and relatively high accessibility (e.g., adjacent to dirt-roads, close to small settlements). In case the species was detected we made an estimate of the subjected area, approximate population size, subjected habitat type and the level of the habitat degradation / naturalness, in new localities we conducted a search for further individuals in a 300-m radius to assess the subjected are of invasion more accurately. The data collection is still in progress, but because of the potential risk of the species' further spread, we provided in the paper preliminary summary of the results of the survey to draw attention to possible habitats suitable for its establishment (Schmidt et al., unpublished).

The largest locality of the species in Debrecen and four localities with large established populations in the Kiskunság region were selected for a detailed vegetation sampling (Table 1). In each site, 1-m^2-sized plots along an increasing cover gradient of *Sporobolus cryptandrus* were sampled. We sampled reference plots with no *Sporobolus* (cover category I), and plots characterized with 1–25%, 26–50% or 51–75% cover of the species (cover categories II, III and IV, respectively), but in the latter case *Sporobolus* cover rarely exceeded 70%. Altogether, 10 plots per cover group (altogether 40 plots per site) were recorded, the percentage cover of all vascular plant species were assessed in the summer of 2019.

For detailed soil analyses, we sampled the topsoil (<5 cm) with a small spade from 40 random locations per site near the vegetation plots (10 samples for each cover category pooled, about 500 g air-dried soil per pooled sample, 4 pooled samples per site). The following soil characteristics were measured: pH (KCl), soil compactness (this figure is strongly related to the physical texture of the soil; higher scores refer to higher proportion of loam-clay), calcium – $CaCO_3$ (m/m%), humus (m/m%), nitrogen – $NO_2 + NO_3$ content (mg/kg), phosphorous – P_2O_5 (mg/kg), potassium – K_2O (mg/kg). Soil analyses were conducted in an accredited laboratory (SYNLAB, Mosonmagyaróvár, Hungary) based on the standardized methods included in the Hungarian standards MSZ-08–0205:1978 (Evaluation of some chemical properties of the soil. Laboratory tests) and MSZ-08–0206–2:1978 (Determination of physical and hydrophysical properties of soils).

Table 1
Sample sites in Central and East Hungary.

Sample sites	Sample code	Nearest town	GPS coordinates		Habitat type	Population size of *Sporobolus*
Debrecen	D	Debrecen	47.55422 N	21.61537 E	Degraded sand grassland in urban area	4000–6000
Kiskunhalas North	KN	Kiskunhalas	46.48243 N	19.47987 E	Mosaic of natural sand steppe and pine plantations	5000–7000
Katonatelep	KT	Kecskemét	46.95044 N	19.76217 E	Grazed meadow-steppe	200,000–300,000
Airport	A	Kecskemét	46.92774 N	19.72590 E	Sandy old-field (30 +-year-old)	75,000–100,000
Kiskunhalas East	KE	Kiskunhalas	46.40935 N	19.56305 E	Disturbed sandy forest-steppe	1500–2000

2.4. Soil seed banks

We screened the composition of soil seed banks in plots characterized by different levels of *Sporobolus* cover at the Debrecen site. In three plots per cover group, we collected 10 soil cores (10 cm depth and 2 cm diameter) separated to four vertical segments (0–2.5 cm, 2.5–5 cm, 5–7.5 cm and 7.5–10 cm) in the last week of August 2020. Matching vertical segments were pooled per plot. We used the seedling emergence method with bulk reduction by ter Heerdt et al. (1996). Concentrated samples were spread in a thin layer (up to 4–5 mm) on the surface of pots filled with steam-sterilized potting soil. The samples were regularly watered and checked weekly for emerged seedlings. Seedlings were identified and removed; unidentified seedlings were transplanted and grown until the final identification. Emergence lasted about 11 weeks in the autumn of 2020, from 28th August until 15th November. At the end of the germination period, we identified all seedlings at the highest possible taxonomic level. As we conducted a preliminary germination experiment in the spring, we were able to distinguish the seedlings of *Sporobolus cryptandrus* from the seedlings of native C3 grasses at a very early stage. Other C4 grasses typical in the region were almost absent from the plots (e.g., *Cynodon dactylon*) or were present with low density only in seed banks and flowered already very early in the pots (*Eragrostis minor*). Only a small fraction of the seedlings perished before identification to a respective family, genus or species (8 individuals, less than 0.4% of all seedlings, omitted from analyses). Altogether 28 taxa were identified at the species level. We were not able to identify non-septate *Juncus* (1 seedling, treated as *J. conglomeratus/effusus*), or *Epilobium* seedlings (3 seedlings, *Epilobium* sp.) on the species level, and we also pooled the seedlings of *Arenaria leptoclados* and *A. serpyllifolia* as *A. leptoclados*. Seedlings of short-lived small *Veronica* species (*V. polita, V. triphyllos, V. verna*) were pooled as *Veronica* sp. (altogether 65 individuals). For some graminoid seedlings we were able to identify them only at the family level – Poaceae (altogether 38 individuals – these were most likely the seedlings of *Poa angustifolia* or *Lolium perenne*).

2.5. Germination experiment

A greenhouse experiment was conducted to test the effects of increasing seed burial depth (0, 0.5 and 1 cm soil) and increasing levels of litter cover (0, 150 and 300 g/m^2) and their interaction on the germination potential of *S. cryptandrus* in a full-factorial design with nine treatments in five replications (resulting in 45 pots total). For the selection of the soil and litter cover thicknesses we used a modified version of the experimental setup published by Sonkoly et al. (2020). *S. cryptandrus* seeds were collected in 2019 and dry-stored at room temperature (20–25 ºC) in the seed collection of the Department of Ecology at the University of Debrecen. A total of 45 pots filled with steam-sterilized potting soil were used in the experiment and 25 *Sporobolus* seeds were spread out evenly on the surface of each pot (in total 1125 seeds were sown). We used the same sterilized potting soil and the litter of *Festuca rupicola* for covering the seeds. The germination experiment lasted ten weeks from 26th March until 27th May 2020. The seedlings were regularly counted and removed. Only those seedlings were counted which appeared at the surface of the treatment. We registered the number of established seedlings weekly and removed and registered the perished ones – so we were able to calculate the seedling survival rates for the entire experiment.

2.6. Statistical analyses

We calculated species richness (S, number of species), Shannon diversity (H, based on ln) and evenness scores (following Pielou, 1975, where Evenness = H/log(S), and H refers for Shannon diversity and S for species richness) to analyse vegetation and seed bank patterns in plots with increasing cover of *Sporobolus*. The effect of *Sporobolus* cover on the selected vegetation characteristics were analysed using GLMM, where '*Sporobolus* cover' was included as a fixed factor and 'sampling site' as a random factor; the dependent variables were species richness, Shannon diversity, and evenness without the inclusion of *Sporobolus* presence and its cover. The effect of litter cover, soil burial and their interaction on the number of germinated seedling and survival rates were analysed by two-way ANOVAs, where the fixed factors were 'litter cover' and 'soil burial depth'. The effect of '*Sporobolus* cover' and 'soil layer' (included as fixed factors) on the species richness, Shannon diversity and evenness (dependent variables) of the seed bank were analysed by two-way ANOVAs.

The vegetation composition of the five sites were compared with a PCA ordination, where the main data matrix was the species composition of the plots characterized with different *Sporobolus* cover (at each mass locality site, where several thousand individuals of the species were present, altogether 10 plots of the same *Sporobolus* cover group were pooled, each cover group was represented by one pooled plot, in total four pooled plots per site, *Sporobolus cryptandrus* and its cover was excluded from the main data matrix). The secondary matrix (predictor variable) contained the *Sporobolus* cover (one pooled sample per *Sporobolus* cover group, in total four pooled scores per site). The correlation between the pooled cover of *Sporobolus cryptandrus* and the soil parameters was analysed using Pearson product moment correlation (altogether 20 pooled samples, one per each cover group in each site). We used FDiversity and R 3.6.3 (Casanoves et al., 2011; and R Core Team, 2020; for species richness, Shannon diversity and evenness), IBM SPSS 26.0 (IBM Corp. Released, 2019; for GLMM, ANOVA and correlations) and CANOCO 4.5 (ter Braak and Šmilauer, 2002; for PCA) program packages for the statistical analyses.

3. Results

3.1. Habitat preference of Sporobolus cryptandrus in Hungary

During the detailed field surveys, surprisingly, more than 620 individual locations of the species were detected in Central and East

Hungary, with most of the locations in the Kiskunság region. In the city of Debrecen, the species was detected in variously degraded and frequently mown urban grasslands situated between blocks of flats, or at road verges, parking lots, and tramlines. In contrast to the urban localities in Debrecen, in the Kiskunság region all *Sporobolus* stands were found in rural landscapes. A remarkable amount of the detected *Sporobolus* populations occur in dry sandy habitats, mainly in disturbed or strongly degraded stands of open sand grasslands, or in closed, desiccated interdune grasslands which typically originate from more wet interdune *Molinia* meadows. Large populations were found along artificial linear landscape elements, such as dirt roads, motocross trails, and plowed fire buffer zones. Furthermore, the species colonized sandy areas plowed recently (edges of young tree plantations) or during the last three decades. We also found the species in old-fields of various age, both young old-fields characterized by short-lived weeds (e.g., *Anthemis ruthenica, Ambrosia artemisiifolia* or *Bromus tectorum*) and old old-fields already dominated by perennial grasses (e.g., *Festuca pseudovina, Cynodon dactylon* and *Bothriochloa ischaemum*). Further land use types with intense disturbance were also found to facilitate the spread of *Sporobolus cryptandrus*, as we found populations in grasslands formerly or recently overgrazed by sheep, and in the close vicinity of game feeders. Invasion of *Sporobolus* was also detected in grasslands that were burned 10–20 years ago, and successfully regenerated since then (apart from the presence of *Sporobolus*) and consisting of the species of natural sandy grasslands (e.g., *Festuca vaginata, Koeleria glauca, Stipa pennata, Alkanna tinctoria, Dianthus serotinus* and *Silene otites*). Moreover, *Sporobolus cryptandrus* spreads in drought-affected stands of open sandy grasslands co-dominated by *Festuca vaginata* and *Stipa pennata*. The southern slopes of sand dunes are typical drought-affected habitats where the destruction of *Festuca vaginata* tussocks by severe droughts is typical, and *Sporobolus* can take its place. *Sporobolus* appeared in the dried-out stands of closed interdune grasslands and in the northern part of the Kiskunság (near Kecskemét) we found it also in the dried-out meadow steppes (with meadow soils). Although primary incursion of *Sporobolus* into natural habitats has not been detected, we found that it can spread to natural open sandy grasslands from the neighboring disturbed, invaded habitats, where it potentially threatens rare sandy species such as *Dianthus diutinus*, which is a priority species of European community interest. An important observation is that the shade-tolerance of *Sporobolus cryptandrus* is rather low; in the shaded parts of the invaded patches only sparse populations of *Sporobolus* were found.

3.2. Soil and vegetation characteristics of the selected sites

Soil analyses of the five study sites revealed that the soil pH ranged between 6.16 and 7.41, with the lowest score in Debrecen (acidic sand deposits) and higher scores were typical in the sample sites of the Kiskunság region (calcareous sand deposits). The physical soil texture type expressed by soil compactness ranged from sand to clay loam, with some sites with a higher load of nutrients, especially in phosphorous (D and KT sites) and potassium (D, KT, and A sites) (Table 2). None of the measured soil parameters were correlated with the cover of *Sporobolus cryptandrus*.

Studying the selected five sites, we found that both increasing *Sporobolus* cover and the sampling site significantly affected most of the studied variables of vegetation without the inclusion of the *Sporobolus* cover in the calculations (Table 3). In all sites, we detected an increase in species richness, Shannon diversity and evenness scores from cover group I to II and then a rapid decline was detected for most variables (Fig. 3 A-C). These trends were clearly shown also on the ordination diagram (Fig. 4). The ordination clearly revealed that the markedly different vegetation composition of different sites was "homogenized" by the increasing cover of *Sporobolus*, and almost all other species were negatively affected by the high cover of the invasive species (Fig. 4). Detailed vegetation compositional data of plots on which Fig. 4 was based is summarized in Electronic Appendix 2.

3.3. Seed banks

Altogether 2132 seedlings of 32 taxa were germinated from the samples of soil seed banks, including in total 320 seedlings of *Sporobolus cryptandrus*. Beside of *Sporobolus*, *Arenaria leptoclados/serpyllifolia, Portulaca oleracea, Potentilla argentea, Digitaria sanguinalis* and *Cerastium semidecandrum* were the most frequent species in the seed bank with 508, 492, 200, 153 and 104 seedlings, respectively. These six taxa provided more than 83% of the total seed bank (see more details in Electronic Appendix 3). The seed density of *Sporobolus* ranged from 1114 to 3077 seeds/m^2 considering the pooled seed bank data for the 30 cores (0–10 cm layer) per site (Electronic Appendix 3). Increasing *Sporobolus* cover negatively affected the total seedling number of other species (Fig. 6), and also species richness, Shannon diversity and evenness of the seed bank (Table 4, Fig. 5 A-C). The cover of *Sporobolus* did not significantly affect the seed bank density of *Sporobolus* itself; we detected soil seed banks of *Sporobolus* even in the closely located reference stands

Table 2

Soil characteristics of the study sites (mean±SE). Measured units: pH (KCl), calcium – CaCO$_3$ (m/m%), humus (m/m %), nitrogen – NO$_2$ + NO$_3$ content (mg/kg), phosphorous – P$_2$O$_5$ (mg/kg), potassium – K$_2$O (mg/kg). Soil compactness is strongly related to the physical texture of the soil; higher scores refer for higher proportion loam-clay fine soil components (e.g., some physical soil texture types are the following: sand = 25–30, sandy loam = 31–37, loam = 38–42, clay-loam = 43–50).

Site	Sample code	pH (KCl)	Soil compactness	CaCO$_3$	Humus	Nitrogen	Phosphorous	Potassium
Debrecen	D	6.16 ± 0.07	43.40 ± 2.29	0.13 ± 0.02	3.18 ± 0.36	2.81 ± 0.99	385.80 ± 53.69	340.60 ± 33.24
Kiskunhalas North	KN	7.02 ± 0.10	30.40 ± 0.68	1.85 ± 0.22	1.20 ± 0.20	2.68 ± 0.20	38.68 ± 5.50	55.28 ± 9.13
Katonatelep	KT	7.15 ± 0.06	43.00 ± 1.34	1.08 ± 0.43	2.30 ± 0.22	3.68 ± 0.69	112.20 ± 19.68	171.80 ± 11.16
Airport	A	7.47 ± 0.01	41.80 ± 1.11	2.53 ± 0.44	2.11 ± 0.13	1.89 ± 0.19	58.24 ± 11.66	120.40 ± 1.78
Kiskunhalas East	KE	7.41 ± 0.04	34.00 ± 1.41	2.68 ± 0.26	0.94 ± 0.25	2.35 ± 0.42	37.70 ± 5.63	53.24 ± 4.59

Table 3
Effect of increasing cover of *Sporobolus cryptandrus* on vegetation characteristics of the subjected plots (GLMM, significant values are indicated with boldface, $p < 0.05$, sampling site were included as a random factor in the analyses).

Vegetation characteristic	*Sporobolus* cover	
	$F_{3,196}$	p
Species richness	**18.909**	**< 0.001**
Shannon diversity	**3.663**	**0.013**
Evenness	**3.463**	**0.017**
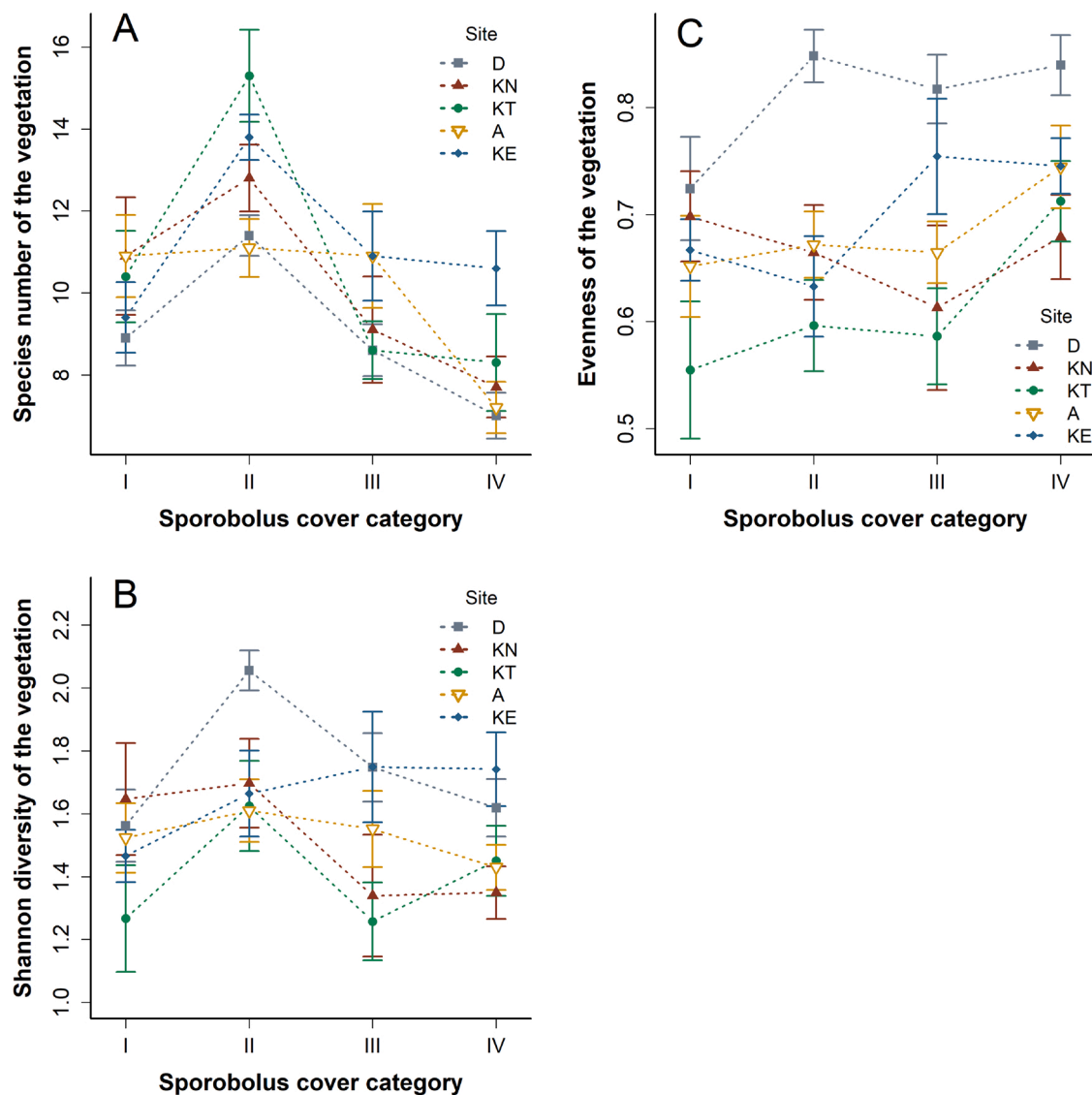
Fig. 3. The relationship between *Sporobolus* cover categories and the species numbers (A), Shannon diversity (B) and evenness (C) of the vegetation in the study sites, calculated excluding *Sporobolus* itself. Sites: D = Debrecen site, KN = Kiskunhalas North, KT = Katonatelep, A = Airport, KE = Kiskunhalas East. *Sporobolus* cover categories were the following: 1 = 0%, 2 = 1–25%, 3 = 26–50% or 4 = 51–75%. Error bars represent standard error.

with no cover of the species. The soil layer significantly affected almost all seed bank characteristics, with decreasing scores towards to the deeper soil layers (Figs. 5 and 6). Seedlings of *Sporobolus* emerged from all studied soil layers (Fig. 6). An interaction between the soil layers and *Sporobolus* cover was detected only in the case of seed bank density of *Sporobolus* and evenness of the seed bank
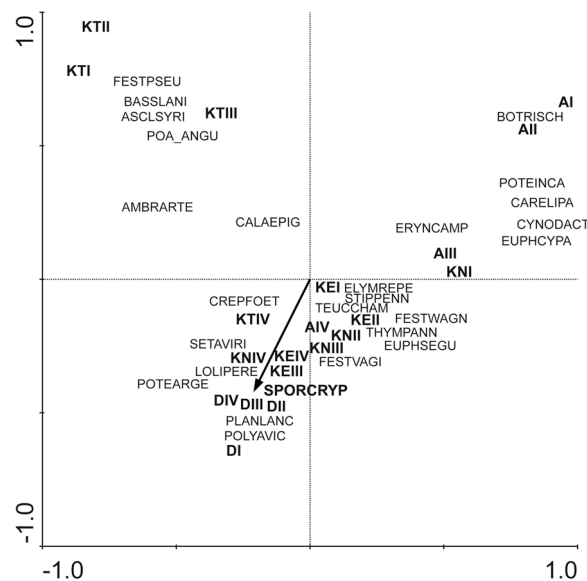
Fig. 4. PCA triplot with the 25 most abundant species (Eigenvalues are 0.289 and 0.187 for the first and second axis, respectively). Vegetation composition of the mass locality sites with different cover of *Sporobolus*. Main matrix is the species abundances without Sporobolus (10 plots per site and Sporobolus cover categories were pooled, four pooled plots per site are included (I-IV). Secondary matrix (added arrow by weighted averaging) was the cover of *Sporobolus cryptandrus*. Sites: D = Debrecen site, KN = Kiskunhalas North, KT = Katonatelep, A = Airport, KE = Kiskunhalas East. Species are abbreviated using the first four letters of the genus names and four letters of the species names. Species abbreviations are the following: SPORCRYP = *Sporobolus cryptandrus*, CYNODACT = *Cynodon dactylon*, BOTRISCH = *Bothriochloa ischaemum*, CARELIPA = *Carex liparocarpos*, FESTPSEU = *Festuca pseudovina*, POA_ANGU = *Poa angustifolia*, POTEINCA = *Potentilla incana*, FESTWAGN = *Festuca wagneri*, BASSLANI = *Bassia laniflora*, EUPHCYPA = *Euphorbia cyparissias*, FESTVAGI = *Festuca vaginata*, EUPHSEGU = *Euphorbia seguieriana*, STIPPENN = *Stipa pennata*, POL-YAVIC = *Polygonum aviculare*, PLANLANC = *Plantago lanceolata*, ASCLSYRI = *Asclepias syriaca*, ERYNCAMP = *Eryngium campestre*, LOLIPERE = *Lolium perenne*, POTEARGE = *Potentilla argentea*, ELYMREPE = *Elymus repens*, THYMPANN = *Thymus pannonicus*, TEUCCHAM = *Teucrium chamaedrys*, AMBRARTE = *Ambrosia artemisiifolia*, CALAEPIG = *Calamagrostis epigeios*, SETAVIRI = *Setaria viridis*, CREPFOET = *Crepis foetida* subsp. *rhoeadifolia*.

Table 4
Effect of *Sporobolus cryptandrus* cover on seed bank composition of the subjected plots. Significant effects were denoted with boldface (two-way ANOVA).

	Sporobolus cover		Soil layer		*Sporobolus* cover × Soil layer	
Characteristic	$F_{3,47}$	p	$F_{3,47}$	p	$F_{9,47}$	p
Seedling number						
Total	2.442	0.082	**12.465**	**< 0.001**	1.503	0.189
Sporobolus	2.727	0.060	**12.845**	**< 0.001**	**2.913**	**0.012**
Other species excluding *Sporobolus*	**3.848**	**0.019**	**10.133**	**< 0.001**	2.024	0.069
Species richness	**11.626**	**< 0.001**	**50.652**	**< 0.001**	0.264	0.980
Shannon diversity	**23.346**	**< 0.001**	**26.845**	**< 0.001**	1.622	0.151
Evenness	**8.659**	**< 0.001**	2.482	0.079	1.612	0.154

(Table 4).

*3.4. Germination characteristics*

Nearly 24% of all *Sporobolus* seeds germinated during the experiment. The highest total germination rate was detected in pots with low soil burial depth all without litter cover (Fig. 7). Both litter and soil cover significantly affected the total germination rate and the seedling survival in the germination experiment, but there was no interaction between these factors (Table 5). The total germination rate was the lowest in pots with low to high burial depth all with high litter cover, but even from these pots some seedlings appeared at the surface and were established until the end of the project. Considering all litter treatments, the highest total germination rate was detected with low soil cover and not in the case of no soil cover. Seedling survival rates showed high fluctuations in most treatments, even in treatments with relatively high survival rates, there were pots with relatively low survival rates. The lowest mean survival rates were detected for the treatments with no soil/high litter cover and high soil/high litter cover (Fig. 7).
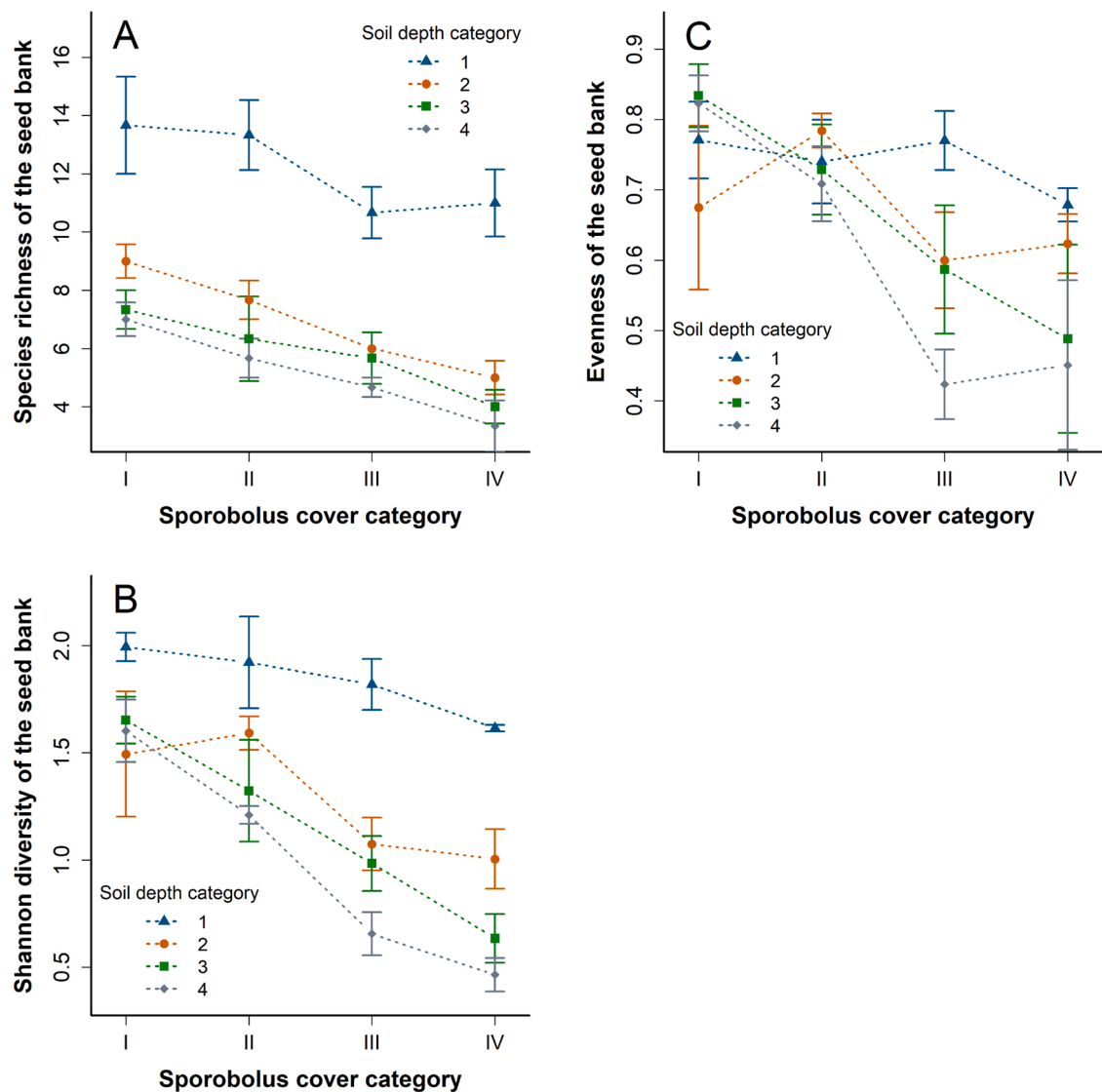
Fig. 5. The relationship between *Sporobolus* cover categories and species richness (A), Shannon diversity (B) and evenness (C) of the seed bank, calculated excluding *Sporobolus* itself. *Sporobolus* cover categories were the following: 1 = 0%, 2 = 1–25%, 3 = 26–50% or 4 = 51–75%. Soil depth categories: 1 = 0–2.5 cm, 2 = 2.5–5 cm, 3 = 5–7.5 cm, 4 = 7.5–10 cm. Error bars represent standard error.

4. Discussion

Dry grassland habitats are in general less threatened by invasive species (Chytrý et al., 2009; Guarino et al., 2021) compared to wetlands or forested habitats; however, there are high differences between its different subtypes. It was reported by Botta-Dukát (2008) that while open rocky grasslands and halophytic habitats, also including alkali grasslands are less threatened by invasive species, sand grasslands have a much higher probability of being invaded (Botta-Dukát, 2008). It was reported based on the MÉTA Database (Molnár et al., 2007) that 50–70% of the total area of sand steppes and open sand grasslands is subjected to plant invasion (most likely by invasive trees *Robinia pseudoacacia, Ailanthus altissima* or *Elaeagnus angustifolia,* ore some clonal forbs like *Asclepias syriaca*) (Botta-Dukát, 2008). In the Kiskunság region, *Sporobolus cryptandrus* has also established in relatively undisturbed sandy grasslands. It is especially alarming that the species has established also in steppe grasslands in the Ukrainian and Russian steppe regions (Demina et al., 2018). As *S. cryptandrus* is considered to be one of the most drought-resistant species of short-grass prairies (see for example Tilley et al., 2009), further potential occurrences and its spread can be forecasted in dry sand regions or degraded rocky habitats of Europe due to the ongoing climate change.
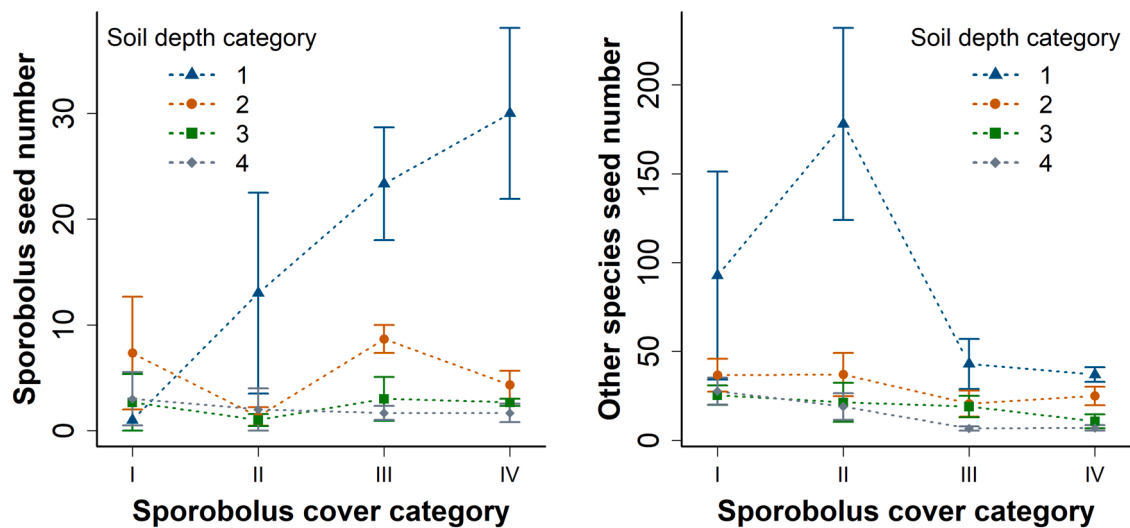
Fig. 6. The relationship between *Sporobolus* cover categories and *Sporobolus* seed bank (left) and the density of the seed bank of other species (right). *Sporobolus* cover categories were the following: 1 = 0%, 2 = 1–25%, 3 = 26–50% or 4 = 51–75%. Soil depth categories: 1 = 0–2.5 cm, 2 = 2.5–5 cm, 3 = 5–7.5 cm, 4 = 7.5–10 cm. Error bars represent standard error.
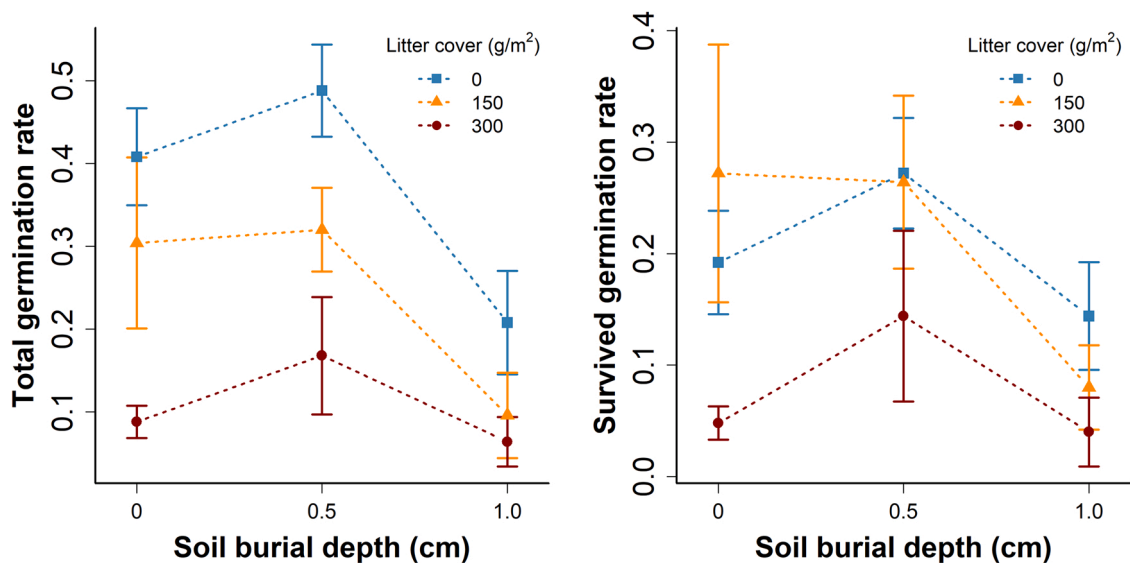
Fig. 7. Effect of litter and soil covering on the total number of germinated seedlings (left) and seedling survival (right) of *Sporobolus cryptandrus*.

Table 5
Effect of litter and soil cover on total germination rate and seedling survival of *Sporobolus cryptandrus* (two-way ANOVA, significant values are indicated with boldface, $p < 0.05$).

	Litter cover		Soil cover		Litter cover × Soil cover	
Germination	$F_{2,45}$	p	$F_{2,45}$	p	$F_{4,45}$	p
Total germination rate	**14.139**	**< 0.001**	**9.005**	**0.001**	0.932	0.456
Seedling survival	**4.153**	**0.024**	**3.777**	**0.032**	0.612	0.657

4.1. Effect of S. cryptandrus on the vegetation and seed banks of sand grasslands

Species-specific information on the aspects of the seed bank formation and early establishment patterns of an invasive species is crucial for developing strategies for its suppression and for the prevention of its further spread (Gioria et al., 2012; Sonkoly et al.,

2020). We found that increasing cover of *S. cryptandrus* is associated with the decreasing species richness and abundance of subordinate species both in the vegetation and seed banks. We also found a rather weak but facilitative effect of the low-abundance establishment of *S. cryptandrus* on the species richness of other species both in the vegetation and seed banks of the subjected grasslands. Similar facilitative effects were detected by Kelemen et al. (2015) in the case of the native species *Festuca pseudovina*, a community dominant perennial grass characteristic in dry alkali grasslands. The most likely explanation of the phenomenon could be that the establishment of the drought-tolerant species also mitigates the microclimatic extremities of the dry habitat and thus facilitates the establishment and survival of others (e.g., Eviner, 2004) – especially that of short-lived species in the habitat (e.g., *Arenaria leptoclados*, *Portulaca oleracea* or *Cerastium semidecandrum*). This type of facilitation was also detected for the invasive species *Asclepias syriaca* from the region (Szitár et al., 2018). However, this 'nurse' effect was not detected in plots with a high cover of the species. The facilitative effect of dominant perennials (including, in our case, *Sporobolus*) mostly occurs through the facilitation of the germination and early establishment of subordinate species, but this positive interaction can turn into competition for light or space (Liancourt et al., 2005; Le Roux et al., 2013). The sign of the interaction between plant species is also density-dependent; a low density of a facilitator species can have positive effects, but it can turn to negative interaction above a certain density of the species (Kelemen et al., 2019). This is in line with our findings as the richness and abundance of subordinated species in the vegetation and seed banks was higher in plots with a low density of *Sporobolus* than in plots without *Sporobolus,* but a higher density of the species had an overall negative effect. However, it should be noted that the observatory nature of our analysis does not allow for certain conclusions regarding the causality of the relationship between *Sporobolus* cover and vegetation and seed bank characteristics, and further manipulative experiments of this issue are needed.

Viable seeds of the species were detected from all soil layers. This indicates that the species is able to form a persistent seed bank as also indicated by similar results from natural prairie communities in North America (Coffin and Lauenroth, 1989; Pérez et al., 1998; Clements et al., 2007). However, the seed bank density was rather low in the three deeper soil layers and increasing *Sporobolus* abundance in the vegetation only increased *Sporobolus* seed bank density in the uppermost layer. This may be an indirect evidence of the ongoing spread and quite recent establishment of the species in the study site (i.e., only a small number of seeds were able to reach the deeper soil layers in the limited time). The detected seed density scores for *Sporobolus* are comparable to some studies in native prairie habitats where high densities of the species were typical (up to 3414 seeds/m^2, Clements et al., 2007). It cannot be excluded, however, that the frequent mowing at the sampled urban grassland occurring before seed maturation affects the seed production and seed bank accumulation of the species in spite of its ability of late and secondary flowering. This latter issue should be clarified later when the seed banks of all sites will be assessed.

4.2. Effect of litter and soil cover on the germination of the species

We found that germination of *Sporobolus cryptandrus* was negatively affected by soil burial and litter cover, but there was no interaction between the two factors. Some seedlings emerged in pots even with the highest litter and soil cover levels. These results were in line with findings of Sonkoly et al. (2020) who studied how soil burial depth and litter cover affect the germination of 11 invasive species and found that most species were able to germinate even with 2 cm soil burial combined with 600 g/m^2 litter cover. The small-seeded *S. cryptandrus* had the highest seed germination rates with 0.5 cm soil burial depth with no litter cover, which is also in line with Sonkoly et al. (2020) who found that litter cover had a significant negative effect on the germination of the studies species and that the effect of litter was stronger for small-seeded species than for large-seeded ones. The detected seed germination rates of *Sporobolus* were rather low compared to some other invasive grasses, but quite similar and even a bit higher compared to the formerly reported germination/viability rates after warm stratification (Sartor and Malone, 2010). As seeds were collected in the previous year, these results suggest that the seeds can survive even longer periods of dry storage without the significant loss of their viability.

4.3. Open research questions and conservation outlook

By definition, those species can be considered as transformer invasive species "that change the character, condition, form, or nature of ecosystems" (Richardson et al., 2000). Based on our results, *Sporobolus cryptandrus* can be considered as a transformer invasive species, whose spread poses a high risk for dry sand and steppe grasslands in Eurasia, especially in the steppe climatic zone. However, to develop an appropriate strategy for its suppression, we need further information on the following crucial aspects of its life history, population dynamics and spread. First, in-depth genetic analyses (e.g., a phylogeographic study using a genomic method) are needed to clarify the likely origin of the established populations and to interpret the means of its long-distance dispersal making it possible to evaluate the pace of its spread and population growth. Second, we need further information on its competitive ability including not only data on the aboveground competition but also information of its allelopathic ability and root competition. Third, it would be necessary to assess the seed banks of sites with different site history and establishment time of the species to evaluate the density and the development speed of its soil seed banks. Fourth, a full-factorial manipulative experiment with a planned partial/total elimination of *S. cryptandrus* from plots with different cover of the species would greatly enhance the knowledge on its effects on vegetation composition. Lastly, for its effective suppression it is vital to study its possible enemies in its native area and to assess the capacity of traditional management types (grazing or mowing) to control the species, not excluding the possibility of its eradication using mechanical (e.g., shading) and/or chemical methods.

After *S. cryptandrus* discovery in Hungary, with a targeted field survey we detected the species in more than 620 individual locations. In our opinion the current situation is a clear phenomenon of a cryptic invasion (Jarić et al., 2019) and there is a high possibility that the species will be detected in other open and dry sandy areas in Hungary but also in other regions of Central Europe, which

underlines the need for a careful monitoring of sand areas in the future. Based on our literature review we can say that naturalized populations of the species were so far detected in Mediterranean regions or regions of Eastern Central and Eastern Europe characterized by a semi-arid, at least moderately continental climate. However, with the forecasted climate change scenarios, other sandy areas in more northern regions may become suitable for its establishment and spread.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01942.

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