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Research Article

Explosive spread of sand dropseed (*Sporobolus cryptandrus*), a C_4 perennial bunchgrass, threatens unique grasslands in Hungary (Central Europe)

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Abstract

Sporobolus cryptandrus is a C_4 perennial bunchgrass native to extensive areas of North America. As a non-native species, it has been reported from several continents, and it has been described as a transformer species in sand steppes of Central and Eastern Europe. However, its spreading ability across the landscape and within habitats has not been quantified, and factors determining its success have not yet been assessed.

In this study, we focused on the largest stronghold of *S. cryptandrus* invasion in Hungary, where the species was first recorded in 2016, and investigated its present distribution in the landscape by mapping along dirt roads. In a separate local study in a heavily infested sand dune site of 2 km^2, we assessed the infestation level and factors affecting the species' establishment.

Our landscape-scale mapping found that in April 2023, the distribution of *S. cryptandrus* encompassed a largely contiguous 600 km^2, with documented presence from 282 1-km^2 mapping units. The species occurred more than 5 m away from roads in 71 mapping units, mostly in the centre of its distribution area. *Sporobolus cryptandrus* presence was negatively related to soil organic matter content and positively related to sand content. At the local scale, we found the species in 39% of vegetation plots in a sand dune site originally covered by Pannonic sand steppes, a priority habitat in the EU Habitats Directive. *Sporobolus cryptandrus* presence at this site was negatively related to the total cover of resident grassland but, surprisingly, was unrelated to the distance from roads. Collectively, these results suggest that primary spread occurs mostly along roads; these roadside populations likely serve as sources for establishment in neighbouring grasslands, but subsequent mass invasion becomes independent from roads.

Together with the species' broad macroclimatic tolerance in North America and reported mass invasion events in Ukraine and Russia, our results suggest that *S. cryptandrus* likely poses a broad-scale threat to Eurasian dry grasslands, in particular on coarse-textured sandy soils with low vegetation cover.

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Introduction

Invasive grasses pose serious threats to natural communities by substantially altering the biodiversity and functioning of ecosystems (D'Antonio and Vitousek 1992; Williams and Baruch 2000). On a global scale, the Poaceae family is highly represented among naturalised alien species, with greater proportion of perennial than annual grasses (Pyšek et al. 2017). Furthermore, about half of the invasive perennial grass species of the world have a C_4 photosynthetic pathway (Sage et al. 1999; Weber 2017), which may promote their expansion in the future when the frequency of episodic heat events, fire, and forest canopy opening are projected to increase (Sage and Kubien 2003). Nevertheless, introduced C_4 perennial bunchgrasses are relatively rare in the European flora (Weber 2017).

Sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) is a C_4 NAD-ME perennial bunchgrass (Koteyeva et al. 2023), which has a wide native distribution range in North America (southern Canada, the United States except for its south-eastern part, and northern Mexico; Holub and Jehlík 1987; Peterson et al. 2007; Kartesz 2015), and is also native to Argentina (Cavagnaro 1988; Rauber et al. 2020). The status of this species in its native range varies from endangered or threatened rare species in some north-eastern states of the USA (Connecticut Department of Energy and Environmental Protection 2015; New Hampshire Official Rare Plants List 2020) to a common species that can occur even along roadsides in the Intermountain Region (Kartesz 2015; Tilley et al. 2022). *Sporobolus cryptandrus* is typically associated with sandy soils and open habitats with bare soil surfaces (Ramaley 1939; Albertson and Weaver 1944; Hulett et al. 1966, 1988). This is a characteristic species of the vegetation in sand hill areas of the Great Plains (Saskatchewan, Nebraska, and Colorado), both as a pioneer species of rolling sand dunes and as a frequent component of sand grasslands on stabilised dunes and level uplands (Ramaley 1939; Hulett et al. 1966). In addition, sand dropseed may be one of the dominant grasses in the herbaceous layer associated with the shrub *Artemisia filifolia* in sandsage prairies in sand dune areas (Hulett et al. 1988). *Sporobolus cryptandrus* is a common species of short grass and mixed grass prairies in the central and southern Great Plains, but is usually abundant only on sandy soils and in areas denuded by drought (Albertson and Weaver 1944; Shiflet 1994). In Argentina, sand dropseed is usually a low-abundance species (< 5% cover) in pampa grasslands and in the grass layer of shrublands (Cavagnaro 1988; Rauber et al. 2020).

Outside of its native range, casual or naturalised populations of *S. cryptandrus* have been reported from numerous locations in Eurasia (from Spain to Japan), Australia and New Zealand (Suppl. material 1). Although *S. cryptandrus* has been detected primarily in disturbed habitats, such as roadsides, along dirt roads, overgrazed or formerly burnt grasslands, ploughed sandy areas, and mown urban grasslands, it can also successfully enter natural plant communities (Nobis et al. 2015; Maltsev et al. 2017; Demina et al. 2018; Török et al. 2021). Recent studies from Central and Eastern Europe, including Hungary, highlight that this grass has

become a transformer invasive species (Maltsev et al. 2017; Demina et al. 2018; Török et al. 2021; Hábenczyus et al. 2022). *Sporobolus cryptandrus* was found to be the only perennial grass among the neophyte species of Hungarian and Russian sand steppes originally dominated by perennial bunchgrasses (Csecserits et al. 2016; Maltsev et al. 2017). The high cover of *S. cryptandrus* in sand steppes was found to be associated with reduced species richness and abundance of subordinate species, homogenised vegetation composition, or even a complete replacement of the originally dominant native perennial grasses (Maltsev et al. 2017; Török et al. 2021; Hábenczyus et al. 2022). Therefore, a detailed assessment of the spreading ability and rate of this grass at the landscape and local scales, as well as the factors determining its invasion success, is urgently needed.

The overall objective of our study was to investigate the current distribution of *S. cryptandrus* at the species' largest naturalised population in Hungary and identify factors associated with its successful spread at the landscape and local scales. At the landscape scale, we mapped *S. cryptandrus* along dirt roads and neighbouring habitats and tested if the species' presence is related to soil characteristics and specific habitats. At the local scale, we assessed the species frequency, and tested if its occurrence is related to distance from roads and the total cover of resident grassland in a heavily infested site of Pannonic sand steppes, a priority habitat type of the EU Habitats Directive (Natura 2000 code: 6260*; Directive 2013) and a critically endangered habitat (Janssen et al. 2016).

Methods

Study region

In Hungary, *S. cryptandrus* was discovered in 2016, near the city of Kiskunhalas (Danube–Tisza Interfluve, Central Hungary) and in the city of Debrecen (eastern Hungary; Török et al. 2021). A historical record of the species was documented in 1927 from the city of Győr (north-western Hungary; Polgár 1933), but the data has not been confirmed since then. Currently, *S. cryptandrus* occurrences have been reported from three regions of Hungary: Danube–Tisza Interfluve (several populations between the city of Lajosmizse (Central Hungary) and the village of Ásotthalom (southern Hungary)), Northern Great Plain (in the city of Debrecen and close to the city of Létavértes), and Western Transdanubia (near the village of Mezőörs; Suppl. material 1).

The study was conducted in the southern part of the Danube–Tisza Interfluve, Central Hungary, where the largest number of *S. cryptandrus* occurrence data was recorded prior to our systematic mapping (Suppl. material 1). The climate of the region is temperate continental with a sub-Mediterranean influence. Mean annual temperature is 10.4 °C, and mean annual precipitation is 500–550 mm with a mid-summer drought typical in July and August (1961–1990; Kovács-Láng et al. 2000). Dominant soil types are coarse-textured calcareous sandy soils with high (> 90%) sand content and low (< 3%) humus content (Kovács-Láng et al. 2000; Kröel-Dulay et al. 2019). Major habitat types include agricultural fields, tree plantation forests of native and alien species, secondary grasslands on previous arable lands, and the remnants of natural Pannonic sand forest steppe mosaic of open and closed grasslands, and juniper-poplar shrublands (Fig. 1).

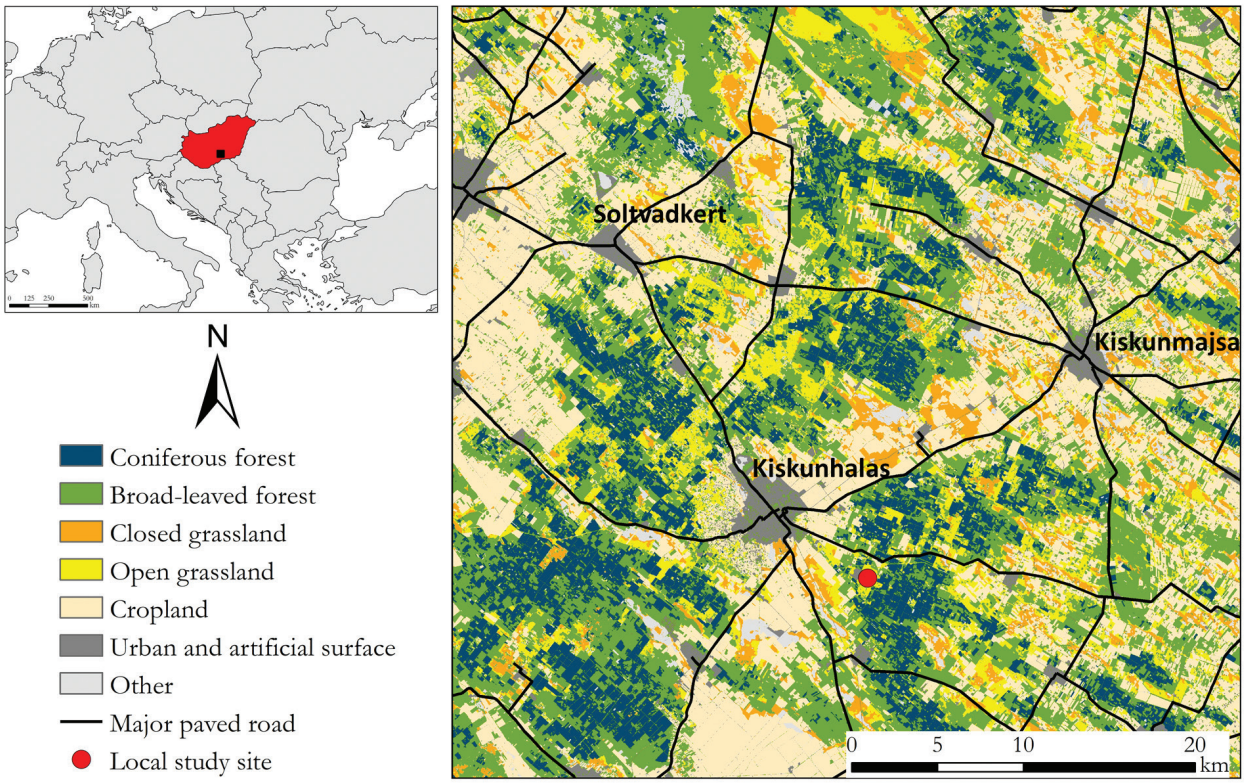


Figure 1. The setting of the study area in Central Europe and Hungary (red), and its habitat map. The red symbol on the habitat map indicates the local study site. The land cover information is based on the Ecosystem Map of Hungary (Tanács et al. 2022).

Landscape-scale mapping

Since we planned to map the current distribution of *S. cryptandrus*, we did not have an *a priori* defined study area. As a starting point, we used *S. cryptandrus* occurrence data from the database of the Kiskunság National Park and from the co-authors of this paper, in the vicinity of the first record of the species, south-east of the city of Kiskunhalas (Török et al. 2021). Note that these data were spatially aggregated and temporally uneven, thus not suitable for reconstructing the invasion dynamics of *S. cryptandrus* between 2016 and 2022.

We implemented the mapping by driving slowly (max 15 km/h) on dirt roads and visually searching for *S. cryptandrus* individuals along the roads. We decided to sample along dirt roads because (a) large populations of *S. cryptandrus* were reported to occur along dirt roads (Török et al. 2021), (b) the low speed allowed us to spot *S. cryptandrus* also in the neighbouring vegetation, and (c) this method made it possible to systematically sample a relatively large area within a reasonable timeframe. The mapping was carried out in early spring (between February and April) 2023. According to our experiences, the dry *S. cryptandrus* bunches and flowering stems from the previous summer are easily recognisable in the open vegetation along the dirt roads as well as in the neighbouring grasslands and forest understory at this time of the year (Fig. 2).

During mapping, a new *S. cryptandrus* occurrence was only recorded when we were at least 120 m (checked on GPS) from an already documented occurrence. We recorded both the presence along the road, defined as within 5 meters of the road edge, and the presence further away from the road, defined as more than 5 meters from the road edge. Based on our field experience, we think that we can,



Figure 2. *Sporobolus cryptandrus* in the study area, south-east of the city of Kiskunhalas. The species most frequently grows on and along dirt roads (upper left picture; 7 February, 2023), but it can also form monodominant patches away from roads (upper right picture; 7 February, 2023). It can establish and grow in natural grasslands (lower left picture; large green tussocks in the foreground are *S. cryptandrus*, whereas small yellowish bunches are native *Festuca vaginata*, 13 September, 2022) and take over dominance (lower right picture; 13 September, 2022). Pictures were taken by G. Kröel-Dulay and A. Rigó.

with high probability, spot average-sized *S. cryptandrus* individuals to at least 30 m in open grasslands, where the species occurs. Starting in the close vicinity of the first reported occurrence (recorded in 2016) and moving gradually away, we sampled all dirt roads unless they were closer than 1 km to an already sampled parallel road. We gradually expanded the search area based on newly detected occurrences, until no additional occurrences were found within a ca. 2 km radius from the outermost occurrences. In the case of already known or accidentally found sporadic occurrences, we only searched their neighbourhood. Mapping in some areas was constrained by the lack of dirt roads or inaccessibility (e.g. fenced areas). While driving, we recorded not only *S. cryptandrus* occurrences, but also the tracks we drove, in order to report the verified absence of the species.

For the visualisation of *S. cryptandrus* distribution in the landscape scale, we plotted our data using the EEA reference grid cells of the ETRS89-LAEA Europe coordinate system (EPSG 3035; EEA 2013) with a 1-km resolution. We distinguished three grid cell states: (1) "presence", where *S. cryptandrus* was observed during our sampling or beforehand, (2) "verified absence", where we drove at least 500 m, but no *S. cryptandrus* was found during our sampling (or beforehand), and (3) "no data", where we drove less than 500 m and no *S. cryptandrus* was found during our sampling (or beforehand). Within the grid cells where *S. cryptandrus* was present, we identified cells where the species was recorded more than 5 m

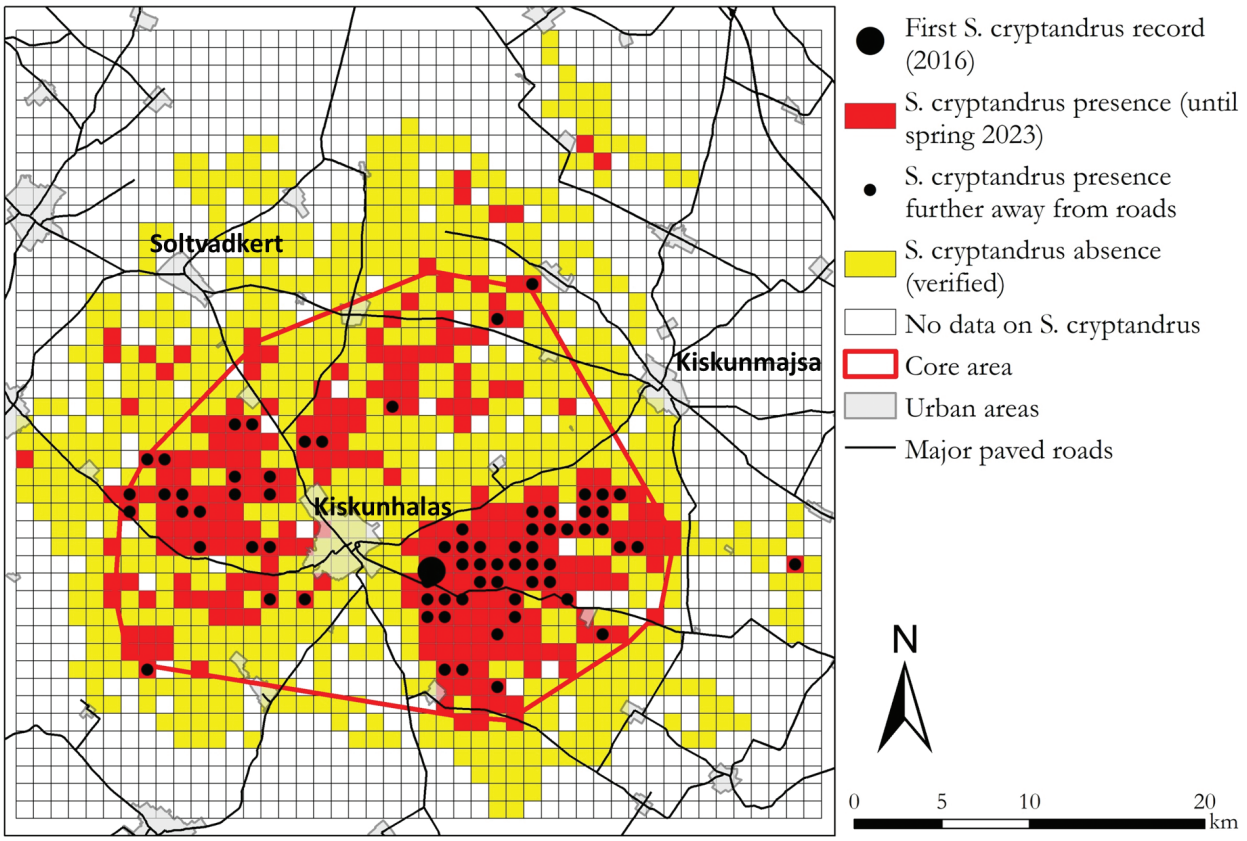


Figure 3. Distribution of *Sporobolus cryptandrus* within the study area at a 1-km resolution in April 2023 and the first documented record in 2016. Verified absence denotes cells where at least 500 m dirt roads were sampled, and no *S. cryptandrus* was found, while no data denotes cells that were not sampled, or less than 500 m dirt roads were sampled and no *S. cryptandrus* was found. The core area was defined as the convex hull around the outermost occupied cells that are not separated from the large areas of mostly contiguous distribution (occupied cells) by more than one empty cell. *Sporobolus cryptandrus* presence further away from roads means cells where the species was present more than 5 m away from roads (in almost all of these cases, it was found also along the roads).

away from the road edge. We defined the core area of the current distribution (April 2023) as the convex hull around the outermost occupied cells that are not separated from the large areas of mostly contiguous distribution (occupied cells) by more than one empty cell (Fig. 3). We defined the core area for two reasons. First, we think that this area is a more robust measure of the state of invasion than the convex hull of all known occurrences, because it is less sensitive to one or a few data points. Second, we used *S. cryptandrus* occurrences within the core area for further analysis on preferences to soil and habitat types, because these relationships may not be visible in areas with extremely few occurrences. All maps were created using ESRI ArcMap 10.8 GIS software (ESRI 2020).

Local survey in a highly infested grassland site

We studied the local-scale distribution of *S. cryptandrus* in a heavily infested sand dune system close to the first record of the species within the study area (coordinates: 46.414, 19.550 EPSG 4326; Fig. 1) in July 2022. Please note that the peak of plant biomass production in sand grasslands is usually in June, thus sampling in July provided a reliable estimate of species abundances in this system. Within a ca. 2 km^2 area covered predominantly by Pannonic sand steppes, we selected 100

randomly located 16 m^2 plots for vegetation sampling. As we aimed to sample sand steppes, a randomly selected plot location was skipped, and a new plot location was generated, if it fell on a road, in a shrubby or forested patch, or closer than 50 m to a previously sampled plot. In each plot, we recorded the presence and estimated the percentage cover of *S. cryptandrus*, as well as all other vascular plants that reached at least 1% cover.

Statistical analysis

Statistical analyses were performed using R version 4.1.1 (R Core Team 2022). For statistical analysis on what environmental factors may be related to the present distribution at the landscape scale, we first generated absence data points within the core area by randomly placing points to the tracks that we drove using the Generate Points Along Lines tool of ESRI ArcMap 10.8. The spatial constraint was that a new absence point should be at least 120 m from a presence or an already chosen absence point. Finally, we ended up with a total of 5715 points, 873 presence and 4842 absence points within the core area. For each point, we gathered soil and habitat information as potential environmental factors that may be related to *S. cryptandrus* presence. Soil sand content (%) and soil organic matter (SOM) content (%) were derived from the DOSoReMI database (https://dosoremi.hu/en/; Pásztor et al. 2020). For habitat information, we used the presence/absence of major habitat types (open grassland, closed grassland, cropland, coniferous forest, broad-leaved forest) within a 20-m radius around each point, derived from the Ecosystem Map of Hungary (Fig. 1; Tanács et al. 2022). This buffer zone was used because *S. cryptandrus* presence/absence localities were studied along dirt roads, which are often habitat boundaries, and we wanted to include only habitats in the close vicinity of each point.

We modelled the effect of habitat types, and the percentage sand and SOM contents of the soil on the presence of *S. cryptandrus* with three separate binomial generalized linear models. We used separate models because sand and SOM contents were correlated, and habitat types were also related to soil properties. For the three models, we first used all sampling points but found significant spatial autocorrelation in the residuals based on Moran's tests in the DHARMa R package (Hartig 2022). To avoid spatial autocorrelation, we selected a subset of 500 random points from the 5715 points, with a minimum distance of 500 m between them, and repeated the analyses on this subset. In the case of the subset models, we did not detect any spatial autocorrelation; therefore, we used these models to present the results.

In order to explain *S. cryptandrus*' presence within a highly infested grassland site in the local survey, we included the distance from the nearest dirt road and the total cover of resident grassland as explanatory variables in two separate binomial generalized linear models. The dirt road map was obtained by digitizing frequently used roads from a satellite image, and we used the Near tool in ESRI ArcMap 10.8 to get a distance measure for each plot (n = 100). The cover of resident grassland was obtained by summing up the percentage cover of each species present in the given plot (without *S. cryptandrus*). Plots with *S. cryptandrus* cover above 5% (15 plots) were left out of this analysis, because a substantial *S. cryptandrus* cover may itself induce a decrease in the cover of the resident species. We tested for but found no spatial autocorrelation in the model residuals by using the DHARMa

R package (Hartig 2022). All models were checked visually for and fulfilled the homoscedasticity assumption of the residuals. Results were visualised with the ggplot2 package (Wickham 2011).

Results

We sampled (drove) a total of 1326 km and detected 902 *S. cryptandrus* occurrences (with the constraint that neighbouring occurrences are at least 120 m from each other), spread over 266 1-km^2 units of the EEA reference grid. After merging these with previous data collected between 2016 and 2022, *S. cryptandrus* occurred in 282 mapping units (red cells in Fig. 3). Its presently known distribution extends 46 km in an east-west and 45 km in a north-south direction. Within the 591 km^2 core area (Fig. 3), *S. cryptandrus* occurred in 268 mapping units (45%). The species occurred more than 5 m away from roads in 71 mapping units, mostly in the centre of its distribution (Fig. 3).

Across the core area of its present distribution in the study area, the probability of *S. cryptandrus* presence was negatively related to soil organic matter content (χ^2 = 43.71, df = 1, p < 0.001; Fig. 4a, Suppl. material 2) and positively related to sand content (χ^2 = 11.12, df = 1, p < 0.001; Fig. 4b). Furthermore, the probability of *S. cryptandrus* presence along dirt roads was positively related to the presence of open grasslands (χ^2 = 19.25, df = 1, p < 0.001) and coniferous forests (χ^2 = 24.00, df = 1, p < 0.001), negatively related to the presence of croplands (χ^2 = 17.09, df = 1, p < 0.001), and unrelated to the presence of closed grasslands (χ^2 = 0.21, df = 1, p = 0.649) and broad-leaved forests (χ^2 = 0.01, df = 1, p = 0.947; Fig. 4c).

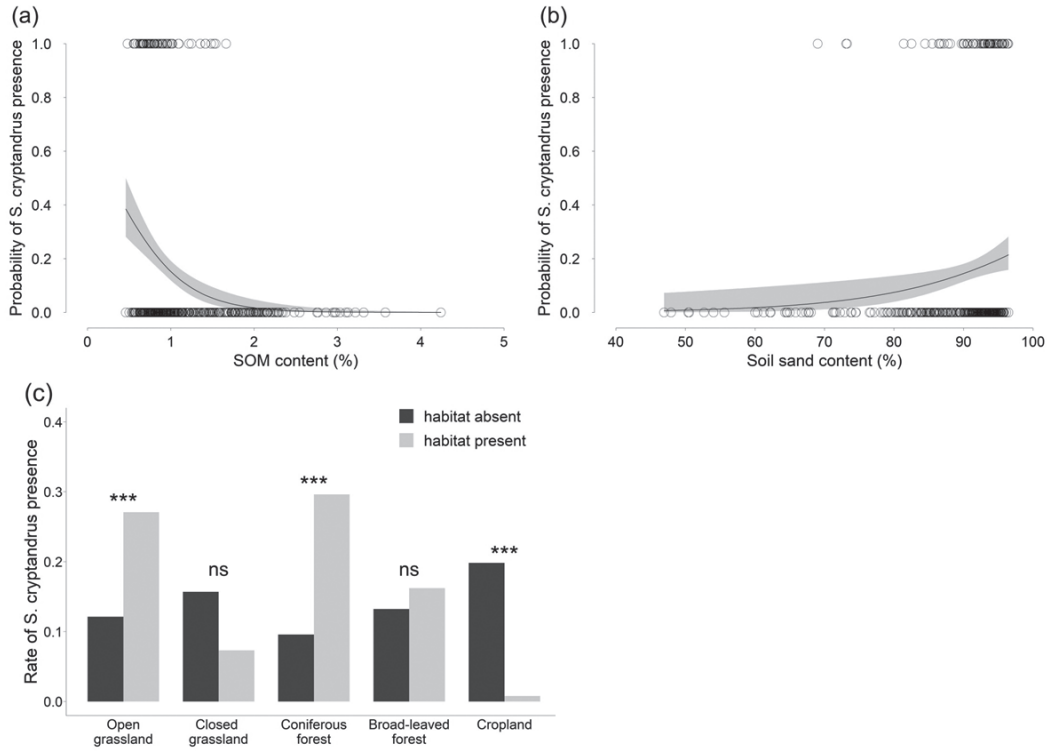


Figure 4. The relationship between the probability of *Sporobolus cryptandrus* presence at the landscape scale and **a** soil organic matter (SOM) content **b** soil sand content, and **c** the presence or absence of major habitat types within a 20-m radius around the sampling points along dirt roads.

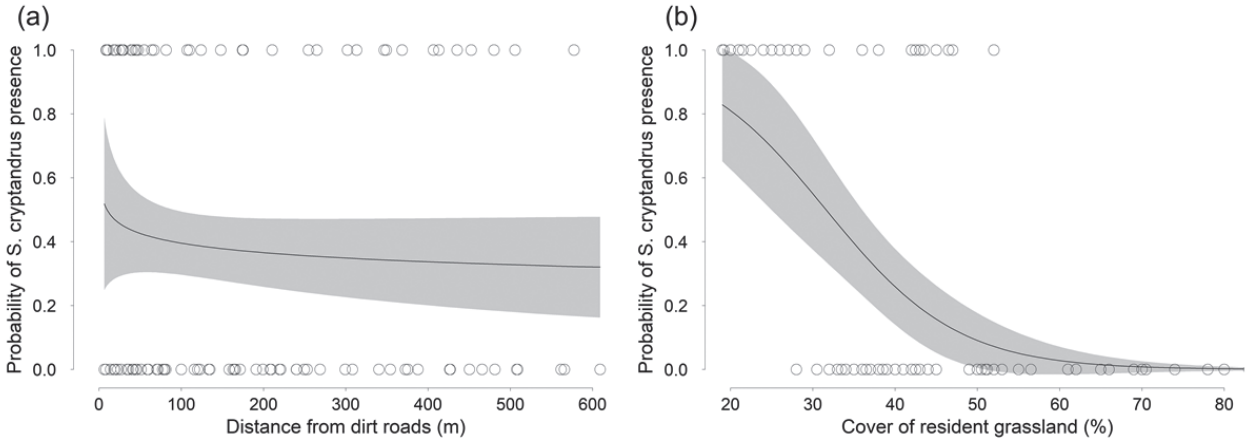


Figure 5. The modelled relationship between the probability of *Sporobolus cryptandrus* presence in plots within a heavily infested open grassland site and **a** the distance from the nearest dirt road (n = 100) and **b** the total cover of the resident grassland community (n = 85). To study the relationship with the total cover, we left out plots with the *S. cryptandrus* cover over 5%, because we wanted to avoid *S. cryptandrus* substantially affecting the resident community in our samples.

In the heavily infested Pannonic sand steppe site in the middle of *S. cryptandrus* distribution, the species was present in 39% of vegetation plots, and out of these, *S. cryptandrus* was the dominant species (i.e. species with the highest cover in a study plot) in nine vegetation plots. The probability of *S. cryptandrus* presence was not related to how far a plot was located from dirt roads (χ^2 = 1.07, df = 1, p = 0.300; Fig. 5a, Suppl. material 2). By contrast, it was strongly negatively related to the total cover of resident grassland (χ^2 = 27.16, df = 1, p < 0.001; Fig. 5b), ranging from 80% probability in grasslands of 20% cover to very low probability in grasslands of 50% cover or higher.

Discussion

Our systematic mapping showed that in April 2023, *S. cryptandrus* had a largely contiguous distribution in a 591 km^2 area, occurring in about half of the mapping units within this area. This is striking because the species was first recorded in the region in 2016 (Török et al. 2021), and there have been only sporadic reports since then (Suppl. material 1), which indicates a very high spreading rate. Although the exact date of the establishment of the species in the area is unknown, it most likely happened not long before the first discovery in 2016 (Török et al. 2021), given the large size of the species' tussocks (up to 1 m high with inflorescences; Fig. 2) and the high intensity of botanical and ecological field surveys in the region.

The fast spreading of *S. cryptandrus* may be explained by its prolific seed production (a single panicle can produce ten thousand seeds; Weaver and Hansen 1939), effective seed dispersal (very small caryopses can easily be carried by the wind, and the pericarp becomes mucilaginous when moist; Peterson et al. 2007), and a large soil seed bank (Török et al. 2024). In addition, the species' ability to tolerate a wide range of climatic conditions may also have contributed to its rapid expansion in this semiarid sand dune system. In its native range, *S. cryptandrus* is described as an extremely drought-tolerant species adapted to sites receiving 175–410 mm mean annual precipitation (Tilley et al. 2009), and it also occurs even in cool climates with mean annual temperatures as low as 1 °C (Hulett et al. 1966). The rate of spread we found for *S. cryptandrus* (ca. 100 km^2 y^{-1} on average since its first record

in 2016) is in the higher part of a broad range (0.006–333 km^2 y^{-1}) of long-distance dispersal rates reported in the literature for alien herbaceous perennial species in their invaded range, and about fourfold higher than that of another invasive C_4 perennial bunchgrass, *Eragrostis lehmanniana* in Arizona grasslands (24.6 km^2 y^{-1}; Pyšek and Hulme 2005).

We detected *S. cryptandrus* further away from roads in 26% of occurrences (in almost all of these cases, the species was found also along the roads), particularly in the centre of the core area, in the vicinity of the first record of the species, where dirt roads were highly infested with *S. cryptandrus*. This distribution pattern suggests that *S. cryptandrus* spreads primarily along dirt roads but has an ability to enter natural grasslands (Fig. 2). These results indicate that *S. cryptandrus* has a greater invasion potential than other invasive species of open sand grasslands in the region. The annual *Ambrosia artemisiifolia* and *Cenchrus incertus* are also associated with dirt roads, but rarely colonise the adjacent intact natural vegetation (Szigetvári 2002). The perennial *Asclepias syriaca* was reported to be most abundant in tree plantations and old fields (Csecserits et al. 2016; Kelemen et al. 2016), and can only rarely invade natural sand grasslands (Albert et al. 2014; Csecserits et al. 2016).

We found that the presence of *S. cryptandrus* is positively related to the sand content of the soil, which is in agreement with previous reports on the species. In fact, the common English name of *S. cryptandrus* is sand dropseed, which reflects its preference for sandy soils in its native range (Ramaley 1939; Albertson and Weaver 1944; Hulett et al. 1966, 1988). In addition, its introduced populations are also frequently found on sandy soils (Gugnacka-Fiedor and Adamska 2010; Nobis et al. 2015; Török et al. 2021), and mass invasion events, in particular, took place in sand dune systems as well as on sandy floodplain terraces and riverbanks (Gouz and Timoshenkova 2017; Maltsev et al. 2017; Demina et al. 2018; Maltsev and Sagalaev 2018; Török et al. 2021). The probability of *S. cryptandrus* occurrence was negatively related to soil organic matter content. Although this relationship was kind of expected since sandy soils usually have low SOM, the relationship for SOM content was much stronger than for sand content: no plot with SOM over 1.8% had *S. cryptandrus*. This suggests that SOM may have a strong predictive power when estimating the species' potential future distribution.

The relationships of *S. cryptandrus* occurrence with the presence of specific habitats were consistent with the correlations between the species' presence and soil characteristics. The probability of *S. cryptandrus* presence along dirt roads was positively related to the presence of open grasslands and coniferous forests, habitat types that typically appear on soils with high sand and low soil organic matter content in the region (Kröel-Dulay et al. 2019). By contrast, the probability of *S. cryptandrus* occurrence along roads was negatively associated with the presence of croplands, which usually have soils with relatively high SOM and low sand contents. This is nicely exemplified by the broad southwest-to-northeast belt across our study area that is dominated by croplands (Fig. 1) and has few *S. cryptandrus* occurrences (Fig. 3). Note that areas northwest of this less suitable belt and thus separated from the first record and potential source of invasion, have a more fragmented *S. cryptandrus* distribution, with fewer instances where the species occurs further away from roads. This broad-scale pattern suggests that unfavourable landscapes may somewhat slow down, but do not ultimately prevent the spread of *S. cryptandrus*.

Our local survey in a sand dune site showed that once established, *S. cryptandrus* can become very frequent (it was present in 39 out of 100 random vegetation plots)

in natural sand grasslands within about six years. Furthermore, these occurrences were not correlated with the distance from dirt roads but were associated with low (< 50%) cover of the resident grassland. These results suggest that when *S. cryptandrus* enters natural grasslands, its further spread may become independent from dirt roads. Moreover, *S. cryptandrus* has become even dominant in several stands (in nine vegetation plots) since its first record in 2016. This implies that, as a dominant species, *S. cryptandrus* likely has a strong impact on community structure and ecosystem functions. Previous studies in the region demonstrated that the high cover of *S. cryptandrus* was associated with reduced species richness, increased vegetation height, and decreased abundance of certain plant functional groups (e.g. other perennials and insect-pollinated species; Török et al. 2021; Hábenczyus et al. 2022). However, long-term monitoring studies that follow the process of invasion in permanent plots are needed to provide a detailed description of how *S. cryptandrus* invasion affects natural sand grasslands; we have already started such studies.

Collectively, the results of our landscape- and local-scale study revealed that *S. cryptandrus* has an ability to spread very fast along dirt roads, and these roadside populations likely serve as sources for its establishment in neighbouring grasslands, where the invasion of this grass poses a serious threat primarily to open perennial grasslands on unproductive sandy soils. These grasslands, the Pannonic sand steppes, are a priority habitat type of the EU Habitats Directive (Natura 2000 code: 6260*; Directive 2013). They harbour a high number of species endemic to the Pannonian biogeographical region (Fekete et al. 2014; Riezing 2023). This habitat type is considered critically endangered in the European Red List of Habitats (Pannonian and Pontic sandy steppe, E1.1a; Janssen et al. 2016), and 98% of the area of Pannonic sand steppes in Hungary were already lost in the last 230 years (Biró et al. 2018). Their remaining stands are already among the vegetation types that are most heavily infested by alien plant species in the country (Botta-Dukát 2008), and *S. cryptandrus* now becomes an additional serious threat.

The preference of *S. cryptandrus* to open grasslands at this stage of its invasion may be related to the fact that bare soils can provide a more favourable environment for seed germination of this grass. Previous studies reported that both diurnal temperature fluctuations, which are larger in bare soil than in soil beneath a closed grassland canopy (Thompson et al. 1977), and the presence of light increased the germination percentage of *S. cryptandrus* seeds (Sabo et al. 1979). However, it does not necessarily mean that more closed grasslands will not be in danger in the future. Consistent with this possibility, previous studies, both in our study area (near the city of Kiskunhalas) and in southern Russia, reported that *S. cryptandrus* can enter sand steppe habitats where the total vegetation cover (without *S. cryptandrus*) exceeds 50% (Demina et al. 2018; Hábenczyus et al. 2022). Together with the species' high spreading rate and its ability to be a transformer invasive species reported from Russia, Ukraine, and Hungary (Gouz and Timoshenkova 2017; Maltsev et al. 2017; Demina et al. 2018; Török et al. 2021; Hábenczyus et al. 2022), our results suggest that *S. cryptandrus* likely poses a broad-scale threat to Central and Eastern European grasslands on sandy soils.

The rapid spread of *S. cryptandrus* and its potential risk for natural sand grasslands call for developing effective management strategies against the species. Given the large population size and area covered by the species in our study area, full eradication is unrealistic. Therefore, preventing *S. cryptandrus* from further spread along dirt roads and particularly from entering natural grasslands should be the

priorities for action. Our results highlight the need for regular monitoring of dirt roads in actual infested and high-risk areas, and for blocking roads in sites where *S. cryptandrus* are present in high densities. Our map on the current distribution of *S. cryptandrus* may help to identify roads that should be carefully monitored for new infestations within and around the study area, and newly established and small populations should be eradicated. Regarding the natural grassland sites where *S. cryptandrus* already reached relatively high abundance, further studies are needed to assess how various habitat management practices (e.g. grazing, mowing, prescribed burning or their combination) affect the competition between *S. cryptandrus* and resident native plant species. Finally, if the mass invasion of *S. cryptandrus* cannot be stopped or at least slowed down, representative stands of unique Pannonic sand steppes should be designated, which are intensively surveyed and actively kept free of the species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

Data that support the findings of this study are available from the authors upon reasonable request. R scripts used for data analysis are available in Suppl. material 2.

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Supplementary material 1

Global distribution of sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) as an alien plant species based on literature data

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Data type: xlsx

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Link: https://doi.org/10.3897/neobiota.95.124667.suppl1

Supplementary material 2

R scripts and the results of binomial generalized linear models used to test the effect of explanatory variables on the presence of *Sporobolus cryptandrus*

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Data type: pdf

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