






RESEARCH ARTICLE

Increasing abundance of an invasive C_4 grass is associated with larger community changes away than at home

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Abstract

Aim: We evaluated stands of the invasive grass, *Sporobolus cryptandrus* in its native North American range and its non-native European range, where it is a recent invader. Our aim was to reveal how the species' increasing abundance affects functional diversity and the ecosystem service-provisioning capacities of plant communities in both ranges.

Location: Sand grasslands in the Kiskunság, Hungary and in Montana, USA.

Methods: All vascular plant species and their relative abundances were recorded in a stratified random manner in 1 m × 1 m plots in each range, using the following cover categories of *Sporobolus* as strata: 1%–25%, 26%–50%, 50%–75%, and 75%–100%. The functional characteristics of the plant communities in the two continents were compared. We performed comparisons of the communities both with and without including *Sporobolus*.

Results: Increasing *Sporobolus* cover resulted in a lower functional diversity and species richness, reduced average specific leaf area and increased the height of whole plant communities in both ranges but these effects were significantly stronger in the non-native stands. *Sporobolus* also negatively affected the cover of insect-pollinated plant species and the proportion of native perennials, switching the rest of the community from perennial-dominated to annual-dominated. In plant communities without *Sporobolus*, increasing *Sporobolus* cover led to a higher specific leaf area and seed mass in both ranges, but average height was decreasing along the *Sporobolus* abundance gradient in the native range, whereas it was increasing in the non-native range.

Conclusions: The spread of *Sporobolus*, away from its native range, leads to the impoverishment of host communities and compromises the biomass and floral resource-provisioning capacity of the vegetation to higher trophic levels. Tackling the spread of this new invader should therefore be a priority task.

KEYWORDS

dry grassland, ecosystem functions, functional diversity, native range, plant invasion, plant traits

1 | INTRODUCTION

Biological invasion involves the successful introduction, establishment and subsequent spread of species outside their native range, which may be driven by human activities (Essl et al., 2018). The invasion success of an alien species is the outcome of several factors, including the characteristics of the resident community (invasibility) as well as the functional properties of the introduced species (Hejda et al., 2009). Although invasibility is apparently context-dependent, and general statements should always be interpreted circumspectly, there are three reasonable aspects to highlight. The most important factors determining the susceptibility of the recipient community to invasion are: (1) altered disturbance regime, (2) empty niches proceeding from ineffectively used resources, and (3) the low diversity or low competitive ability of the resident species (Davis et al., 2000; Lonsdale, 1999; Mack et al., 2000). By contrast, the functional traits of species related to physiology, biomass allocation, growth rate, size, and fitness are of the greatest importance in promoting the invasion success of non-native species (van Kleunen & Richardson, 2007).

There is a large body of evidence that the spread of invasive species can negatively affect subjected ecosystems (Bellard et al., 2016; Kumschick et al., 2015; Vilà & Hulme, 2017). Adverse impacts of invasive alien species include the suppression of native species (Kelemen et al., 2016; Pal et al., 2015), loss of overall biodiversity (Bellard et al., 2016), and alteration of community structure (Hejda et al., 2009) and ecosystem functions (Kumschick et al., 2015), all leading to altered ecosystem services and disservices (Milanović et al., 2020). Functional traits can provide a useful tool to quantify and describe the functional properties of communities, thereby giving the opportunity to assess impacts on ecosystems, and translate ecosystem services and disservices into monetary or non-monetary values.

Functional traits are also used to reveal community-level effects, when the impact of an invader or the response of the invaded community is of concern (Davies, 2011; Fried et al., 2019; Funk & Wolf, 2016; Kelemen et al., 2016). The ideal approach to detect invasion-caused changes in native vegetation would be to record the original state of the community, even before introduction of the non-native species, then to follow its spread in real time (Pickett, 1989). However, researchers rarely have the opportunity to study the effects of an invader in this way. Because of this methodological problem, the space for time substitution approach, i.e., comparing invaded and uninvaded sites under the same habitat conditions (Pickett, 1989), has arisen as an alternative to the before–after chronological design. Although this method has its limitations, because it lacks pre-invasion data and inherently supposes causality between the presence of the non-native species and the observed shifts in the native vegetation (Sax et al., 2005), prudently interpreted results of such studies may provide valuable starting points for nature conservation.

The open sand grasslands of Hungary are under particularly high invasive pressure (Botta-Dukát, 2008). The high invasibility of this

habitat type can be linked to heavy human disturbance, mostly related to agricultural activities and the presence of intensively managed, non-native tree plantations (Botta-Dukát, 2008; Csecserits et al., 2016). Furthermore, the area suffers from severe aridification, potentially creating niches for species tolerant to xeric conditions. Widespread invaders include both woody species (*Ailanthus altissima*, *Elaeagnus angustifolia*, and *Robinia pseudoacacia*) and forbs (*Asclepias syriaca*, *Solidago canadensis*, and *Solidago gigantea*) (Iványosi, 2015). In 2016, a North American perennial C_4 bunchgrass, *Sporobolus cryptandrus* (Torr.) A. Gray (sand dropseed) was discovered in these grasslands, and appeared to spread rapidly (Török & Aradi, 2017).

Sporobolus cryptandrus is a prolific seed producer (Brown, 1943) and is one of the most drought-tolerant graminoids in North American short-grass prairie (Wan et al., 1993). In Hungary, *S. cryptandrus* has been detected along busy dirt roads and connecting disturbed areas such as fallows and trash dumps, but it is also invading intact grasslands (Török et al., 2021). The species was accidentally introduced to the Kiskunság region, Hungary, by a shepherd coming home from the United States. The origin of the stands of *S. cryptandrus* in the Nyírség region is still unknown. Considering its high fecundity and drought resistance (Demina et al., 2018), *S. cryptandrus* may become an extremely dangerous invasive species of sand regions in Hungary and elsewhere.

Although *S. cryptandrus* has been reported from several countries as a non-native species, its ecological effects on the invaded vegetation have not been assessed. We have limited understanding of whether this species will integrate into the recipient plant communities and play a role similar to that in its native range, or by escaping its biotic limitations in the new environment, will suppress the native vegetation and transform its functional profile. Because the guild of xeric C_4 bunch grasses is scarce in the Hungarian flora, we hypothesize that the latter outcome is more probable across a range of functional traits and other community characteristics. In particular, we addressed the following questions:

1. How does the increasing abundance of *S. cryptandrus* affect the diversity of plant communities in its non-native (Hungarian) compared with its native (North American) range?
2. How does the increasing abundance of *S. cryptandrus* influence the functional community characteristics in the two regions?

2 | METHODS

2.1 | Study area

We surveyed grassland patches in the native (North American) and the newly colonized non-native (Hungarian) ranges of *S. cryptandrus*. The North American native stands were located near the towns of Helena, Pipestone, and Three Forks (Montana, USA) (Figure 1a,b). The climate of the region is continental, with long and cold winters and hot summers. The mean annual temperature is 6–7°C and the mean annual precipitation is 250–350 mm.

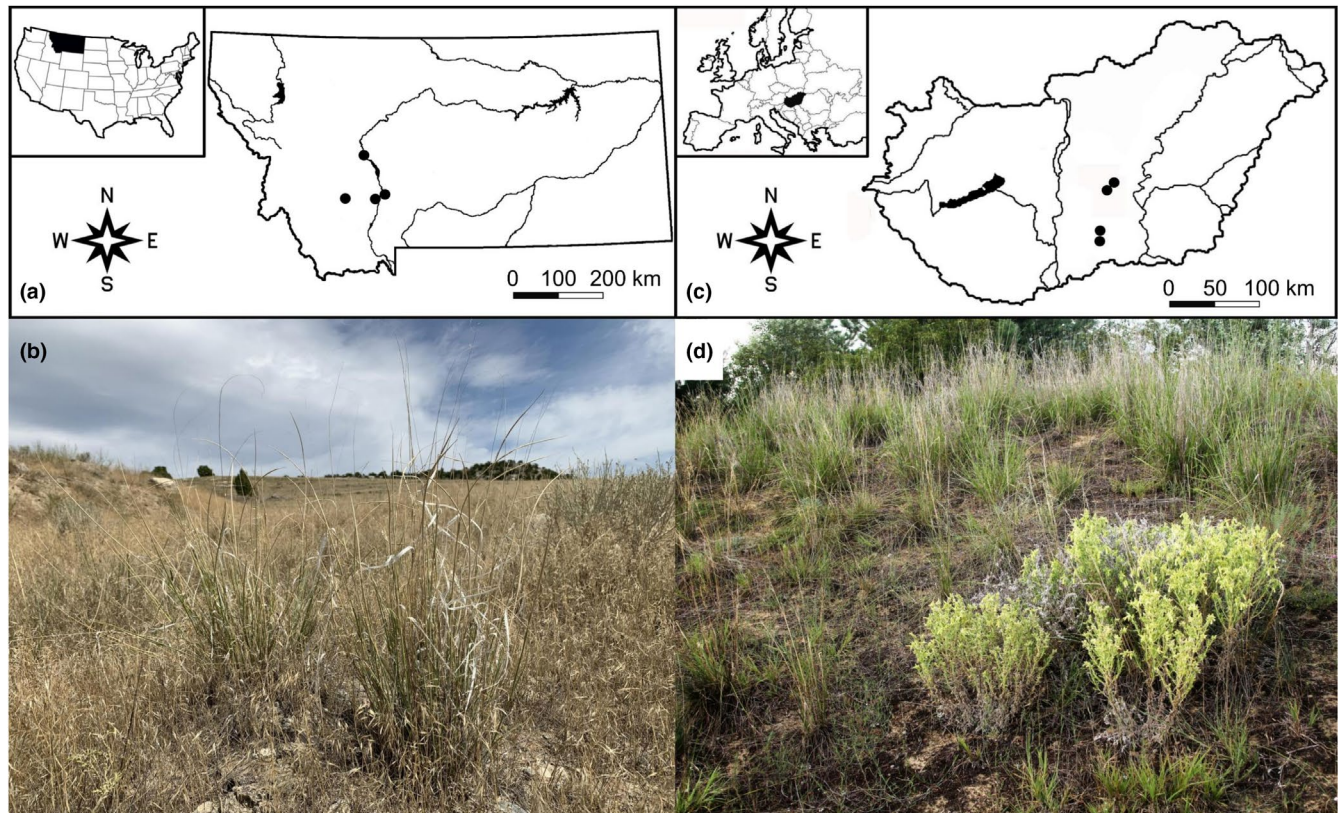


FIGURE 1 Maps and photographs of the localities of the surveyed sites in the native (North American) and the non-native (Hungarian) ranges of *Sporobolus cryptandrus*. (a) Map of the North American sites; (b) map of the Hungarian sites; (c) native habitat and habitus of *S. cryptandrus* in Montana (photograph by R. Pál); (d) invaded open grassland in the Kiskunság region (photograph by A. Kelemen)

Soils are loamy, fine- and medium-textured and have low organic matter content. The potential vegetation types of the area are: Rocky Mountain lodgepole pine forest, Rocky Mountain montane Douglas-fir forest and woodland, montane sagebrush steppe and Great Plains mixed-grass prairie. Typical land uses are dry farming and grazing. The studied populations of the plant occurred in Great Plains mixed-grass prairie ecological systems (Luna & Vance, 2017), more specifically in *Pascopyrum smithii*–*Nassella viridula* grasslands. In addition to the two dominant grass species, *Bouteloua gracilis*, *Hesperostipa comata*, *Koeleria macrantha*, and *S. cryptandrus* are also abundant. Forbs, such as *Achillea millefolium*, *Artemisia ludoviciana*, *Artemisia frigida*, and *Sphaeralcea coccinea* are typical members of this community (Hirsch, 1985). Because mechanical disturbance by grazing and human activity is relatively frequent in these habitats, *Bromus tectorum* has become a frequent invader.

Sporobolus cryptandrus is a widespread species in North America, ranging from Canada to Mexico (Holub & Jehlík, 1987; Nobis et al., 2015). Although native, or even “threatened” or “endangered” in Connecticut and New Hampshire, respectively, it is considered as a ruderal, or even invasive species in some of the western regions of North America (Darbyshire, 2003; Holm et al., 1977). In its native range, *S. cryptandrus* grows in sandy soils and dry riverbeds, on rocky slopes and calcareous ridges, along roadsides, in woodlands and desert grasslands (Peterson et al., 2003). Outside its native range,

the species has been introduced to Australia, Japan, New Zealand, Russia and several countries in Europe (Gouz & Timoshenkova, 2017; Holub & Jehlík, 1987; Murr, 1902; Nobis et al., 2015; Randall, 2017; Ryves et al., 1996).

Sporobolus cryptandrus appeared as an invasive species in the Kiskunság Sand Ridge, a lowland region of Hungary, Central Europe (Figure 1c,d). The studied stands of *S. cryptandrus* were located near the towns of Kecskemét and Kiskunhalas. The region is characterized by a continental climate with a moderate sub-Mediterranean influence (Erdős et al., 2018). Mean annual temperature is 11–12°C and mean annual precipitation is 550–600 mm (peak in early summer; Tölgyesi et al., 2016). The soil is coarse-grained calcareous sand with low organic matter content. The potential natural vegetation is forest-steppe, but only a small proportion of the original land cover has been spared from intensive land use, such as crop production and associated surface drainage processes, overgrazing and plantations of drought-tolerant, non-native trees (Bíró et al., 2013; Iványosi, 2015). Fragments of open sandy grasslands dominated by *Stipa pennata*, *Festuca vaginata* and/or *Festuca wagneri* remained mainly in nature reserves. Secondary grasslands composed of annual graminoids such as *Bromus tectorum* and *Secale sylvestre*, or non-native, ruderal forbs, such as *Ambrosia artemisiifolia* and *Conyza canadensis* are widespread. *Sporobolus cryptandrus* has been recorded both in secondary and natural grasslands.

2.2 | Data collection

We selected four sites both in the native and non-native *S. cryptandrus* habitats (Figure 1) between July and September 2019. We established 1 m × 1 m plots in each site in a stratified random manner, using the following cover gradient categories of *S. cryptandrus* as strata: 1%–25%, 26%–50%, 50%–75%, and 75%–100%. We aimed to select ten plots for each cover category in all sites; however, because some categories were underrepresented, we obtained a total of 101 plots in the USA and 153 plots in Hungary. We recorded the percentage cover of all vascular plant species in the plots, including *S. cryptandrus*.

Because the functional role of organisms in ecosystems depends on their traits rather than on their taxonomical affiliation, we used a trait-based approach to study the effects of increasing *S. cryptandrus* cover on the vegetation. We considered a wide range of traits, encompassing the entire life history of the species and their ecosystem-level effects (Table 1). Leaf-height-seed (LHS) traits, including leaf area (LA), specific leaf area (SLA), vegetative plant height and thousand-seed mass (hereafter seed mass) provide information on interspecific interactions (Klimešová & Pyšek, 2011; Westoby, 1998); SLA also correlates with photosynthetic efficacy and palatable biomass for herbivores (Wilson et al., 1999). Pollination type, complemented with the mean range of flowering period makes a link between plants and pollinators by providing information about floral resources. We used growth form (a simplified version of the original Raunkiaer's life forms; Raunkiaer, 1934) as a proxy to describe the general appearance of the vegetation. In the case of species missing from the available databases, we used trait values of the most closely related, morphologically similar species published in the database. If multiple records were provided for a species, we used the average value.

2.3 | Data analyses

To characterize the diversity of the surveyed grasslands, we used plot-level species richness and Rao's quadratic entropy, including all the collected traits in the analysis. The latter is a measure of functional diversity, expressing the mean functional distance between two randomly chosen species in the plots, while also accounting for the abundances of the species (Botta-Dukát, 2005). For the continuous traits, we calculated community-weighted means (CWMs) for each plot, whereas for categorical variables we used the cumulative cover of each category without any transformation. We prepared linear mixed-effect models to quantify the effects of *S. cryptandrus* cover, region (i.e., Montana and Hungary) and their interaction on the vegetation descriptors. We used site identity within a region as a random factor. The values of the response variables and the cover values of *S. cryptandrus* were scaled prior to fitting the linear mixed-effect models. We involved traits that are widely used to trace community-level changes or responses, and supposedly reflect ecosystem functions. Ecosystem functions are determined by whole plant communities but the direct effects of *S. cryptandrus* may be better understood if scrutinizing only the rest of the vegetation along the *S. cryptandrus* cover gradient. Therefore, we performed the analysis in two ways: (1) using whole vegetation data sets together with *S. cryptandrus*, and (2) reduced data sets by omitting *S. cryptandrus*.

All analyses were performed in R (version 4.0.3., R Core Team, R Foundation for Statistical Computing, Vienna, AT). Rao's quadratic entropy and CWMs were calculated with the 'dbFD' function of the *FD* package (R version 1.0-12, R Core Team, R Foundation for Statistical Computing, Vienna, AT). We used the 'lmer' function of the *lme4* package (Bates et al., 2015) to build the linear mixed-effect models, and the 'Anova' function of the *car* package (Fox & Weisberg, 2019) to test the effect of the predictors. We used the

TABLE 1 Description of the functional traits used for the study

Name of trait	Data type	Source	Note
Specific leaf area (SLA)	Numeric (mm ² /mg)	Kleyer et al. (2008) (LEDA Traitbase), Kattge et al. (2011) (TRY database), Lhotsky et al. (2016), USDA NRCS (2021)	
Thousand-seed mass	Numeric (g/1,000 seeds)	Török et al. (2013, 2016), USDA NRCS (2021)	
Leaf area (LA)	Numeric (cm ²)	Kleyer et al. (2008) (LEDA Traitbase), Kattge et al. (2011) (TRY database), Lhotsky et al. (2016), USDA NRCS (2021)	
Plant height	Numeric (cm)	Király (2009), USDA NRCS (2021)	Maximized to 100 cm
Flowering period	Numeric (month)	Király (2009), USDA NRCS (2021)	
Pollination type	Nominal with three categories: insect-, wind- and self-pollination	Kühn et al. (2004) (BioFlor database), USDA NRCS (2021)	If more than one type occurs, we chose the more common one
Growth form	Nominal with two categories: short-lived (therophytes and hemitherophytes) and perennials (chamaephytes, geophytes and hemicryptophytes)	Király (2009)	Simplified version of the original Raunkiaer's life forms

'rsq' function of the *rsq* package (R version 2.2, R Core Team, R Foundation for Statistical Computing, Vienna, AT) to obtain marginal R^2 values, which represent the proportion of variation explained by the fixed-effects factors.

3 | RESULTS

3.1 | Whole plant communities

We detected a total of 60 and 110 plant species in the USA and Hungary, respectively (Appendix S1; Appendix S2). Species numbers were generally higher in the Hungarian, non-native range and decreased along the *S. cryptandrus* gradient, whereas no significant trend was detected in the American, native range (Figure 2a; Appendix S3). Functional diversity decreased with increasing *S. cryptandrus* cover; however, no difference was detected between the native and non-native regions (Figure 2b; Appendix S3).

SLA and seed mass decreased with increasing *S. cryptandrus* cover in both regions (Figure 3a; Appendix S3). Higher *S. cryptandrus* cover was associated with a higher overall vegetation height in both regions, with a steeper increase in the non-native range (Figure 3b; Appendix S3). No significant impact of *S. cryptandrus* cover was detected on the CWMs of LA (Appendix S3).

Increasing *S. cryptandrus* cover shifted the mean start date of flowering in the communities to earlier times in the non-native range, whereas no such effect was detected in the native range. At the same time, the flowering end month was pushed to later times in both ranges, but the trend was steeper in the non-native range. Overall, these findings indicate an extended mean range of the flowering period for the plant communities in both regions, (Figure 3c,d; Appendix S3). The cover and proportion of wind-pollinated species increased (Figure 4a,c; Appendix S4), and the cover and proportion of insect- and self-pollinated plant species decreased along the gradient of *S. cryptandrus* cover both in the USA and Hungary (Figure 4b,d; Appendix S4). Considering the absolute cover of vegetation, perennials made up most of the vegetation in both ranges (Figure 5b; Appendix S4). However, the proportion of perennial species, and cover and proportion of short-lived species showed changes along the *S. cryptandrus* gradient only in the non-native range (Figure 5a–d; Appendix S4).

3.2 | Plant communities without *S. cryptandrus*

When omitting *S. cryptandrus* and scrutinizing only the rest of the plant communities, we did not detect any significant changes in functional diversity along the *S. cryptandrus* cover gradient (Figure 2c; Appendix S3). SLA increased with increasing *S. cryptandrus* cover in both regions (Figure 3e; Appendix S3). Higher *S. cryptandrus* cover was associated with lower LA in the non-native, Hungarian range, but not in the native range (Appendix S3). Vegetation height decreased in the native range, but slightly increased in Hungary with

increasing *S. cryptandrus* cover, although the relationship was rather weak ($R^2 < 0.1$) (Figure 3f; Appendix S3). The average seed mass of the surveyed communities did not change along the *S. cryptandrus* cover gradient. (Appendix S3).

The mean start or end times of flowering did not change significantly in the non-native range, but both parameters decreased in the native range, indicating that the overall flowering period shifted to earlier times (Figure 3g,h; Appendix S3). Increasing *S. cryptandrus* cover

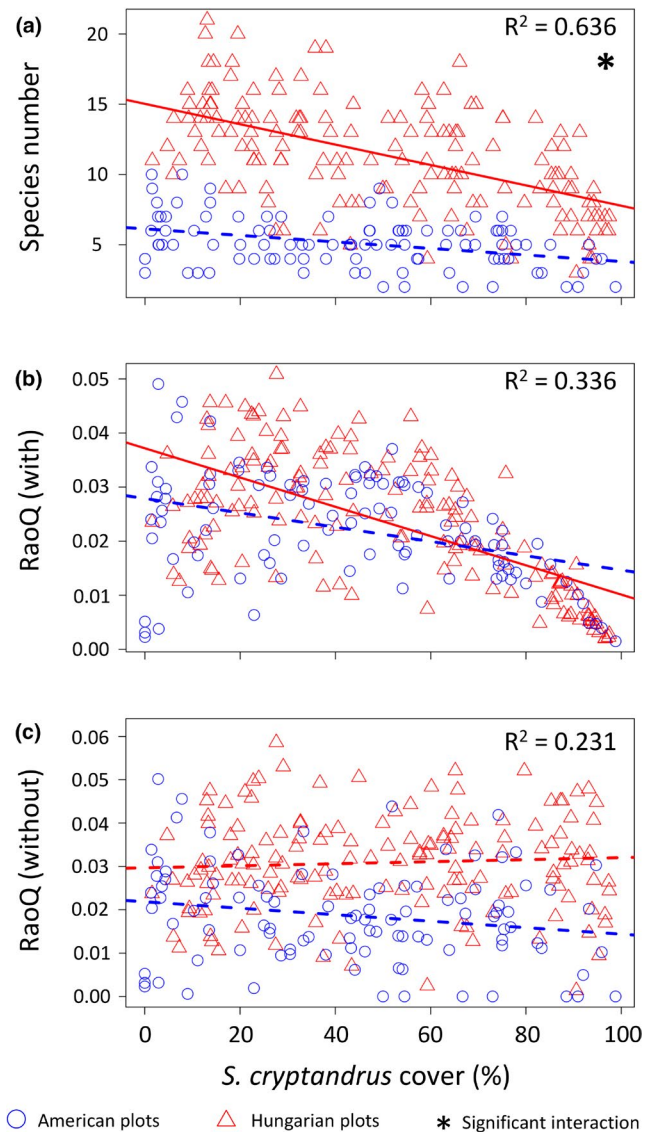


FIGURE 2 Community-weighted means (CWMs) of species number and functional diversity (Rao's quadratic entropy) along the gradient of increasing *Sporobolus cryptandrus* cover. (a) Plot-level species number of the whole plant community as a function of increasing *S. cryptandrus* cover; (b) functional diversity as a function of increasing *S. cryptandrus* cover, for the whole plant community (with *S. cryptandrus*); and (c) functional diversity as a function of increasing *S. cryptandrus* cover, for the rest of the vegetation (without *S. cryptandrus*). Trend-lines show the trends of linear models used for illustration. Solid lines indicate a significant effect ($p < 0.05$) of *S. cryptandrus* cover on the CWMs of the dependent variables

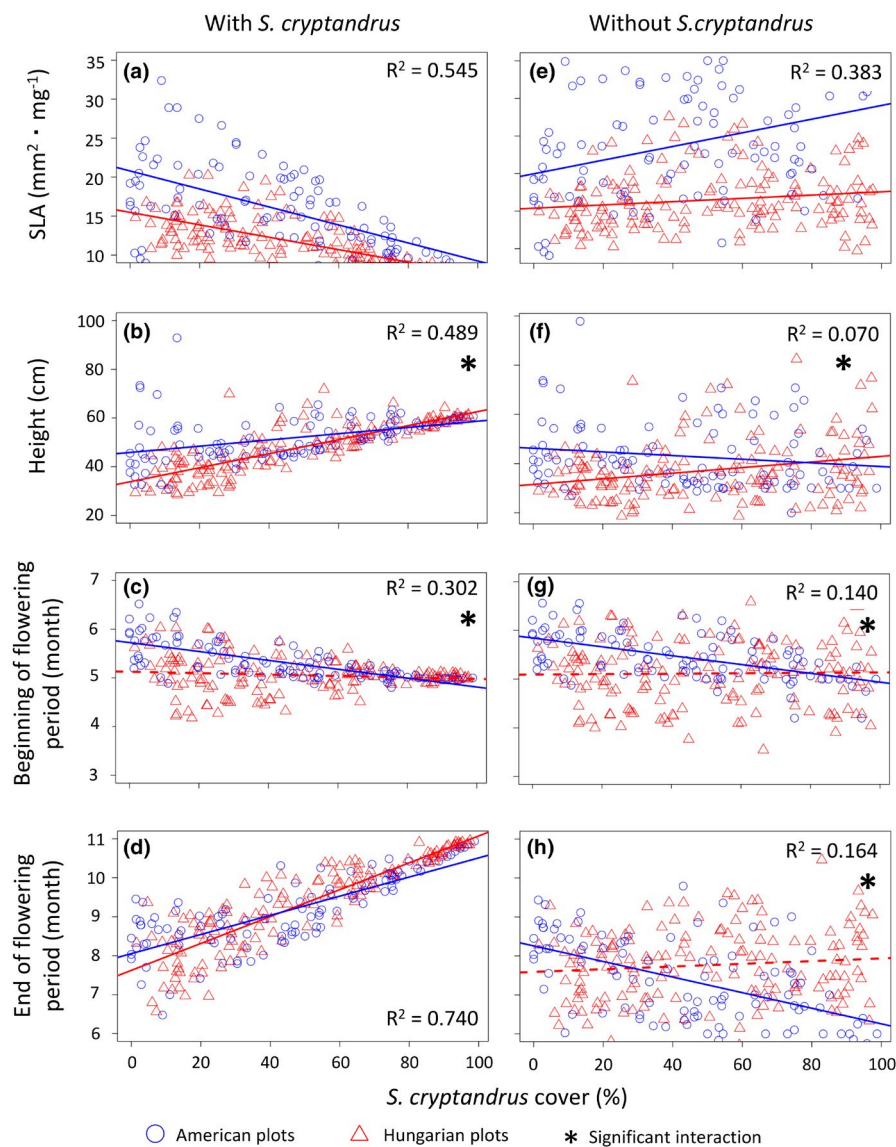


FIGURE 3 Community-weighted means (CWMs) of specific leaf area (SLA), height, and average beginning and end of flowering period along the gradient of increasing *Sporobolus cryptandrus* cover in the whole plant communities (a–d) and in the rest of the vegetation (e–h). Lines show the trends of linear models and are used only for illustration because the random term is not considered for them. Solid lines indicate a significant effect ($p < 0.05$) of *S. cryptandrus* cover on the CWMs of the dependent variables, dashed lines indicate a non-significant effect of *S. cryptandrus* cover

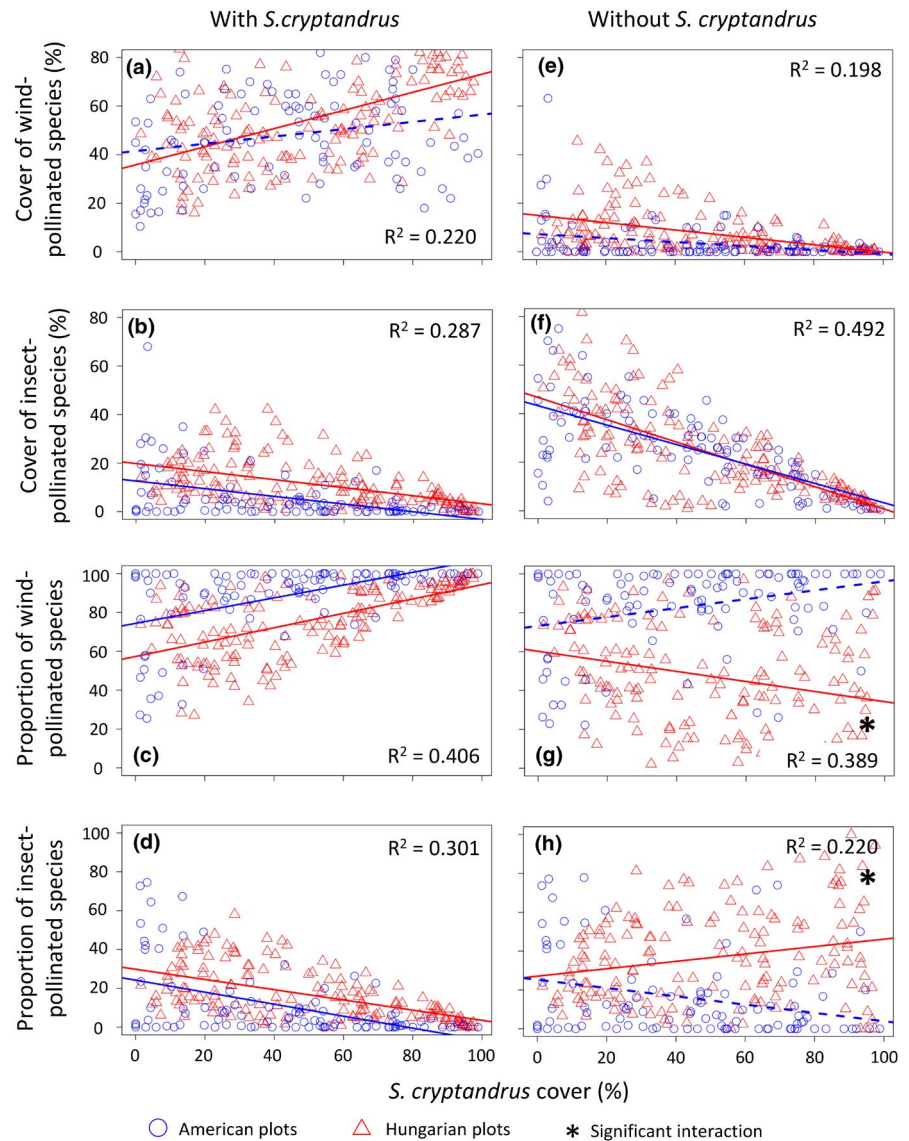
obviously was associated in lower absolute cover of insect-, self-, other wind-pollinated, short-lived and other perennial species in both regions as the species took over their place (Figures 4e,f and 5e,f; Appendix S4). For proportional relations of the different pollination types, we found no changes in the native range along the gradient of *S. cryptandrus* cover. In the non-native range, however, increasing *S. cryptandrus* cover was associated with a decreasing proportion of other wind-pollinated species and an increasing proportion of insect-pollinated species (Figure 4g,h; Appendix S4). The proportion of other perennial species decreased, whereas the proportion of short-lived species increased along the *S. cryptandrus* cover gradient in Hungary, but in the USA, only the proportion of annual species showed a decreasing trend along the *S. cryptandrus* gradient (Figure 5g,h; Appendix S4).

4 | DISCUSSION

In this study we compared the diversity and functional trait composition of plant communities along the gradient of *S. cryptandrus*

cover in the native, North American and a non-native, Hungarian range of the species. Species entering into a non-native range always stand the chance of having similar effects on plant community properties and on the vegetation in the two ranges, i.e., it integrates into the community in the non-native range contributing to diversity and ecosystem functions resembling the patterns in its native range. Provided that this latter outcome is confirmed, the species may be of lower management concern. However, if *S. cryptandrus* is associated with heavier functional community changes than in the native range, it represents a higher conservation risk and should receive more attention. According to our findings, the latter scenario is unfortunately more probable. Taxonomic diversity declined more sharply with increasing *S. cryptandrus* cover in the non-native range than in the native range, and several of the functional properties also reacted more intensely to the cover gradient, indicating abrupt functional transformation, potentially with far-reaching bottom-up consequences on the invaded ecosystem (see also Scherber et al., 2010, López-Núñez et al., 2015, and Boscutti et al., 2020 for similar findings for other invasive species).

FIGURE 4 Cover and proportion of insect- and wind-pollinated plant species along the gradient of increasing *Sporobolus cryptandrus* cover in the whole plant communities (a–d) and with *S. cryptandrus* omitted (e–h). Lines show the trends of linear models and are used for illustration only because the random term is not considered for them. Solid lines indicate a significant effect ($p < 0.05$) of *S. cryptandrus* cover on the CWMs of the dependent variables, dashed lines indicate a non-significant effect of *S. cryptandrus* cover



As for taxonomic diversity, the sharp decline in the values in the non-native range may be the effect of competitive exclusion of the native species. *Sporobolus cryptandrus* is capable of high biomass and seed production even in harsh environmental conditions owing to its C_4 photosynthetic pathway and extensive rhizosphere (Brown, 1943; Wan et al., 1993), which both allow for monopolizing resources compared with native C_3 species.

Other species of the genus *Sporobolus* are known for producing allelopathic compounds (Rasmussen & Rice, 1971), which may also be a driver of species loss. Plant species in the non-native range may have a lower ability to tolerate allelopathy compared with those species that have coexisted with *S. cryptandrus* for evolutionary time scales in the native range. This mechanism has been emphasized for the success of several other invasive plants, such as *Centaurea diffusa* (Hiero & Callaway, 2003) but needs confirmation for *S. cryptandrus*. Our functional diversity scores, which expressed the average difference in the traits between two species of a plot, did not show a significant decreasing trend when we omitted *S. cryptandrus*. Because allelopathy is not necessarily

specific to species with certain trait values, in the presence of a species producing allelopathic compounds we cannot expect a sharp trait convergence, which could result in a detectable decline in functional diversity.

Unlike overall functional diversity, the analysis of individual traits proved to be more useful in understanding the functional changes associated with the invasion (see also te Beest et al., 2015 and Funk et al., 2016). Trait CWMs were heavily modified along the gradient of *S. cryptandrus* cover, and in many cases the changes were stronger in the non-native range, where resident species were naïve to *S. cryptandrus*. In its native range, *S. cryptandrus* had higher abundance in communities consisting of species with high SLA and seed mass, short stature and a short-lived life form. In the non-native range, not only high photosynthetic and growth rate, but also tall stature was necessary for plant species to persist in sites dominated by *S. cryptandrus*. Here, only those species that are good competitors but at the same time ruderals were able to coexist with *S. cryptandrus*, such as *Ambrosia artemisiifolia*, *Asclepias syriaca*, *Conyza canadensis* and *Falcaria vulgaris*. Except for the latter, these species are also

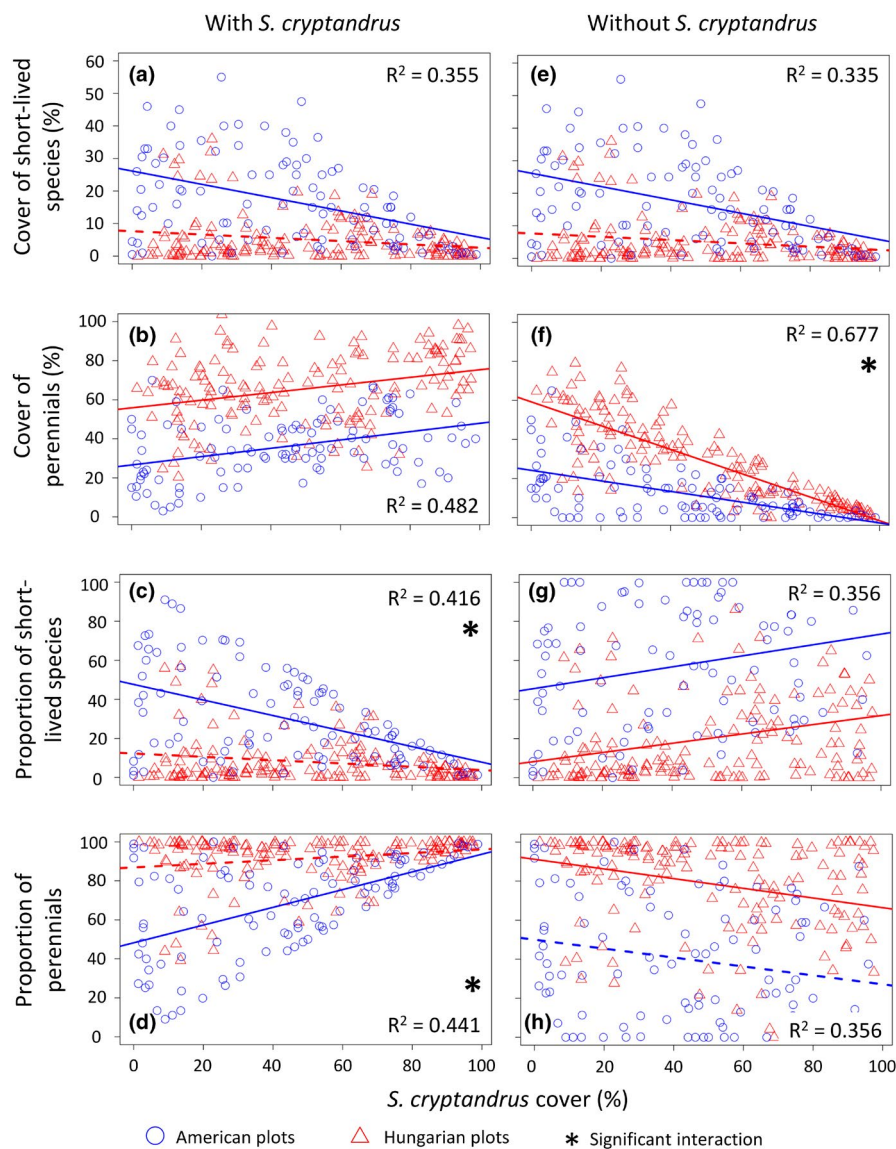


FIGURE 5 Cover and proportion of annuals and perennials along the gradient of increasing *Sporobolus cryptandrus* cover in the whole plant communities (a–d) and with *S. cryptandrus* omitted (e–h). Lines show the trends of linear models and are used only for illustration because the random term is not considered in them. Solid line indicates a significant effect ($p < 0.05$) of *S. cryptandrus* cover on the community-weighted means of the dependent variables, dashed lines indicate a non-significant effect of *S. cryptandrus* cover

non-native. Short species could persist in Hungarian *S. cryptandrus*-dominated grasslands only when having high SLA and ruderal life strategy (such as *Bromus tectorum*, *Cynodon dactylon* and *Secale sylvestre*).

Exotic grasses with a C_4 assimilation type are typically successful invaders in grasslands, where regular fires serve as important abiotic disturbance regulating the ecosystem (Reed et al., 2005; Williams & Baruch, 2000). Species like *Andropogon bladhii*, *Imperata cylindrica* or *Panicum coloratum* entering a habitat as a non-native newcomer may outcompete native vegetation by exerting intense competition on native species for light, nutrients and water, modifying the carbon cycle, and ultimately decreasing the diversity of the invaded community (Brooks et al., 2004; Jose et al., 2002; Reed et al., 2005). Except for the decrease in diversity, the case of *S. cryptandrus* differs from the above-mentioned invasive grasses. Hungarian sandy grasslands are arid habitats, but their natural disturbance regime does not include frequent fire events. Most relevant C_4 grasses in the invaded regions are *Bothriochloa ischaemum* and *Cenchrus incertus*. *Bothriochloa ischaemum* is a native species

in Hungary, however, it may reach local dominance as the canopy of sympatric grasses opens up on disturbance (Zólyomi & Fekete, 1994). Although the increasing cover of *Bothriochloa ischaemum* may result in degraded community composition and decreased diversity (Dee et al. 2016), its functional effects are unknown. *Cenchrus incertus* is not native to Hungary and has the potential to cover considerable areas (Török et al., 2003), but it is a pioneer annual weed of arable lands, with little ability to enter natural or semi-natural grassland communities (Botta-Dukát & Balogh, 2008). As such, *S. cryptandrus* presents the first non-native C_4 grass invading Hungarian sandy drylands and potentially causing conservation issues.

Plant invasions often lead to the disruption of pollination and seed-dispersal mutualistic interactions (Traveset & Richardson, 2006); thus, invasive plants can pose significant threat to specialist interactions and can have detrimental effects on entire food webs through a bottom-up pathway (Scherber et al., 2010). Our results suggest that *S. cryptandrus* is one of these highly problematic species outside its native range. *Sporobolus cryptandrus* is characterized by

a long flowering period (May–November), but it is a wind-pollinated species, thus it does not offer floral resources for pollinators. In invaded Hungarian grasslands, increasing *S. cryptandrus* cover was associated with heavily suppressed insect-pollinated plant species, which presumably has a cascading negative effect on native pollinators.

Owing to the potential transformative effects of *S. cryptandrus* on the plant communities in its non-native range, there is an urgent need for interventions (1) to reduce its abundance where already established and (2) to protect intact grasslands from future establishment of the species. Removal by herbivores is often a viable option for invasion control (Firn et al., 2013). American studies reported that *S. cryptandrus* provides satisfactory forage for livestock (Frolik & Shepherd, 1940) but poor forage for wildlife (Gould, 1978; Stubbendieck et al., 1992), and exhibits variable responses to grazing (Kleiner, 1983; Voigt & Oaks, 1985). Because grazing involves the potential of dispersal by ectozoochory (Milotić et al., 2017), it may facilitate further the expansion of prolific seed producers, such as *S. cryptandrus*. Mechanical control before seed setting (e.g., mowing) may be more preferable than grazing, although this requires further testing. *Sporobolus cryptandrus* shows various responses to herbicides (Biondini et al., 1986; Jacoby et al., 1982; Schuster, 1976) and does not respond well to severe soil disturbance (Webb & Guthery, 1983). Non-selective herbicides may also have destructive effects on non-target species (Mason & French, 2007; McAlpine et al., 2018; Szitár & Török, 2008), creating open space for new or further invasion, thus entailing similar risks to that of soil surface disturbance (Csecserits et al., 2016; Pinke et al., 2011). Thus, considering the traits of *S. cryptandrus* and the available literature on its control, suppressing its further invasion seems a difficult challenge for conservation managers.

In conclusion, *S. cryptandrus* has the potential to become a harmful invader in its non-native range because it suppresses other species more effectively and its traits become dominant more rapidly in the community along its abundance gradient compared with in its native range. The multiple effects on the mean trait scores of the native flora are likely to entail ecosystem-level functional changes, as seen globally for many other invasive plant species, and grasses in particular (Weidlich et al., 2020). Aridification, hitting southeast Europe (Kertész & Mika, 1999; Rakonczay, 2007) and the increasing global atmospheric carbon dioxide level will presumably give further advantage to *S. cryptandrus* over native grassland species, and forecasts the appearance of other invasive C_4 grasses, of which the host communities in this region are unsaturated. Our study highlights the immense threat that this and similar species may pose, and calls for a high vigilance to identify C_4 grasses at the earliest possible stage of spreading, while we also urge the more rapid development of locally adapted intervention protocols.

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AUTHOR CONTRIBUTIONS

P.T. conceived the study. All authors collected the data. A.A.H. analyzed the data. A.A.H. and C.T. led the writing of the paper. All authors critically contributed to the revisions.

DATA AVAILABILITY STATEMENT

Data are archived in the Dryad data repository: <https://doi.org/10.5061/dryad.612jm645g>.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. List of species recorded in North American study sites.

Appendix S2. List of species recorded in Hungarian study sites.

Appendix S3. Test results of the linear mixed-effects models prepared for the continuous functional descriptors of the whole plant community and the rest of the vegetation, excluding *S. cryptandrus*.

Appendix S4 Test results of the linear mixed-effects models prepared for the levels of the categorical functional descriptors of the whole plant community and the rest of the vegetation, excluding *S. cryptandrus*.

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