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Spreading of recently introduced North American sand dropseed (*Sporobolus crytrandus*) threatens European native dry grassland arthropods

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Running title: Invasive grass threatens native arthropods

Abstract

1. Invasive plants can fundamentally impact ecosystems. As arthropods play prominent roles in ecosystem functioning via their food webs, understanding how plant invasion affects arthropod communities is essential.

2. We studied the impact of the invasive grass (*Sporobolus cryptandus*) on arthropods (ground beetles, orthopterans, spiders, and true bugs) across three habitat types in Hungary: forest-steppe, open sand grassland, and meadow steppe. We compared the species composition of arthropod groups and the abundance of species of conservation interest between invaded and control plots. We also identified species unique to either control or invaded plots. Additionally, we analysed the species richness and abundance of arthropod groups along a gradient of the invader density (low, medium, high, as well as control).

3. We found that species composition between invaded and control plots only differed for vegetation-dwelling true bugs and orthopterans, with several species unique to control plots. Their species richness and/or abundance decreased with increasing *Sporobolus* cover, varying among habitats. Interestingly, low *Sporobolus* cover increased the species richness and abundance of ground beetles and the abundance of vegetation-dwelling, primarily web-building spiders. However, the conservation value of true bug, grasshopper and ground beetle species was reduced in invaded compared to control sites.

4. We conclude that low *Sporobolus* cover may temporarily increase arthropod species richness and abundance, but this effect is likely short-lived before *Sporobolus* rapidly gains dominance due to its fast spreading rate. Ultimately, *Sporobolus* invasion can reduce arthropod diversity, particularly affecting species of high conservation value.

Keywords: abundance, carabids, exotic, invasion, orthopterans, species richness, spiders, steppe, true bugs

Introduction

The spreading of non-native species is one of the most severe threats to biodiversity in terrestrial ecosystems (Pyšek et al., 2020), and thus also one of the main global drivers of ecosystem change (Millennium Ecosystem Assessment, 2005). Plant species invasion may lead to changes in native plant community composition and diversity, microclimatic conditions, and soil properties (Ehrenfeld, 2003; Pehle & Schirmel, 2015; Vitousek et al., 1996). Accordingly, invasive plants can affect arthropod communities as well, but the responses of arthropod communities to plant invasion are often contradicting (Bezemer et al., 2014; Litt et al., 2014). Most studies reported a significant decrease in arthropod diversity and abundance in response to plant invasions (Litt et al., 2014). However, some studies found neutral or even positive effects of invasive plants on arthropods, suggesting that invasive plants may attract pollinators (Bartomeus et al., 2008; Graves & Shapiro, 2003; Kovács-Hostyánszki et al., 2022), provide alternative resources for generalist herbivores (Emery & Doran, 2013), and create favourable conditions for certain species (Pearson, 2009).

Arthropods are essential components of the biodiversity and functioning of terrestrial ecosystems. They have a prominent role in pollination, herbivory, decomposition, nutrient cycling, and as food resources for many vertebrates (Yang & Gratton, 2014). Thus, understanding how arthropod communities respond to the spreading of a non-native plant is crucial for biodiversity conservation. It is particularly important in conservation areas, which harbour diverse arthropod communities with many specialist species, such as Eurasian dry grassland remnants in Europe (Cizek et al., 2012; Torma et al., 2014; van Swaay, 2002).

The Kiskunság region of Hungary represents a transition zone between temperate deciduous forests and continental steppes, forming mosaics of forested and open habitat patches (Erdős et al., 2015, 2018). Several habitat types in the region are listed among the priority habitats of Annex 1 of the EU Habitats Directive (e.g., 2340* Pannonic inland dunes, 6260* Pannonic sand steppes). These habitats still harbour a unique flora and fauna characterised by several endemic or endangered species. Unfortunately, the region is highly influenced by non-native plant species (Botta-Dukát, 2008), owing to the largely missing, formerly widespread traditional grazing management, lowering water table and climate change. We have restricted information on the effects of these non-native plants on grassland arthropods, with perhaps the only exception being common milkweed (*Asclepias syriaca*). Common milkweed has been

intensively studied in Hungary and throughout Europe. However, study results suggest significant but mixed effects of common milkweed on arthropods (Follak et al., 2021).

Sand dropseed (*Sporobolus crytandus*), a C4 grass species of North American origin, was recently discovered in Hungary (Török & Aradi, 2017) and has become an invasive species within a few years, particularly in the Kiskunság (Hábenczyus et al., 2022; Török et al., 2021). In contrast to the other *Sporobolus* species (e.g., *S. neglectus* and *S. vaginiflorus*) introduced into Europe, the spreading of sand dropseed is not limited to road margins and ruderal sites but also affects natural, semi-natural dry grasslands (Bauer & Verloove, 2023; Kröel-Dulay et al., 2024). In sand steppes, sand dropseed invasion significantly reduces the species richness and abundance of subordinate plants, homogenises the vegetation composition and can even lead to the complete replacement of the originally dominant native grasses (Hábenczyus et al. 2022; Török et al. 2021). Although sand dropseed is also spreading in Western Russian and Ukrainian steppe habitats (Alekseev et al., 1996; Demina et al., 2018; Gouz & Timoshenkova, 2017; Kuvaev & Stepanova, 2014; Maltsev & Sagalaev, 2018), we have no information about the effects of the invasion of sand dropseed on the diversity of arthropod communities. To fill this knowledge gap, we examined the effect of sand dropseed invasion on dry grassland arthropod communities in the Kiskunság region, Hungary.

The extent of the threat posed by invasive plants may vary among different habitats since habitat characteristics affects both the establishment and dominance of non-native plants in the community (Chytrý et al., 2009; Guarino et al., 2021). In addition, the density of invaders increases as invasions progress. Thus, studying the role of invasive plant density is useful for understanding ecological processes at different stages of invasion and predicting its future impacts. For example, Foster et al. (2021) concluded that the conflicting results of studies on the effects of the invasive spotted knapweed (*Centaurea stoebe*) were probably due to the different densities of the invaders in the study areas. However, the role played by the alien species' density has seldom been explored. To evaluate the effects of sand dropseed invasion into native grasslands, we sampled arthropod communities on plots established along a gradient of the invasive grass density in three characteristic and high-nature-value habitat types: forest-steppe, open sand grassland, and meadow steppe.

Different taxonomical or functional arthropod groups often respond differently to plant invasion (Bezemer et al., 2014). Therefore, we applied a multi-taxon approach, sampling both

ground-dwelling and vegetation-dwelling arthropods. In general, changes in the compositional diversity of vegetation affect the diversity of vegetation-dwelling, primarily herbivorous arthropods, whereas structural diversity is more related to that of ground-dwelling, mostly predatory arthropods (Lengyel et al., 2016; Torma et al., 2023). We selected spiders (Araneae), ground beetles (Coleoptera: Carabidae), true bugs (Hemiptera: Heteroptera), and orthopterans (Orthoptera) as study taxa since they are species-rich and abundant groups in grassland ecosystems and play different roles in ecosystem functioning. The majority of orthopterans and true bugs are important primary consumers in grasslands and provide a rich prey resource for several predators (Neff et al., 2019). Herbivorous insects are likely to be significantly affected by plant invasion, as they are directly related to plant species composition and diversity (Tallamy et al., 2021). Spiders and ground beetles are common predatory arthropods in many terrestrial ecosystems, although some ground beetle species are granivorous or omnivorous. Usually, they do not rely directly on plant species composition, even though plant invasions may indirectly affect them through changes in vegetation structure or prey availability (Gratton & Denno, 2005; Khum et al., 2023). Finally, we explored the effect of invasion on particular species of high conservation value. These species are typically xerothermic species that prefer bare sandy soil surfaces, adapted to the semi-arid conditions. They are associated strongly with the critically endangered Pannonian sandy habitats (Janssen et al., 2016) and are therefore of conservation importance in the European Union.

We addressed the following research questions:

- i) Does the sand dropseed invasion influence the species richness, composition and abundance of arthropod communities?
- ii) Does the effect of sand dropseed invasion vary between selected habitat types and arthropod groups?
- iii) Does the response of arthropod communities to sand dropseed invasion relate to its density?
- iv) Does the number and abundance of the species of high conservation value differ between invaded and control sites?

Materials and methods

Study region and habitats

We carried out the study in the Kiskunság sand ridge in the Danube-Tisza interfluvium in Hungary, Central Europe (Fig. 1.). Kiskunság region has a continental climate with a mean annual temperature of 11°C and a mean annual precipitation of 550–600 mm (Dövényi et al., 2010). The soil is coarse-grained calcareous sand with low organic matter content. We selected our study sites in three different habitat types: forest-steppe (hereafter: FS), open sand grassland (hereafter: OG), and meadow steppe (hereafter: MS) (Fig. 1.). In the studied FS sites, smaller and larger patches of poplar trees (*Populus alba*) and shrubs (*Crataegus monogyna* and *Juniperus communis*) form a mosaic with sand grassland patches. Habitat conditions, including vegetation, are quite similar between OG and the grassland patches of sandy FS (Erdős et al., 2015). This similarity is also reflected in the similarity of arthropod communities, although the relatively small grassland patches of FS and the surrounding shrubs and trees could influence the composition and diversity of arthropod communities (Gallé & Torma, 2009; Kaur et al., 2019). In open sand grasslands, which are characterised by significant bare sand surface, the dominant plants are the tussock-forming, short-growing fescue grasses (*Festuca vaginata* and *F. wagneri*). Subordinate plants are other grasses (e.g., *Stipa borysthénica*) and drought-tolerant dicots (e.g., *Fumana procumbens*, *Euphorbia seguieriana*, *Alkanna tinctoria*). Meadow steppes are also characterised by the dominance of the tussock-forming, short-growing fescue grasses (*F. rupicola* and *F. wagneri*), but forming more dense vegetation together with several subordinate plants (e.g., *Chrysopogon gryllus*, *Poa angustifolia*, *Pseudolysimachion spicatum*, *Salvia pratensis*, and *Dianthus pontederiae*).

Arthropod sampling and study design

In each habitat type, we selected five invaded vegetation plots and five corresponding control plots in the nearby vegetation, where sand dropseed was not present, resulting in 3×5 plot-pairs for sampling (Table S1). The plots were 15 × 15 m, a reasonable size even for a small invaded area. Due to the early invasion stage, the number of patches invaded by sand dropseed was limited, and their area was usually small, ca. 400–800 m². Typically, only the patches with higher sand dropseed cover exceeded 1000 m². Control plots situated 20 m from the edge of the invaded plots were characterised by the same habitat conditions, i.e. same vegetation type, succession status and site history. The mean distance between plot-pairs within habitat types was 413 ± 34 m (mean ± SEM). Furthermore, in accordance with previous studies on sand dropseed invasion in

these sites (c.f. Török et al., 2021), we classified the invaded plots into three density categories: low (1–20% mean cover), medium (21–50%) and high (above 50%). We assessed the sand dropseed cover in three 5×5 m quadrats in each invaded plot.

For sampling ground-dwelling true bugs, spiders, and ground beetles, we used pitfall traps (white 500 ml plastic cups, 8.5 cm in diameter) filled with a 50% ethylene glycol–water solution. The traps were equipped with transparent plastic funnels to avoid vertebrate bycatch and a plastic roof was placed over each trap to prevent the preservative from dilution (Császár et al., 2018). In each plot, we placed three pitfall traps in a row 10 m apart, resulting in a total of 90 traps. The traps were active for two weeks in one sampling period. We sampled vegetation-dwelling true bugs, spiders, and orthopterans, using a sweep-net with a diameter of 40 cm. In a sampling period, we performed 2×25 sweeps on sunny, windless days in each plot. We conducted the sampling procedures in the main vegetation period between the 19th of June and the 21st of July. During this period, pitfall trapping and sweep-netting were repeated two and three times, respectively. Arthropods were identified at the species level based on morphological characters (detailed information about literature used for identification is available in Supplementary material, Table S2). The nomenclature follows Cigliano et al. (2017), Müller-Motzfeld (2004), Wachmann et al. (2004–2012), and World Spider Catalog (2023).

Data analyses

To assess the overall effect of sand dropseed invasion on the different arthropod groups, we applied distance-based redundancy analyses (dbRDA, Bray-Curtis dissimilarity) using the vegan R package (Oksanen et al., 2020). The effect of invasion (invaded and control), habitat type (FS, OG, and MS) and their interaction on the species composition of arthropod groups was tested by *anova* function. In addition, we applied the indicator species approach of Dufrêne and Legendre (1997) to identify species associated with invaded or control plots in the different habitat types. In this method, indicator values are calculated by combining specificity (i.e., the abundance of the species in a given site group) and fidelity (i.e., the probability of finding the species at sites belonging to that site group). We used the *multipatt* function in the indicpecies R package (De Cáceres and Legendre, 2009). The function searches for indicator species for both individual site groups and combinations of site groups (De Cáceres et al., 2010).

To reveal the responses of different arthropod groups to sand dropseed density, we separately analysed the species richness and abundance (activity-density in the case of pitfall trapping) of each arthropod group per sampling method. For analyses, arthropod species data were pooled by sampling plots, resulting in 60 (3 habitats $\times$ 5 plot-pairs $\times$ 2 repetitions) and 90 (3 habitats $\times$ 5 plot-pairs $\times$ 3 repetitions) statistical samples in case of pitfall trapping and sweep-netting, respectively. We analysed the effect of sand dropseed invasion on arthropod communities with generalised linear mixed-effects models (GLMMs, Poisson models) using the lme4 R package (Bates et al., 2015). In the case of data overdispersion, we used negative binomial models. We used species richness and abundance of arthropod groups as response variables, and sand dropseed coverage class (low, medium, high, and control), habitat type (FS, OG, and MF), and their interaction as fixed effects. Sampling sites (i.e., plot-pairs) and repetitions (i.e., sampling periods) were incorporated into models as separate random effects. We conducted post hoc comparisons with the help of the emmeans R package (Lenth, 2020). In separate models, we also compared species richness and abundance of high conservation value arthropod species between invaded and control sites. In these models, habitat type was considered as a random factor (sampling pairs nested in habitat types). Based on the expert knowledge of the authors, we selected the species of high conservation value (Table S2). We considered species of high conservation value according to the following criteria: i) dry grassland specialists (steppe, forest-steppe or open sand grassland species), ii) rare in Central Europe and iii) also rare or only locally abundant in Hungary. We excluded dry grassland specialists that are widespread and common in Hungarian grasslands.

All analyses were conducted in the R environment (R Development Core Team, 2023).

Results

We collected 3639 adult specimens of 159 species (28 orthopteran, 84 true bug, and 47 spider species) by sweep-netting, and 2314 adult specimens of 124 species (29 ground beetle, 42 true bug, and 53 spider species) by pitfall trapping, including 9 grasshopper, 30 true bug, 29 spider and 9 ground beetle species of high conservation value (Table S2).

Vegetation-dwelling arthropods

We found a significant effect of invasion, habitat type, and their interaction on the species composition of orthopterans and true bugs (Table 1). Invaded plots were distinct from control plots, particularly in OG and FS sites, as shown in the ordination diagrams (Fig. 2). Additionally, invaded plots tended to cluster together, especially in the case of true bugs, suggesting the homogenization of communities due to the invasion. However, only habitat type had a significant effect on the species composition of spiders (Table 1). We identified indicator species for each habitat type, and a number of them were associated with both FS and OG sites (Table S4). Several vegetation-dwelling species, particularly among true bugs, were exclusively associated with the control or invaded plots (Table 2). The majority of species of high conservation value were associated with the control plots. Species associated with the invaded plots were mostly found in MS sites, whereas species associated with control plots were found in each habitat type.

Habitat type affected the species richness and abundance of orthopterans, whilst sand dropseed invasion influenced only their abundance (Table 3; Table S3; Fig. 3 a,b). In addition, we found a significant interacting effect of habitat type and invasion on the abundance of orthopterans. Orthopteran abundance was significantly lower in plots with high sand dropseed cover compared to plots with low and medium cover and controls (Fig. 3b). However, the significant interaction suggested that this pattern could vary between the orthopteran communities in different habitat types. Orthopteran abundance was significantly lower in the plots with high sand dropseed cover in FS sites and in the plots with medium and high cover in OG sites, compared to the controls. In contrast, orthopteran abundance increased in the plots with low cover compared to the plots with high cover and controls in MS sites (Fig. 4). Only sand dropseed invasion significantly influenced the species richness and abundance of true bugs (Table 3; Table S3). Both the species richness and abundance of true bugs were lower in plots with medium and high sand dropseed cover compared to control plots (Fig. 3c,d). There were no significant differences in any other cases. Habitat type significantly affected the species richness of spiders, whilst sand dropseed invasion affected their abundance (Table 3; Table S3). Their abundance was higher in plots with low sand dropseed cover than the control plots, but no significant differences existed in any other cases (Fig. 3e,f).

For species of high conservation value, the species richness of grasshoppers did not differ between invaded and control sites ($t = -1.747$, $p = 0.084$), but their abundance was significantly lower in invaded sites ($t = -3.874$, $p < 0.001$) (Fig. 6a,b). Both the species richness ($t = -5.584$, p

< 0.001) and abundance ($t = -4.888$, $p < 0.001$) of true bugs of conservation importance were significantly lower in invaded sites (Fig. 6a,b). We found no significant differences in the number ($t = 1.417$, $p = 0.160$) and abundance ($t = 1.638$, $p = 0.105$) of spider species (Fig. 6a,b).

Ground-dwelling arthropods

In contrast to plant-dwelling arthropods, only the habitat type influenced significantly the species composition of ground-dwelling arthropod groups (Table 1). Accordingly, most indicator species were associated with a given habitat type regardless of sand dropseed invasion (Table S4). We found only a few ground-dwelling species that were exclusively associated with control or invaded plots (Table 2).

Habitat type significantly affected the species richness of ground-dwelling true bugs, whilst sand dropseed invasion did not affect their species richness and abundance (Table 3; Table S3; Fig. 5a,b). Similarly, only habitat type, but not the invasion, affected spider species richness and abundance significantly (Table 3; Table S3; Fig. 5c,d). Both habitat type and sand dropseed invasion showed significant effects on the species richness and abundance of ground beetles (Table 3; Table S3). Ground beetle species richness was significantly higher in plots with low sand dropseed cover compared to plots with medium and high cover and controls (Fig. 5e). Ground beetle abundance was also higher in plots with low cover compared to plots with medium and high cover. Still, compared to controls, the difference was only near significant ($p = 0.055$) (Fig. 5f).

Concerning species of high conservation value, their numbers were significantly lower in invaded sites in the case of true bugs ($t = -2.539$, $p = 0.014$) and ground beetles ($t = -2.411$, $p = 0.020$), in contrast to their abundance (for true bugs: $t = -1.644$; $p = 0.107$; for ground beetles: $t = -1.072$, $p = 0.289$) (Fig. 6c,d). We found no significant differences in the number ($t = 0.835$, $p = 0.408$) and abundance ($t = -0.739$, $p = 0.463$) of spider species between invaded and control sites (Fig. 6c,d).

Discussion

We studied the impact of the recently introduced, invasive sand dropseed (*Sporobolus cryptandrus*) on arthropod communities in open sand grassland, forest steppe, and meadow steppe habitats. We found neutral or even positive effects of the emerging invasion on predatory

spiders and partly omnivorous/phytophagous ground beetles, whilst the invasion overall negatively affected the vegetation-dwelling, primarily herbivorous orthopterans and true bugs. However, the effects of invasion depended on the density of sand dropseed and varied between habitat types. Overall, sand dropseed negatively affected the arthropod species of high conservation value.

Responses of Orthoptera to invasion varied between habitat types

The species composition of orthopterans differed between invaded and control plots, particularly in OG and FS habitats. These changes in species composition were presumably driven by changes in orthopteran abundance. Sand dropseed invasion affected their abundance, but did not affect species richness. The abundance of orthopteran communities responds quickly and sensitively to changes in vegetation, whether it is due to grassland management or plant invasion (Torma et al., 2019; Yoshioka et al., 2010). Additionally, several studies have reported that while herbivore abundance decreases in response to invasive plants, species richness remains unaffected (Litt et al., 2014). We also found that orthopteran abundance decreased in OG and FS sites, particularly in plots with high sand dropseed cover, in contrast to MS sites, where orthopteran abundance did not change or even increased in plots with low sand dropseed cover. Responses of food generalists to plant invasion are often varied, and in some cases, facilitation of native herbivores has also been reported (De Groot et al., 2007; Samways & Moore, 1991). On the one hand, non-native plants may serve as additional resources for generalist herbivores (García-Robledo & Horvitz, 2011; Graves & Shapiro, 2003). Jonas et al. (2002) found that an invasive grass, which proved to be a suitable food plant for grasshoppers, positively affected them. Although the majority of collected orthopterans were grasshoppers, sand dropseed, being a C4 grass, is presumably less preferable to grass-feeding herbivores due to the unfavourable C:N ratio and the high amount of sclerenchyma (Pinder & Kroh, 1987; Heckathorn et al., 1999). In addition, the Eurasian steppe zone is characterised by the prevailing dominance of C3 grasses (Hurka et al., 2019), and insect herbivores that live in Eurasian grasslands are presumably less adapted to C4 grasses than insect herbivores in, e.g., African savannahs (van Bergen et al., 2016). It seems that sand dropseed is not a suitable host plant for native insect herbivores, which confirms the fact that alien plants have rarely been proven to be suitable food plants for native herbivorous insects (Bezemer et al., 2014; Talamy et al., 2021). On the other hand, a non-native

plant may increase the architectural complexity and/or species diversity of vegetation thus positively affecting generalist herbivores (Gallé et al., 2023). Török et al. (2021) have previously reported that low cover of sand dropseed increased the species richness of plant communities, which could be favourable for some generalist herbivores or even omnivorous species such as *Roeseliana roeselii*.

However, even the high sand dropseed cover did not cause reduced orthopteran abundance in MS sites, in contrast to OG and FS sites. Increasing cover of non-native grass species can reduce the abundance of grasshoppers, which prefer open vegetation, as opposed to grasshoppers, which prefer closed vegetation (Litt & Steidl, 2010). Numerous grasshopper species collected in FS and OG sites, such as *Stenobothrus fischeri* and *Calliptamus barbarus*, prefer bare soil surfaces and short, sparse vegetation (Cigliano et al. 2017; Iorgu & Iorgu, 2008). Presumably, these species reacted much more adversely to the increasing vegetation height and cover due to sand dropseed invasion than eurytopic species (e.g. *Chorthippus brunneus* and *Euchorthippus declivus*), or species with a preference for closed grasslands (e.g., *Ch. dichrous*), which were associated with MS sites. Arthropods need to adapt to the harsh environment in the semidesert-like OG and FS habitats; thus, some life-history trait states are favoured (drought tolerant, thermophile, preference for bare soil surface, etc.). This environmental filtering of species may lead to low functional diversity but a high degree of habitat specialisation in arthropod communities (Gallé et al., 2018). The different responses of orthopteran communities to invasion in the different habitat types were presumably due to the presence of more habitat specialists in OG and FS sites. There are greater impacts of invasive grasses on native grasshoppers when they are habitat specialists, as opposed to habitat generalists (Yoshioka et al., 2010). However, the invasion vulnerability of native herbivores has rarely been examined as a function of their habitat specificity.

Vegetation-dwelling, but not ground-dwelling true bugs were affected by invasion

We found that sand dropseed invasion had a severe impact on the species composition of vegetation-dwelling true bugs, and could homogenise their communities. Additionally, both their abundance and species richness decreased with increasing sand dropseed cover, regardless of the habitat type. Generally, food specialist herbivores are more vulnerable to plant invasion than generalists, as they have little or no flexibility in their choice of host plant species (De Groot et

al., 2007; Harvey & Fortuna, 2012). Numerous true bugs are specialised to a restricted number of host plants, most of which are dicots (Wachman et al. 2004-2012). It was previously shown that with increasing sand dropseed cover, the cover of insect-pollinated dicots decreased in the study sites (Hábenczyus et al., 2022). The results of indicator species analysis underpin the sensitivity of food specialist herbivores to invasion since the majority of true bugs, which avoided invaded plots, were mono-, or oligophagous species having clear host plant preferences (e.g., *Dicranocephalus albipes*, *Oncochila scapularis*, *Emblethis ciliatus* feed on *Euphorbia*, and *Polymerus unifasciatus* feeds on *Galium*). However, several food generalist species also showed sensitivity to sand dropseed invasion (e.g., *Chorosoma gracile*, *Eurygaster dilaticollis*, and *Phimodera humeralis*). These species have a strong affinity to their habitats (Wachman et al. 2004-2012), suggesting again that habitat specialisation may have an important role in the response of true bugs to plant invasion besides trophic specialisation. In addition, some of them feed exclusively on grasses, suggesting that sand dropseed is not a suitable host plant for native herbivores.

An unexpected finding was, however, the lack of any significant effect of sand dropseed on ground-dwelling true bug communities. In contrast, the invasive common milkweed could affect the species richness and abundance of ground-dwelling true bugs (Gallé et al., 2023). In terms of species-specific responses, except for the above-mentioned *E. ciliatus*, the majority of frequent ground-dwelling species (*Pionosomus opacellus*, *Aellopus atratus*, *Ocethostethus opacus*, and *Acalypta gracilis*) were not affected by sand dropseed. Although many ground-dwelling species have a strong affinity to dry sandy grasslands and often to their host plant species as well (Gallé et al., 2010; Polchaninova et al., 2016; Torma & Körmöcz, 2008), ground-dwelling hemipterans are presumably less dependent on vegetation composition than vegetation-dwelling ones (Orabi et al., 2011). Ground-dwelling species are usually more affected by soil surface conditions, such as the physical structure and temperature, which influence their locomotion and activity (Torma & Gallé, 2011). The studied habitats are dominated by tussock-forming fescue grasses, and the presence of sand dropseed tussocks might not cause pronounced changes in the vegetation structure at the soil level. Presumably, sand dropseed also cannot alter the microclimate in this harsh environment, contrary to the well-known impacts of common milkweed (Follak et al., 2021). However, the physiognomy of common milkweed is very different from grasses, and for example, their broad leaves have a significant shading effect on the soil surface (Gallé et al.,

2023). Lastly, mosses and lichens are also key components for true bugs in sandy areas; the cover of mosses and lichens can influence the herbivores feeding on them, e.g. the *Acalypta* species, and it may affect the diversity and population density of ground-dwelling true bugs in general as they may serve as shelters for them (Spungis, 2005; Torma & Gallé, 2011). However, the sand dropseed seems to have a negative effect on dicotyledons, while it has less of an effect on grasses, mosses and lichens (Hábenczyus et al., 2022).

Low sand dropseed cover supported vegetation-dwelling, but not ground-dwelling spiders

Overall, we found almost no effect of invasion on spiders, except for the increased abundance of vegetation-dwelling spiders in plots with low sand dropseed cover. Sand dropseed is a high grass compared to dominant fescue species, and its low cover increases the structural complexity of vegetation (Kröel-Dulay et al., 2024). Increased vegetation complexity could be advantageous for spiders, providing more attachment points for web building, thus improving their hunting success (Pearson, 2009). In addition, low sand dropseed cover was shown to support the plant species richness (Török et al., 2021) and higher plant species richness often leads to higher structural complexity of vegetation, providing higher web site diversity for spiders (Finch et al., 2008; Rypstra et al., 1999). However, as the sand dropseed cover increased, the plant species diversity decreased, and the vegetation structure became more homogeneous (Török et al., 2021). The North American cobweb spider *Euryopis saukea*, a small myrmecophagous spider, with a preference for xerothermic open habitats, was associated with invaded plots in FS and OG sites. In addition, the well-known, large orb web spider *Argiope bruennichi* preferred invaded plots in MS sites, supporting the idea that the vegetation structure altered by low sand dropseed cover is particularly advantageous for web-building spiders.

Besides vegetation structure, microclimate and soil moisture are also crucial for ground-dwelling spiders (Carvalho et al., 2011; Entling et al., 2007). For example, many spiders are very sensitive to desiccation. Unlike some insects, spiders cannot extract moisture from atmospheric water vapour (Pultz, 1987). Therefore, soil moisture or litter humidity is particularly important for them (Wagner et al., 2003). If a non-native plant can alter these conditions, ground-dwelling spider communities respond sensitively to plant invasion (Schirmel & Buchholz, 2013). For example, the common milkweed invasion affected the species richness of ground-dwelling spiders via reduced soil moisture and temperature (Gallé et al., 2023). However, similarly to

ground-dwelling true bugs, the lack of changes in community-level patterns of ground-dwelling spiders suggests that the presence of sand dropseed did not cause pronounced changes in the habitat conditions at the soil level. Even though, there were some species, e.g., *Hogna radiata*, a large wolf spider, that avoided invaded plots.

Low sand dropseed cover supported ground beetles

Similar to spiders, the responses of ground beetles to plant invasion often varied according to the impact of the invasive plants on vegetation structure, soil moisture, microclimate, and the availability of prey (Schirmel et al., 2011; Pehle & Schirmel, 2015). Medium and high sand dropseed cover did not influence ground beetle species richness and abundance, coinciding with the findings in the other ground-dwelling arthropod groups. However, low sand dropseed cover even increased their species richness and abundance, presumably via the increased plant species richness. Carabidae is a diverse taxon in the sense of trophic behaviour of species, and herbivorous (seed predator) ground beetles can be supported by higher plant species richness (Liu et al., 2015; Lundgren et al., 2011). In addition, some species (*Harpalus* spp., *Amara* spp.) are proven to be able to adapt to consuming seeds of alien plants (Brust & House, 1988), which may result in increasing abundance and homogenisation of ground beetle communities (Hansen et al., 2009; Topp et al., 2008). The studied ground beetle communities were dominated by the genus *Harpalus*, which mainly consists of seed predator species and some of them (*H. servus*, *H. picipennis*) preferred invaded plots, but only in certain habitats. Sand dropseed is a prolific seed producer (Brown, 1943), that may be advantageous for seed predators, except for large species. Its seeds are very small and large ground beetles prefer heavier seeds (Fischer et al., 2021; Honek et al., 2007). In addition, seed energy content also influences seed predation rates (Gaba et al., 2019). However, we have no information on whether native carabid beetles consume sand dropseed seeds.

Sand dropseed negatively affected the arthropod species of high conservation value

Except for spiders, sand dropseed reduced the species richness and/or abundance of arthropods of high conservation value. In the case of vegetation-dwelling true bugs and orthopterans, it coincided with the response of the total assemblages. However, the number of ground-dwelling true bug and ground beetle species of high conservation value was also lower in sites invaded by

sand dropseed, in contrast to the species number of their total assemblages. Many species of high conservation value also showed species-specific responses, such as *S. fischeri*, *C. barbarus*, *Ph. humeralis*, *D. albipes*, *Ch. gracile*, *E. ciliatus* (cfr. Table 2). Many of these specialist species of high conservation value are endangered or even extinct in other Central European countries according to the national red lists (cfr. Holuša et al., 2017; Kment et al., 2017; Rabitsch, 2012; Štepanovičová & Bianchi, 2001; Řezáč et al., 2015, Veselý et al. 2017). Thus their conservation in Hungary, where sand habitats still harbour their stable populations, should be a high priority.

Conclusion

Based on the results, we can assert that the spreading of sand dropseed seriously threatens dry grassland arthropod communities, particularly the species of high conservation value. Although we agree with the conclusion of numerous studies that the impact of invasive plants on different taxonomic and/or functional groups of arthropods can often vary and even be contradictory (Litt et al., 2014). We suggest that, habitat specialisation and substrate preference of arthropods, even in the case of herbivores, play essential roles in their reaction to plant invasion in addition to their trophic level and food specialisation. However, we have to note, that all the slight positive effects found in the present study and reported by previous studies on plant communities (Hábenczyus et al., 2022; Török et al., 2021), were due to the low cover of sand dropseed in certain sites. Presumably, low sand dropseed cover may increase the local species richness, but its high density causes reduced diversity and homogenisation of communities. Based on its extremely fast spreading rate, it will probably gain higher coverage in extended areas in the future, suggesting serious consequences for the native flora and fauna. How to control sand dropseed invasion is the focus of some ongoing research in Hungary; for example, its possible suppression by a hemiparasitic plant, *Odontites lutea*. Some studies highlighted the potential role of native parasitic plants in suppressing invasive or dominant species, thus aiding in the restoration of affected habitats (Mládek et al., 2017; Těšitel et al., 2020). However, it is poorly known how such a restoration method affects arthropods (e.g., Tesitel et al., 2025).

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Author contributions

Márton Szabó: Formal analysis; investigation; methodology; writing—original draft; writing—review and editing. **Botond Magyar:** Investigation; methodology; writing – review and editing. **Anna Violetta Nagy:** Investigation; methodology; writing – review and editing. **Nikolett Gallé-Szpisjak:** Methodology; writing – review and editing. **Péter Batáry:** Formal analysis; writing – review and editing. **Attila Torma:** Conceptualisation; formal analysis; investigation; methodology; writing—original draft; writing—review and editing.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The data that support the findings of this study are available at <https://doi.org/10.5061/dryad.cc2fqz6gn> (Szabo_ICDIV_2024 [Dataset]).

Table 1. Effects of sand dropseed invasion, habitat type and their interacting term on the species composition of different arthropod groups according to dbRDAs. Effects on vegetation-dwelling and ground-dwelling groups are listed above and below the dashed line, respectively. Significant results are marked in bold.

	Variance %	F	P
ORTHOPTERA			
invasion	6.97	4.123	< 0.001
habitat	33.46	9.894	0.028
invasion × habitat	19.03	5.626	0.004
HETEROPTERA			
invasion	11.84	5.527	< 0.001
habitat	22.68	5.295	< 0.001
invasion × habitat	14.19	3.311	< 0.001
ARANEAE			
invasion	4.98	1.801	0.149
habitat	24.24	4.392	< 0.001
invasion × habitat	4.68	0.849	0.568
HETEROPTERA			
invasion	22.63	0.480	0.799
habitat	22.63	3.800	0.003
invasion × habitat	4.54	0.762	0.600
ARANEAE			
invasion	1.10	0.385	0.952
habitat	27.35	4.790	< 0.001
invasion × habitat	3.40	0.599	0.904
CARABIDAE			
invasion	0.94	0.373	0.831
habitat	37.16	7.393	< 0.001
invasion × habitat	1.62	0.323	0.949

Table 2. Effects of sand dropseed invasion, habitat type and their interacting term on different arthropod groups according to GLMMs. Effects on vegetation-dwelling and ground-dwelling groups are listed above and below the dashed line, respectively. Significant results are marked in bold.

	Species richness ^P			Abundance ^{nb}		
	χ^2	df	P	χ^2	df	P
ORTHOPTERA						
invasion	4.51	3	0.211	39.2	3	< 0.001
habitat	44.81	2	< 0.001	33.02	2	<0.001
invasion × habitat	8.18	6	0.225	36.41	6	<0.001
HETEROPTERA						
invasion	20.61	3	< 0.001	32.37	3	<0.001
habitat	2.54	2	0.281	4.44	2	0.108
invasion × habitat	5.25	6	0.511	10.03	6	0.123
ARANEAE						
invasion	1.87	3	0.598	8.163	3	0.043
habitat	8.15	2	0.017	3.534	2	0.171
invasion × habitat	2.97	6	0.812	11.49	6	0.074
HETEROPTERA						
invasion	3.41	3	0.332	2.83	3	0.418
habitat	9.19	2	0.01	5.45	2	0.065
invasion × habitat	7.6	6	0.268	0.98	6	0.986
ARANEAE						
invasion	1.85	3	0.604	4.36	3	0.225
habitat	34.12	2	< 0.001	57.44	2	<0.001
invasion × habitat	4.56	6	0.6	2.91	6	0.821
CARABIDAE						
invasion	14.54	3	0.002	11.84	3	0.007
habitat	12.27	2	0.002	20.163	2	<0.001
invasion × habitat	9.03	6	0.172	3.146	6	0.79

^P Poisson model, ^{nb} negative binomial model (except ground-dwelling spider abundance, in which case we did not detect overdispersion)

Table 3. The list of the species, which were associated with invaded (Inv) or control (Ctrl) plots in one or more habitat types according to the multi-level pattern analysis of indicator species. Vegetation-dwelling species and ground-dwelling species are listed above and below the dashed line, respectively. Abbreviation of arthropod groups: Orth - orthopterans, Het - true bugs, Ara - spiders, and Car - ground beetles. Stars indicate the species of high conservation value. For detailed information on the results of the extended Indicator Value method see Table S3.

Species	Group	Forest steppe		Open sand grassland		Meadow steppe	
		Inv	Ctrl	Inv	Ctrl	Inv	Ctrl
<i>Calliptamus italicus</i>	Orth					×	
<i>Roeseliana roeselii</i>	Orth					×	
<i>Berytinus geniculatus</i> *	Het					×	
<i>Berytinus minor</i>	Het					×	
<i>Argiope bruennichi</i>	Ara					×	
<i>Euryopsis saukea</i>	Ara	×		×			
<i>Stenobothrus nigromaculatus</i> *	Orth						×
<i>Dolycoris baccarum</i>	Het						×
<i>Lasiacantha gracilis</i>	Het						×
<i>Polymerus unifasciatus</i>	Het						×
<i>Cheiracanthium pennyi</i>	Ara						×
<i>Oncochila scapularis</i> *	Het				×		×
<i>Stenobothrus fischeri</i> *	Orth				×		
<i>Aelia rostrata</i>	Het				×		
<i>Dicranocephalus albipes</i> *	Het				×		
<i>Trigonotylus caelestialium</i>	Het				×		
<i>Runcinia grammica</i>	Ara				×		
<i>Calliptamus barbarus</i> *	Orth		×		×		
<i>Chorosoma gracile</i> *	Het		×		×		
<i>Eurygaster dilaticollis</i> *	Het		×		×		
<i>Phimodera humeralis</i> *	Het		×		×		
<i>Trigonotylus pulchellus</i> *	Het		×		×		
<i>Chlamydatus saltitans</i>	Het		×				
<i>Europiella artemisiae</i>	Het		×				
<i>Emblethis ciliatus</i> *	Het					×	
<i>Sciocoris deltocephalus</i> *	Het	×	×		×		
<i>Hogna radiata</i>	Ara						×
<i>Syntomus truncatellus</i>	Car						×
<i>Harpalus servus</i> *	Car	×	×	×			
<i>Harpalus picipennis</i> *	Car	×				×	×

Figure legends

Fig. 1. Schematic maps showing the location of the studied habitats.

Fig. 2. Ordination plots from distance-based redundancy analyses (db-RDA, Bray-Curtis index) depict the effect of sand dropseed invasion (inv vs ctrl), habitat type (FS, OG, and MS) and their interaction on vegetation-dwelling orthopterans (a) and true bugs (b). Abbreviations: FS - forest steppe, OG - open sand grassland, MS - meadow steppe, ctrl - control, inv - invaded.

Fig. 3. Estimated means and confidence limits depict the differences in vegetation-dwelling arthropod (orthopterans, true bugs, spiders) species richness and abundance in relation to the invasive sand dropseed cover (control: not present, low: 1-20 %, medium: 21-50%, high: above 50%) on logarithmic (ln) scale. Different letters indicate significant differences between the four treatments based on post hoc comparisons. Abbreviations: ctrl - control, med - medium. For detailed information on post hoc comparisons see Table S2.

Fig. 4. Estimated means and confidence limits depict the differences in ground-dwelling arthropod (true bugs, spiders, ground beetles) species richness and abundance in relation to the invasive sand dropseed cover (control: not present, low: 1-20 %, medium: 21-50%, high: above 50%) on logarithmic (ln) scale. Different letters indicate significant differences between the four treatments based on post hoc comparisons. Abbreviations: ctrl - control, med - medium. For detailed information on post hoc comparisons see Table S2.

Fig. 5. Estimated means and control limits depict the differences in the orthopteran abundance in relation to the invasive sand dropseed cover (control: not present, low: 1-20 %, medium: 21-50%, high: above 50%) within habitat types on logarithm scale. Different letters indicate significant differences between the four treatments, based on post hoc comparisons between treatments within habitat types. Abbreviations: ctrl - control, med - medium. For detailed information on post hoc comparisons see Table S2.

809 Fig. 6. Bar charts (mean $\pm$ SE) depict the differences in the number and abundance of species of
810 high conservation value between sand dropseed-invaded and control sites (a,b - plant-dwelling
811 spiders, true-bugs and orthopterans; c,d - ground-dwelling spiders, true bugs and ground beetles).
812 Stars indicate the level of significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).
813

For Review Only

Spreading of recently introduced North American sand dropseed (*Sporobolus crytrandus*) threatens European native dry grassland arthropods

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Running title: Invasive grass threatens native arthropods

Abstract

1. Invasive plants ~~may can have~~ fundamentally impacts ~~on~~ ecosystems. As arthropods play prominent roles in ecosystem functioning via their food webs, knowing how plant invasion affects arthropod communities is essential.

2. We studied the ~~effect impact~~ of ~~the invasive sand dropseed the invasive grass~~ (*Sporobolus cryptandus*) on arthropods ~~(ground beetles, orthopterans, spiders, and true bugs)~~ across ~~three habitat types in Hungary: forest-steppe, open sand grassland, and meadow steppe~~. We compared ~~the species composition of arthropod groups. species richness and abundance~~. Additionally, we analysed the species richness and abundance of arthropod groups along a gradient of the invader density (low, medium, high, as well as control). ~~in three habitat types of high conservational value (forest-steppe, open sand grassland, and meadow steppe) in Hungary. We sampled vegetation-dwelling arthropods (orthopterans, true bugs, and spiders) by sweep-netting and ground-dwelling arthropods (true bugs, spiders, and ground beetles) by pitfall trapping.~~

3. ~~Orthopteran abundance decreased with increasing sand dropseed cover, but this varied among habitats. Their abundance was even higher in meadow steppe sites with low invasive grass cover compared to controls. The species richness and abundance of vegetation-dwelling true bugs decreased with increasing sand dropseed cover. We found that species composition between invaded and control plots only differed for vegetation-dwelling true bugs and orthopterans, with several species unique to control plots. Their species richness and/or abundance decreased with increasing *Sporobolus* cover, varying among habitats. However, Interestingly, low *Sporobolus* sand dropseed cover increased the species richness and abundance of ground beetles and the abundance of vegetation-dwelling, primarily web-building spiders. However, Nevertheless,~~ the conservation value of true bug, grasshopper and ground beetle species was reduced in invaded compared to control sites.

4. ~~We conclude that low sand dropseed cover may increase arthropod species richness and abundance possibly only for a short period. However, the diversity of arthropods, particularly species of high conservation value, can be reduced in invaded sites. Considering the fast spreading of sand dropseed, we highlight that its invasion threatens the native arthropod fauna of dry grasslands. We conclude that low *Sporobolus* cover may temporarily increase arthropod species richness and abundance, but this effect is likely short-lived before *Sporobolus* rapidly~~

gains dominance due to its fast spreading rate. Ultimately, *Sporobolus* invasion can reduce arthropod diversity, particularly affecting species of high conservation value.

Keywords: abundance, carabids, exotic, invasion, orthopterans, species richness, spiders, steppe, true bugs

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Introduction

The spreading of non-native species is one of the most severe threats to biodiversity in terrestrial ecosystems (Pyšek et al., 2020), and thus also one of the main global drivers of ecosystem change (Millennium Ecosystem Assessment, 2005). Plant species invasion may lead to changes in native plant community composition and diversity, microclimatic conditions, and soil properties (Ehrenfeld, 2003; Pehle & Schirmel, 2015; Vitousek et al., 1996). Accordingly, invasive plants can affect arthropod communities as well, but the responses of arthropod communities to plant invasion are often contradicting (Bezemer et al., 2014; Litt et al., 2014). Most studies reported a significant decrease in arthropod diversity and abundance in response to plant invasions (Litt et al., 2014). However, some studies found neutral or even positive effects of invasive plants on arthropods, suggesting that invasive plants may attract pollinators (Bartomeus et al., 2008; Graves & Shapiro, 2003; Kovács-Hostyánszki et al., 2022), provide alternative resources for generalist herbivores (Emery & Doran, 2013), and create favourable conditions for certain species (Pearson, 2009).

Arthropods are essential components of the biodiversity and functioning of terrestrial ecosystems. They have a prominent role in pollination, herbivory, decomposition, nutrient cycling, and as food resources for many vertebrates (Yang & Gratton, 2014). Thus, understanding how arthropod communities respond to the spreading of a non-native plant is crucial for biodiversity conservation. It is particularly important in conservation areas, which harbour diverse arthropod communities with many specialist species, such as Eurasian dry grassland remnants in Europe (Cizek et al., 2012; Torma et al., 2014; van Swaay, 2002).

The Kiskunság region of Hungary represents a transition zone between temperate deciduous forests and continental steppes, forming mosaics of forested and open habitat patches (Erdős et al., 2015, 2018). Several habitat types in the region are listed among the priority habitats of Annex 1 of the EU Habitats Directive (e.g., 2340* Pannonic inland dunes, 6260* Pannonic sand steppes). These habitats still harbour a unique flora and fauna characterised by several endemic or endangered species. Unfortunately, the region is highly influenced by non-native plant species (Botta-Dukát, 2008), owing to the largely missing, formerly widespread traditional grazing management, lowering water table and climate change. We have restricted information on the effects of these non-native plants on grassland arthropods, with perhaps the only exception being common milkweed (*Asclepias syriaca*). Common milkweed has been

intensively studied in Hungary and throughout Europe. However, study results suggest significant but mixed effects of common milkweed on arthropods (Follak et al., 2021).

Sand dropseed (*Sporobolus crytrandus*), a C4 grass species of North American origin, was recently discovered in Hungary (Török & Aradi, 2017) and has become an invasive species within a few years, particularly in the Kiskunság (Hábenczyus et al., 2022; Török et al., 2021). In contrast to the other *Sporobolus* species (e.g., *S. neglectus* and *S. vaginiflorus*) introduced into Europe, the spreading of sand dropseed is not limited to road margins and ruderal sites but also affects natural, semi-natural dry grasslands (Bauer & Verloove, 2023; Kröel-Dulay et al., 2024).

In sand steppes, sand dropseed invasion significantly reduces the species richness and abundance of subordinate plants, homogenises the vegetation composition and can even lead to the complete replacement of the originally dominant native grasses (Hábenczyus et al. 2022; Török et al. 2021). Although sand dropseed is also spreading in Western Russian and Ukrainian steppe habitats (Alekseev et al., 1996; Demina et al., 2018; Gouz & Timoshenkova, 2017; Kuvaev & Stepanova, 2014; Maltsev & Sagalaev, 2018), we have no information about the effects of the invasion of sand dropseed on ~~how the invasion of sand dropseed affect~~ the diversity of arthropod communities. To fill this knowledge gap, we examined the effect of sand dropseed invasion on dry grassland arthropod communities in the Kiskunság region, Hungary.

The extent of the threat posed by invasive plants may vary among different habitats since habitat characteristics affects both the establishment and dominance of non-native plants in the community (Chytrý et al., 2009; Guarino et al., 2021). In addition, the density of invaders increases as invasions progress. Thus, studying the role of invasive plant density is useful for understanding ecological processes at different stages of invasion and predicting its future impacts. For example, Foster et al. (2021) concluded that the conflicting results of studies on the effects of the invasive spotted knapweed (*Centaurea stoebe*) were probably due to the different densities of the invaders in the study areas. However, the role played by the alien species' density has seldom been explored. To evaluate the effects of sand dropseed invasion into native grasslands, we sampled arthropod communities on plots established along a gradient of the invasive grass density in three characteristic and high-nature-value habitat types: forest-steppe, open sand grassland, and meadow steppe.

Different taxonomical or functional arthropod groups often respond differently to plant invasion (Bezemer et al., 2014). Therefore, we applied a multi-taxon approach, sampling both

ground-dwelling and vegetation-dwelling arthropods. In general, changes in the compositional diversity of vegetation affect the diversity of vegetation-dwelling, primarily herbivorous arthropods, whereas structural diversity is more related to that of ground-dwelling, mostly predatory arthropods (Lengyel et al., 2016; Torma et al., 2023). We selected spiders (Araneae), ground beetles (Coleoptera: Carabidae), true bugs (Hemiptera: Heteroptera), and orthopterans (Orthoptera) as study taxa since they are species-rich and abundant groups in grassland ecosystems and play different roles in ecosystem functioning. The majority of orthopterans and true bugs are important primary consumers in grasslands and provide a rich prey resource for several predators (Neff et al., 2019). Herbivorous insects are likely to be significantly affected by plant invasion, as they are directly related to plant species composition and diversity (Tallamy et al., 2021). Spiders and ground beetles are common predatory arthropods in many terrestrial ecosystems, although some ground beetle species are granivorous or omnivorous. Usually, they do not rely directly on plant species composition, even though plant invasions may indirectly affect them through changes in vegetation structure or prey availability (Gratton & Denno, 2005; Khum et al., 2023). Finally, we explored the effect of invasion on particular species of high conservationnatural value. These species are typically xerothermic species that prefer bare sandy soil surfaces, adapted to the ~~often semidesert-like semi-arid~~ conditions. They are associated strongly with the critically endangered Pannonian sandy habitats (Janssen et al., 2016) and are therefore of conservation importance in the European Union.

We addressed the following research questions:

- i) Does the sand dropseed invasion influence the species richness, composition and abundance of arthropod communities?
- ii) Does the effect of sand dropseed invasion vary between selected habitat types and arthropod groups?
- iii) Does the response of arthropod communities to sand dropseed invasion relate to its density?
- iv) Does the number and abundance of the species of high conservationnatural value differ between invaded and control sites?

Materials and methods

Study region and habitats

We carried out the study in the Kiskunság sand ridge in the Danube-Tisza interfluvium in Hungary, Central Europe (Fig. 1, Table S1). Kiskunság region has a continental climate with a mean annual temperature of 11°C and a mean annual precipitation of 550–600 mm (Dövényi et al., 2010). The soil is coarse-grained calcareous sand with low organic matter content. We selected our study sites in three different habitat types: forest-steppe (hereafter: FS), open sand grassland (hereafter: OG), and meadow steppe (hereafter: MS) (Fig. 1, Table S1). In the studied FS sites, smaller and larger patches of poplar trees (*Populus alba*) and shrubs (*Crataegus monogyna* and *Juniperus communis*) form a mosaic with sand grassland patches. Habitat conditions, including vegetation, are quite similar between OG and the grassland patches of sandy FS (Erdős et al., 2015). This similarity is also reflected in the similarity of arthropod communities, although the relatively small grassland patches of FS and the surrounding shrubs and trees could influence the composition and diversity of arthropod communities (Gallé & Torma, 2009; Kaur et al., 2019). In open sand grasslands, which are characterised by significant bare sand surface, the dominant plants are the tussock-forming, short-growing fescue grasses (*Festuca vaginata* and *F. wagneri*). Subordinate plants are other grasses (e.g., *Stipa borysthénica*) and drought-tolerant dicots (e.g., *Fumana procumbens*, *Euphorbia seguieriana*, *Alkanna tinctoria*). Meadow steppes are also characterised by the dominance of the tussock-forming, short-growing fescue grasses (*F. rupicola* and *F. wagneri*), but forming more dense vegetation together with several subordinate plants (e.g., *Chrysopogon gryllus*, *Poa angustifolia*, *Pseudolysimachion spicatum*, *Salvia pratensis*, and *Dianthus pottederae*).

Arthropod sampling and study design

In each habitat type, we selected five invaded vegetation plots and five corresponding control plots in the nearby vegetation, where sand dropseed was not present, resulting in 3×5 plot-pairs for sampling (Table S1). The plots were 15 × 15 m, a reasonable size even for a small invaded area. Due to the early invasion stage, the number of patches invaded by sand dropseed was limited, and their area was usually small, ca. 400–800 m². Typically, only the patches with higher sand dropseed cover exceeded 1000 m². Control plots situated 20 m from the edge of the invaded plots were characterised by the same habitat conditions, i.e. same vegetation type, succession status and site history. The mean distance between plot-pairs within habitat types was 413 ± 34 m (mean ± SEM). Furthermore, in accordance with previous studies on sand dropseed invasion in

these sites (c.f. Török et al., 2021), we classified the invaded plots into three density categories: low (1–20% mean cover), medium (21–50%) and high (above 50%). We assessed the sand dropseed cover in three 5×5 m quadrats in each invaded plot.

For sampling ground-dwelling true bugs, spiders, and ground beetles, we used pitfall traps (white 500 ml plastic cups, 8.5 cm in diameter) filled with a 50% ethylene glycol–water solution. The traps were equipped with transparent plastic funnels to avoid vertebrate bycatch and a plastic roof was placed over each trap to prevent the preservative from dilution (Császár et al., 2018). In each plot, we placed three pitfall traps in a row 10 m apart, resulting in a total of 90 traps. The traps were active for two weeks in one sampling period. We sampled vegetation-dwelling true bugs, spiders, and orthopterans, using a sweep-net with a diameter of 40 cm. In a sampling period, we performed 2×25 sweeps on sunny, windless days in each plot. We conducted the sampling procedures in the main vegetation period between the 19th of June and the 21st of July. During this period, pitfall trapping and sweep-netting were repeated two and three times, respectively. Arthropods were identified at the species level based on morphological characters (detailed information about literature used for identification is available in Supplementary material, Table S4S2). The nomenclature follows Cigliano et al. (2017), Müller-Motzfeld (2004), Wachmann et al. (2004–2012), and World Spider Catalog (2023).

Data analyses

To assess the overall effect of sand dropseed invasion on the different arthropod groups, we applied distance-based redundancy analyses (dbRDA, Bray-Curtis dissimilarity) using the vegan R package (Oksanen et al., 2020). The effect of invasion (invaded and control), habitat type (FS, OG, and MS) and their interaction on the species composition of arthropod groups was tested by *anova* function. In addition, we applied the indicator species approach of Dufrêne and Legendre (1997) to identify species associated with invaded or control plots in the different habitat types. In this method, indicator values are calculated by combining specificity (i.e., the abundance of the species in a given site group) and fidelity (i.e., the probability of finding the species at sites belonging to that site group). We used the *multipatt* function in the *indicspecies* R package (De Cáceres and Legendre, 2009). The function searches for indicator species for both individual site groups and combinations of site groups (De Cáceres et al., 2010).

~~For analyses, arthropod species data were pooled by sampling plots, resulting in 60 (3~~
~~habitats $\times$ 5 plot-pairs $\times$ 2 repetitions) and 90 (3 habitats $\times$ 5 plot-pairs $\times$ 3 repetitions) statistical~~
~~samples in case of pitfall trapping and sweep-netting, respectively.~~ To reveal the responses of
 different arthropod groups to sand dropseed ~~invasion~~density, we separately analysed the species
 richness and abundance (activity-density in the case of pitfall trapping) of each arthropod group
 per sampling method. For analyses, arthropod species data were pooled by sampling plots,
resulting in 60 (3 habitats $\times$ 5 plot-pairs $\times$ 2 repetitions) and 90 (3 habitats $\times$ 5 plot-pairs $\times$ 3
repetitions) statistical samples in case of pitfall trapping and sweep-netting, respectively. We
 analysed the effect of sand dropseed invasion on arthropod communities with generalised linear
 mixed-effects models (GLMMs, Poisson models) using the lme4 R package (Bates et al., 2015).
 In the case of data overdispersion, we used negative binomial models. We used species richness
 and abundance of arthropod groups as response variables, and sand dropseed coverage class (low,
 medium, high, and control), habitat type (FS, OG, and MF), and their interaction as fixed effects.
 Sampling sites (i.e., plot-pairs) and repetitions (i.e., sampling periods) were incorporated into
 models as separate random effects. We conducted post hoc comparisons with the help of the
 emmeans R package (Lenth, 2020). In separate models, we also compared species richness and
 abundance of high ~~conservation~~natural value arthropod species between invaded and control
 sites. In these models, habitat type was considered as a random factor (sampling pairs nested in
 habitat types). Based on the expert knowledge of the authors, we selected the species of high
~~conservation~~natural value (Table S2). We considered species of high ~~conservation~~natural value
 according to the following criteria: i) dry grassland specialists (steppe, forest-steppe or open sand
 grassland species), ii) rare in Central Europe and iii) also rare or only locally abundant in
 Hungary. We excluded dry grassland specialists that are widespread and common in Hungarian
 grasslands.

~~We applied the indicator species approach of Dufrêne and Legendre (1997) to identify~~
~~species associated with invaded or control plots in the different habitat types. In this method,~~
~~indicator values are calculated by combining specificity (i.e., the abundance of the species in a~~
~~given site group) and fidelity (i.e., the probability of finding the species at sites belonging to that~~
~~site group). We used the *multipatt* function in the *indicspecies* R package (De Cáceres and~~
~~Legendre, 2009). The function searches for indicator species for both individual site groups and~~

~~combinations of site groups (De Cáceres et al., 2010).~~ All analyses were conducted in the R environment (R Development Core Team, 2023).

Results

We collected 3639 adult specimens of 159 species (28 orthopteran, 84 true bug, and 47 spider species) by sweep-netting, and 2314 adult specimens of 124 species (29 ground beetle, 42 true bug, and 53 spider species) by pitfall trapping, including 9 grasshopper, 30 true bug, 29 spider and 9 ground beetle species of high ~~conservation~~^{natural} value (Table S2).

Vegetation-dwelling arthropods

We found a significant effect of invasion, habitat type, and their interaction on the species composition of orthopterans and true bugs (Table 1). Invaded plots were distinct from control plots, particularly in OG and FS sites, as shown in the ordination diagrams (Fig. 2). Additionally, invaded plots tended to cluster together, especially in the case of true bugs, suggesting the homogenization of communities due to the invasion. However, only habitat type had a significant effect on the species composition of spiders (Table 1). We identified indicator species for each habitat type, and a number of them were associated with both FS and OG sites (Table S4). Several vegetation-dwelling species, particularly among true bugs, were exclusively associated with the control or invaded plots (Table 2). The majority of species of high conservation value were associated with the control plots. Species associated with the invaded plots were mostly found in MS sites, whereas species associated with control plots were found in each habitat type.

Habitat type affected the species richness and abundance of orthopterans, whilst sand dropseed invasion influenced only their abundance (Table ~~43~~³; Table S3; Fig. ~~4-3~~³ a,b). In addition, we found a significant interacting effect of habitat type and invasion on the abundance of orthopterans. Orthopteran abundance was significantly lower in plots with high sand dropseed cover compared to plots with low and medium cover and controls (Fig. ~~4b3b~~^{3b}). However, the significant interaction suggested that this pattern could vary between the orthopteran communities in different habitat types. Orthopteran abundance was significantly lower in the plots with high sand dropseed cover in FS sites and in the plots with medium and high cover in OG sites, compared to the controls. In contrast, orthopteran abundance increased in the plots with low cover compared to the plots with high cover and controls in MS sites (Fig. ~~34~~³⁴). Only sand

dropseed invasion significantly influenced the species richness and abundance of true bugs (Table 43; Table S3). Both the species richness and abundance of true bugs were lower in plots with medium and high sand dropseed cover compared to control plots (Fig. 4e3c,d). There were no significant differences in any other cases. Habitat type significantly affected the species richness of spiders, whilst sand dropseed invasion affected their abundance (Table 43; Table S3). Their abundance was higher in plots with low sand dropseed cover than the control plots, but no significant differences existed in any other cases (Fig. 4e3e,f).

For species of high conservation natural-value, the species richness of grasshoppers did not differ between invaded and control sites ($t = -1.747$, $p = 0.084$), but their abundance was significantly lower in invaded sites ($t = -3.874$, $p < 0.001$) (Fig. 4a6a,b). Both the species richness ($t = -5.584$, $p < 0.001$) and abundance ($t = -4.888$, $p < 0.001$) of true bugs of conservation importance were significantly lower in invaded sites (Fig. 4-6a,-b). We found no significant differences in the number ($t = 1.417$, $p = 0.160$) and abundance ($t = 1.638$, $p = 0.105$) of spider species (Fig. 4a6a,b).

~~We identified indicator species for each habitat type, and a number of them were associated with both FS and OG sites (Table S4). Several vegetation-dwelling species, particularly among true bugs, were exclusively associated with the control or invaded plots (Table 2). Species associated with the invaded plots were mostly found in MS sites, whereas species associated with control plots were found in each habitat type.~~

Ground-dwelling arthropods

In contrast to plant-dwelling arthropods, only the habitat type influenced significantly the species composition of ground-dwelling arthropod groups (Table 1). Accordingly, mMost indicator species were associated with a given habitat type regardless of sand dropseed invasion (Table S4). We found only a few ground-dwelling species that were exclusively associated with control or invaded plots (Table 2).

Habitat type significantly affected the species richness of ground-dwelling true bugs, whilst sand dropseed invasion did not affect their species richness and abundance (Table 43; Table S3; Fig. 25-a,b). Similarly, only habitat type, but not the invasion, affected spider species richness and abundance significantly (Table 43; Table S3; Fig. 25-c,d). Both habitat type and sand dropseed invasion showed significant effects on the species richness and abundance of ground beetles

(Table 13; Table S3). Ground beetle species richness was significantly higher in plots with low sand dropseed cover compared to plots with medium and high cover and controls (Fig. 2e5e). Ground beetle abundance was also higher in plots with low cover compared to plots with medium and high cover. Still, compared to controls, the difference was only near significant ($p = 0.055$) (Fig. 25-f).

Concerning species of high ~~conservation~~^{natural} value, their numbers were significantly lower in invaded sites in the case of true bugs ($t = -2.539$, $p = 0.014$) and ground beetles ($t = -2.411$, $p = 0.020$), in contrast to their abundance (for true bugs: $t = -1.644$; $p = 0.107$; for ground beetles: $t = -1.072$, $p = 0.289$) (Fig. 46-c,d). We found no significant differences in the number ($t = 0.835$, $p = 0.408$) and abundance ($t = -0.739$, $p = 0.463$) of spider species between invaded and control sites (Fig. 4e6c,d).

~~Most indicator species were associated with a given habitat type regardless of sand dropseed invasion (Table S4). We found only a few ground-dwelling species that were exclusively associated with control or invaded plots (Table 2).~~

Discussion

We studied the impact of the recently introduced, invasive sand dropseed (*Sporobolus cryptandrus*) on arthropod communities in open sand grassland, forest steppe, and meadow steppe habitats. We found neutral or even positive effects of the emerging invasion on ~~predatory spiders and partly omnivorous/phytophagous ground beetle~~^{earnivorous spiders and ground beetles}, whilst the invasion overall negatively affected the vegetation-dwelling, primarily herbivorous orthopterans and true bugs. However, the effects of invasion depended on the density of sand dropseed and varied between habitat types. Overall, sand dropseed negatively affected the arthropod species of high ~~conservation~~^{natural}-value.

Responses of Orthoptera ~~Orthopteran responses~~ to invasion varied between habitat types

~~The species composition of orthopterans differed between invaded and control plots, particularly in OG and FS habitats. These changes in species composition were presumably driven by changes in orthopteran abundance. Sand dropseed invasion affected their abundance, but did not the affect species richness of orthopterans. The abundance of orthopteran communities responds quickly and sensitively to changes in vegetation, whether it is due to grassland management or~~

plant invasion (Torma et al., 2019; Yoshioka et al., 2010). Additionally, several studies have reported that while herbivore abundance decreases in response to invasive plants, species richness remains unaffected (Litt et al., 2014). Several studies reported that herbivore abundance, but not species richness, decreased in response to invasive plants (Litt et al., 2014). In addition, orthopteran communities often respond to disturbances by changing abundance rather than changing species richness (Torma et al., 2019). We also found that orthopteran abundance decreased in OG and FS sites, particularly in plots with high sand dropseed cover, in contrast to MS sites, where orthopteran abundance did not change or even increased in plots with low sand dropseed cover. Responses of food generalists to plant invasion are often varied, and in some cases, facilitation of native herbivores has also been reported (De Groot et al., 2007; Samways & Moore, 1991). On the one hand, non-native plants may serve as additional resources for generalist herbivores (García-Robledo & Horvitz, 2011; Graves & Shapiro, 2003). Jonas et al. (2002) found that an invasive grass, which proved to be a suitable food plant for grasshoppers, positively affected them. Although the majority of collected orthopterans were grasshoppers, sand dropseed, being a C4 grass, is presumably less preferable to grass-feeding herbivores due to the unfavourable C:N ratio and the high amount of sclerenchyma (Pinder & Kroh, 1987; Heckathorn et al., 1999). In addition, the Eurasian steppe zone is characterised by the prevailing dominance of C3 grasses (Hurka et al., 2019), and insect herbivores that live in Eurasian grasslands are presumably less adapted to C4 grasses than insect herbivores in, e.g., African savannahs (van Bergen et al., 2016). It seems that sand dropseed is not a suitable host plant for native insect herbivores, which confirms the fact that alien plants have rarely been proven to be suitable food plants for native herbivorous insects (Bezemer et al., 2014; Talamy et al., 2021). On the other hand, a non-native plant may increase the architectural complexity and/or species diversity of vegetation thus positively affecting generalist herbivores (Gallé et al., 2023). Török et al. (2021) have previously reported that low cover of sand dropseed increased the species richness of plant communities, which could be favourable for some generalist herbivores or even omnivorous species such as *Roeseliana roeselii*.

However, even the high sand dropseed cover did not cause reduced orthopteran abundance in MS sites, in contrast to OG and FS sites. Increasing cover of non-native grass species can reduce the abundance of grasshoppers, which prefer open vegetation, as opposed to grasshoppers, which prefer closed vegetation (Litt & Steidl, 2010). Numerous grasshopper species collected in

FS and OG sites, such as *Stenobothrus fischeri* and *Calliptamus barbarus*, prefer bare soil surfaces and short, sparse vegetation (Cigliano et al. 2017; Iorgu & Iorgu, 2008). Presumably, these species reacted much more adversely to the increasing vegetation height and cover due to sand dropseed invasion than eurytopic species (e.g. *Chorthippus brunneus* and *Euchorthippus declivus*), or species with a preference for closed grasslands (e.g., *Ch. dichrous*), which were associated with MS sites. Arthropods need to adapt to the harsh environment in the semidesert-like OG and FS habitats; thus, some life-history trait states are favoured (drought tolerant, thermophile, preference for bare soil surface, etc.). This environmental filtering of species may lead to low functional diversity but a high degree of habitat specialisation in arthropod communities ~~a high degree of arthropod communities' habitat specialisation~~ (Gallé et al., 2018). The different responses of orthopteran communities to invasion in the different habitat types were presumably due to the presence of more habitat specialists in OG and FS sites. There are greater impacts of invasive grasses on native grasshoppers when they are habitat specialists, as opposed to habitat generalists (Yoshioka et al., 2010). However, the invasion vulnerability of native herbivores has rarely been examined as a function of their habitat specificity.

Vegetation-dwelling, but not ground-dwelling true bugs were affected by invasion

We found that sand dropseed invasion had a severe impact on the species composition of vegetation-dwelling true bugs, and could homogenise their communities. Additionally, both their abundance and species richness decreased with increasing sand dropseed cover, regardless of the habitat type. Generally, food specialist herbivores are more vulnerable to plant invasion than generalists, as they have little or no flexibility in their choice of host plant species (De Groot et al., 2007; Harvey & Fortuna, 2012). Numerous true bugs are specialised to a restricted number of host plants, most of which are dicots (Wachman et al. 2004-2012). It was previously shown that with increasing sand dropseed cover, the cover of insect-pollinated dicots decreased in the study sites (Hábenczyus et al., 2022). The results of indicator species analysis underpin the sensitivity of food specialist herbivores to invasion since the majority of true bugs, which avoided invaded plots, were mono-, or oligophagous species having clear host plant preferences (e.g., *Dicranocephalus albipes*, *Oncochila scapularis*, *Emblethis ciliatus* feed on *Euphorbia*, and *Polymerus unifasciatus* feeds on *Galium*). However, several food generalist species also showed sensitivity to sand dropseed invasion (e.g., *Chorosoma gracile*, *Eurygaster dilaticollis*, and

Phimodera humeralis). These species have a strong affinity to ~~these~~their habitats (Wachman et al. 2004-2012), suggesting again that habitat specialisation may have an important role in the response of ~~herbivores~~true bugs to plant invasion besides trophic specialisation. In addition, some of them feed exclusively on grasses, suggesting that sand dropseed is not a suitable host plant for native herbivores.

An unexpected finding was, however, the lack of any significant effect of sand dropseed on ground-dwelling true bug communities. In contrast, the invasive common milkweed could affect the species richness and abundance of ground-dwelling true bugs (Gallé et al., 2023). In terms of species-specific responses, except for the above-mentioned *E. ciliatus*, the majority of frequent ground-dwelling species (*Pionosomus opacellus*, *Aellopus atratus*, *Ocethostethus opacus*, and *Acalypta gracilis*) were not affected by sand dropseed. Although many ground-dwelling species have a strong affinity to dry sandy grasslands and often to their host plant species as well (Gallé et al., 2010; Polchaninova et al., 2016; Torma & Körmöcz, 2008), ground-dwelling hemipterans are presumably less dependent on vegetation composition than vegetation-dwelling ones (Orabi et al., 2011). Ground-dwelling species are usually more affected by soil surface conditions, such as the ~~physical structures~~surface's complexity and temperature, which influence their locomotion and activity (Torma & Gallé, 2011). The studied habitats are dominated by tussock-forming ~~Fescue~~fescue grasses, and the presence of sand dropseed tussocks might not cause pronounced changes in the vegetation structure at the soil level. Presumably, sand dropseed also cannot alter the microclimate in this harsh environment, contrary to the well-known impacts of common milkweed (Follak et al., 2021). However, the physiognomy of common milkweed is very different from grasses, and for example, their broad leaves have a significant shading effect on the soil surface (Gallé et al., 2023). Lastly, mosses and lichens are also key components for true bugs in sandy areas; the cover of mosses and lichens can influence the herbivores feeding on them, e.g. the *Acalypta* species, and it may affect the diversity and population density of ground-dwelling true bugs in general as they may serve as shelters for them (Spungis, 2005; Torma & Gallé, 2011). ~~However, the sand dropseed seems to negatively affect dicots, while less so on grasses, mosses, and lichens~~However, the sand dropseed seems to have a negative effect on dicotyledons, while it has less of an effect on grasses, mosses and lichens (Hábenczyus et al., 2022).

Low sand dropseed cover supported vegetation-dwelling, but not ground-dwelling spiders

Overall, we found almost no effect of invasion on spiders, except for the increased abundance of vegetation-dwelling spiders in plots with low sand dropseed cover. ~~We found an increased abundance of vegetation-dwelling spiders in plots with low sand dropseed cover.~~ Sand dropseed is a ~~tussock-forming~~ high grass compared to dominant fescue species, and its low cover increases the structural complexity of vegetation (Kröel-Dulay et al., 2024). Increased vegetation complexity could be advantageous for spiders, providing more attachment points for web building, thus improving their hunting success (Pearson, 2009). In addition, low sand dropseed cover was shown to support the plant species richness (Török et al., 2021) and higher plant species richness often leads to higher structural complexity of vegetation, providing higher web site diversity for spiders (Finch et al., 2008; Rypstra et al., 1999). However, as the sand dropseed cover increased, the plant species diversity decreased, and the vegetation structure became more homogeneous (Török et al., 2021). The North American cobweb spider *Euryopis saukea*, a small myrmecophagous spider, with a preference for xerothermic open habitats, was associated with invaded plots in FS and OG sites. In addition, the well-known, large orb web spider *Argiope bruennichi* preferred invaded plots in MS sites, supporting the idea that the vegetation structure altered by low sand dropseed cover is particularly advantageous for web-building spiders.

Besides vegetation structure, microclimate and soil moisture are also crucial for ground-dwelling spiders (Carvalho et al., 2011; Entling et al., 2007). For example, many spiders are very sensitive to desiccation. Unlike some insects, spiders cannot extract moisture from atmospheric water vapour (Pultz, 1987). Therefore, soil moisture or litter humidity is particularly important for them (Wagner et al., 2003). If a non-native plant can alter these conditions, ground-dwelling spider communities respond sensitively to plant invasion (Schirmel & Buchholz, 2013). For example, the common milkweed invasion affected the species richness of ground-dwelling spiders via reduced soil moisture and temperature (Gallé et al., 2023). However, similarly to ground-dwelling true bugs, the lack of changes in community-level patterns of ground-dwelling spiders suggests that the presence of sand dropseed did not cause pronounced changes in the habitat conditions at the soil level. Even though, there were some species, e.g., *Hogna radiata*, a large wolf spider, that avoided invaded plots.

Low sand dropseed cover supported ground beetles

Similar to spiders, the responses of ground beetles to plant invasion often varied according to the impact of the invasive plants on vegetation structure, soil moisture, microclimate, and the availability of prey (Schirmel et al., 2011; Pehle & Schirmel, 2015). Medium and high sand dropseed cover did not influence ground beetle species richness and abundance, coinciding with the findings in the other ground-dwelling arthropod groups. However, low sand dropseed cover even increased their species richness and abundance, presumably via the increased plant species richness. Carabidae is a diverse taxon in the sense of trophic behaviour of species, and herbivorous (seed predator) ground beetles can be supported by higher plant species richness (Liu et al., 2015; Lundgren et al., 2011). In addition, some species (*Harpalus* spp., *Amara* spp.) are proven to be able to adapt to consuming seeds of alien plants (Brust & House, 1988), which may result in increasing abundance and homogenisation of ground beetle communities (Hansen et al., 2009; Topp et al., 2008). The studied ground beetle communities were dominated by the genus *Harpalus*, which mainly consists of seed predator species and some of them (*H. servus*, *H. picipennis*) preferred invaded plots, but only in certain habitats. Sand dropseed is a prolific seed producer (Brown, 1943), that may be advantageous for seed predators, except for large species. Its seeds are very small and large ground beetles prefer heavier seeds (Fischer et al., 2021; Honek et al., 2007). In addition, seed energy content also influences seed predation rates (Gaba et al., 2019). However, we have no information on whether native carabid beetles consume sand dropseed seeds.

Sand dropseed negatively affected the arthropod species of high ~~conservation~~natural value

Except for spiders, sand dropseed reduced the species richness and/or abundance of arthropods of high ~~conservation~~natural value. In the case of vegetation-dwelling true bugs and orthopterans, it coincided with the response of the total assemblages. However, the number of ground-dwelling true bug and ground beetle species of high ~~conservation~~ natural-value was also lower in sites invaded by sand dropseed, in contrast to the species number of their total assemblages. Many species of high ~~conservation~~natural value also showed species-specific responses, such as *S. fischeri*, *C. barbarus*, *Ph. humeralis*, *D. albipes*, *Ch. gracile*, *E. ciliatus* (cfr. Table 2). Many of these specialist species of high ~~conservation~~natural value are endangered or even extinct in other Central European countries according to the national red lists (cfr. Holuša et al., 2017; Kment et al., 2017; Rabitsch, 2012; Štepanovičová & Bianchi, 2001; Řezáč et al., 2015; Veselý et al.

2017). Thus their conservation in Hungary, where sand habitats still harbour their stable populations, should be a high priority.

Conclusion

Based on the results, we can assert that the spreading of sand dropseed seriously threatens dry grassland arthropod communities, particularly the species of high ~~conservation~~^{natural} value. ~~Even though, we agree with the conclusion of numerous studies stating that the effect of invasive plants on different taxonomic and/or functional groups of arthropods often varies and can be conflicting even~~ Although we agree with the conclusion of numerous studies that the impact of invasive plants on different taxonomic and/or functional groups of arthropods can often vary and even be contradictory (Litt et al., 2014). We suggest that ~~arthropods' habitat specialisation and substrate preference~~, habitat specialisation and substrate preference of arthropods, even in the case of herbivores, play essential roles in their reaction to plant invasion in addition to their trophic level and food specialisation. However, we have to note, that all the slight positive effects found in the present study and reported by previous studies on plant communities (Hábenczyus et al., 2022; Török et al., 2021), were due to the low cover of sand dropseed in certain sites. Presumably, low sand dropseed cover may increase the local species richness, but its high density causes reduced diversity and homogenisation of communities. Based on its extremely fast spreading rate, it will probably gain higher coverage in extended areas in the future, suggesting serious consequences for the native flora and fauna. How to control sand dropseed invasion is the focus of some ongoing research in Hungary; for example, its possible suppression by a hemiparasitic plant, *Odontites lutea*. Some studies highlighted the potential role of native parasitic plants in suppressing invasive or dominant species, thus aiding in the restoration of affected habitats (Mládek et al., 2017; Těšitel et al., 2020). However, it is poorly known how such a restoration method affects arthropods (e.g., ~~Tesitel et al., 2025~~^{Vašíček et al., 2023}).

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786
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794
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796 The authors declare no conflict of interest.

797
798 Data availability statement

799
800 The data that support the findings of this study are available at
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Table 1. Effects of sand dropseed invasion, habitat type and their interacting term on the species composition of different arthropod groups according to dbRDAs. Effects on vegetation-dwelling and ground-dwelling groups are listed above and below the dashed line, respectively. Significant results are marked in bold.

	Variance %	F	P
<u>ORTHOPTERA</u>			
invasion	6.97	4.123	< 0.001
habitat	33.46	9.894	0.028
invasion × habitat	19.03	5.626	0.004
<u>HETEROPTERA</u>			
invasion	11.84	5.527	< 0.001
habitat	22.68	5.295	< 0.001
invasion × habitat	14.19	3.311	< 0.001
<u>ARANEAE</u>			
invasion	4.98	1.801	0.149
habitat	24.24	4.392	< 0.001
invasion × habitat	4.68	0.849	0.568
<u>HETEROPTERA</u>			
invasion	22.63	0.480	0.799
habitat	22.63	3.800	0.003
invasion × habitat	4.54	0.762	0.600
<u>ARANEAE</u>			
invasion	1.10	0.385	0.952
habitat	27.35	4.790	< 0.001
invasion × habitat	3.40	0.599	0.904
<u>CARABIDAE</u>			
invasion	0.94	0.373	0.831
habitat	37.16	7.393	< 0.001
invasion × habitat	1.62	0.323	0.949

Table 12. Effects of sand dropseed invasion, habitat type and their interacting term on different arthropod groups according to GLMMs. Effects on vegetation-dwelling and ground-dwelling groups are listed above and below the dashed line, respectively. Significant results are marked in bold.

	Species richness ^P			Abundance ^{nb}		
	χ^2	df	P	χ^2	df	P
ORTHOPTERA						
invasion	4.51	3	0.211	39.2	3	≤ 0.001
habitat	44.81	2	≤ 0.001	33.02	2	≤ 0.001
invasion $\times$ habitat	8.18	6	0.225	36.41	6	≤ 0.001
HETEROPTERA						
invasion	20.61	3	≤ 0.001	32.37	3	≤ 0.001
habitat	2.54	2	0.281	4.44	2	0.108
invasion $\times$ habitat	5.25	6	0.511	10.03	6	0.123
ARANEAE						
invasion	1.87	3	0.598	8.163	3	0.043
habitat	8.15	2	0.017	3.534	2	0.171
invasion $\times$ habitat	2.97	6	0.812	11.49	6	0.074
HETEROPTERA						
invasion	3.41	3	0.332	2.83	3	0.418
habitat	9.19	2	0.01	5.45	2	0.065
invasion $\times$ habitat	7.6	6	0.268	0.98	6	0.986
ARANEAE						
invasion	1.85	3	0.604	4.36	3	0.225
habitat	34.12	2	≤ 0.001	57.44	2	≤ 0.001
invasion $\times$ habitat	4.56	6	0.6	2.91	6	0.821
CARABIDAE						
invasion	14.54	3	0.002	11.84	3	0.007
habitat	12.27	2	0.002	20.163	2	≤ 0.001
invasion $\times$ habitat	9.03	6	0.172	3.146	6	0.79

^P Poisson model, ^{nb} negative binomial model (except ground-dwelling spider abundance, in which case we did not detect overdispersion)

Table 23. The list of the species, which were associated with invaded (Inv) or control (Ctrl) plots in one or more habitat types according to the multi-level pattern analysis of indicator species extended Indicator Value method. Vegetation-dwelling species and ground-dwelling species are listed above and below the dashed line, respectively. Abbreviation of arthropod groups: Orth - orthopterans, Het - true bugs, Ara - spiders, and Car - ground beetles. Stars indicate the species of high conservation concern value. For detailed information on the results of the extended Indicator Value method see Table S3.

Species	Group	Forest steppe		Open sand grassland		Meadow steppe	
		Inv	Ctrl	Inv	Ctrl	Inv	Ctrl
<i>Calliptamus italicus</i>	Orth					×	
<i>Roeseliana roeselii</i>	Orth					×	
<i>Berytinus geniculatus</i> *	Het					×	
<i>Berytinus minor</i>	Het					×	
<i>Argiope bruennichi</i>	Ara					×	
<i>Euryopsis saukea</i>	Ara	×		×			
<i>Stenobothrus nigromaculatus</i> *	Orth						×
<i>Dolycoris baccarum</i>	Het						×
<i>Lasiacantha gracilis</i>	Het						×
<i>Polymerus unifasciatus</i>	Het						×
<i>Cheiracanthium pennyi</i>	Ara						×
<i>Oncochila scapularis</i> *	Het				×		×
<i>Stenobothrus fischeri</i> *	Orth				×		
<i>Aelia rostrata</i>	Het				×		
<i>Dicranocephalus albipes</i> *	Het				×		
<i>Trigonotylus caelestialium</i>	Het				×		
<i>Runcinia grammica</i>	Ara				×		
<i>Calliptamus barbarus</i> *	Orth		×		×		
<i>Chorosoma gracile</i> *	Het		×		×		
<i>Eurygaster dilaticollis</i> *	Het		×		×		
<i>Phimodera humeralis</i> *	Het		×		×		
<i>Trigonotylus pulchellus</i> *	Het		×		×		
<i>Chlamydatus saltitans</i>	Het		×				
<i>Europiella artemisiae</i>	Het		×				
<i>Emblethis ciliatus</i> *	Het					×	
<i>Sciocoris deltocephalus</i> *	Het	×	×		×		
<i>Hogna radiata</i>	Ara						×
<i>Syntomus truncatellus</i>	Car						×
<i>Harpalus servus</i> *	Car	×	×	×			
<i>Harpalus picipennis</i> *	Car	×				×	×

Figure legends

Fig. 1. Schematic maps showing the location of the studied habitats.

Fig. 2. Ordination plots from distance-based redundancy analyses (db-RDA, Bray-Curtis index) depict the effect of sand dropseed invasion (inv vs ctrl), habitat type (FS, OG, and MS) and their interaction on vegetation-dwelling orthopterans (a) and true bugs (b). Abbreviations: FS - forest steppe, OG - open sand grassland, MS - meadow steppe, ctrl - control, inv - invaded.

Fig. 43. Estimated means and confidence limits depict the differences in vegetation-dwelling arthropod (orthopterans, true bugs, spiders) species richness and abundance in relation to the invasive sand dropseed cover (control: not present, low: 1-20 %, medium: 21-50%, high: above 50%) on logarithmic (ln) scale. Different letters indicate significant differences between the four treatments based on post hoc comparisons. Abbreviations: ctrl - control, med - medium. For detailed information on post hoc comparisons see Table S2.

Fig. 24. Estimated means and confidence limits depict the differences in ground-dwelling arthropod (true bugs, spiders, ground beetles) species richness and abundance in relation to the invasive sand dropseed cover (control: not present, low: 1-20 %, medium: 21-50%, high: above 50%) on logarithmic (ln) scale. Different letters indicate significant differences between the four treatments based on post hoc comparisons. Abbreviations: ctrl - control, med - medium. For detailed information on post hoc comparisons see Table S2.

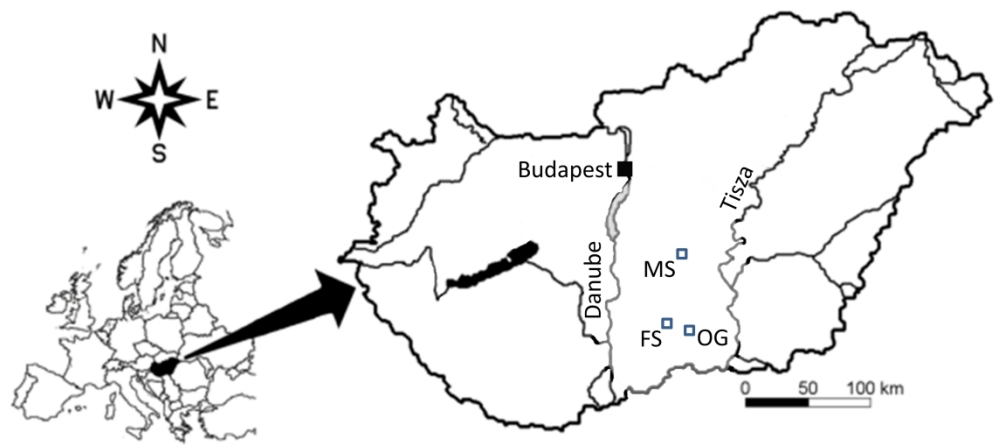
Fig. 35. Estimated means and control limits depict the differences in the orthopteran abundance in relation to the invasive sand dropseed cover (control: not present, low: 1-20 %, medium: 21-50%, high: above 50%) within habitat types on logarithm scale. Different letters indicate significant differences between the four treatments, based on post hoc comparisons between treatments within habitat types. Abbreviations: ctrl - control, med - medium. For detailed information on post hoc comparisons see Table S2.

Fig. 46. Bar charts (mean $\pm$ SE) depict the differences in the number and abundance of species of high conservation natural-value between sand dropseed-invaded and control sites (a,b - plant-

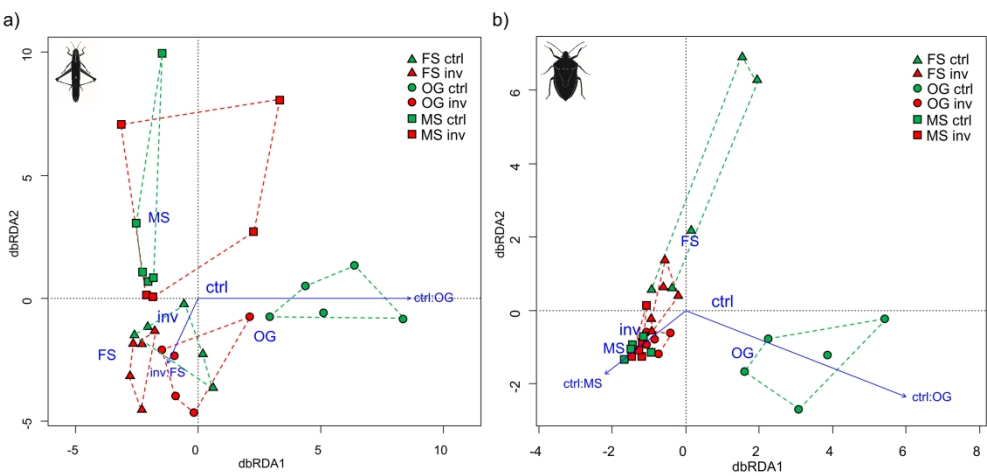
854 dweeling spiders, true-bugs and orthopterans; c_d - ground-dwelling spiders, true bugs and
855 ground beetles). Stars indicate the level of significance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

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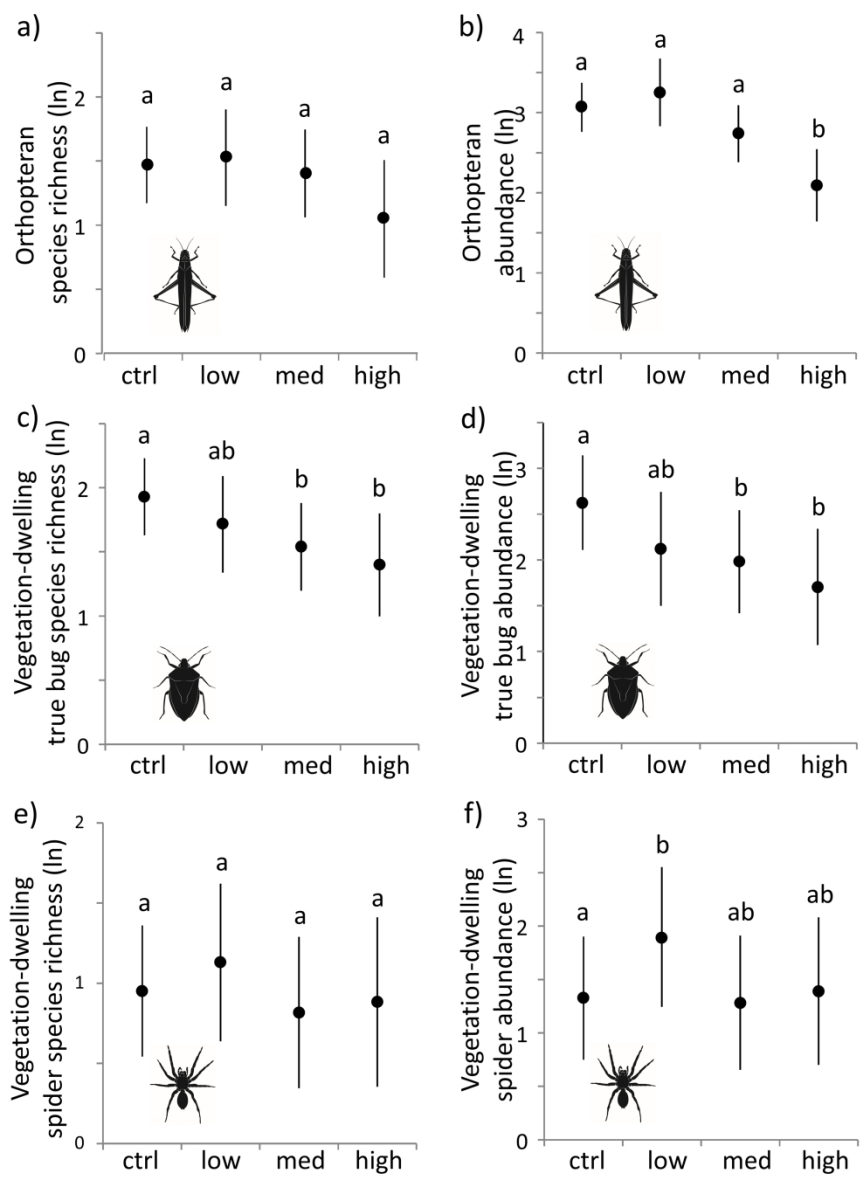
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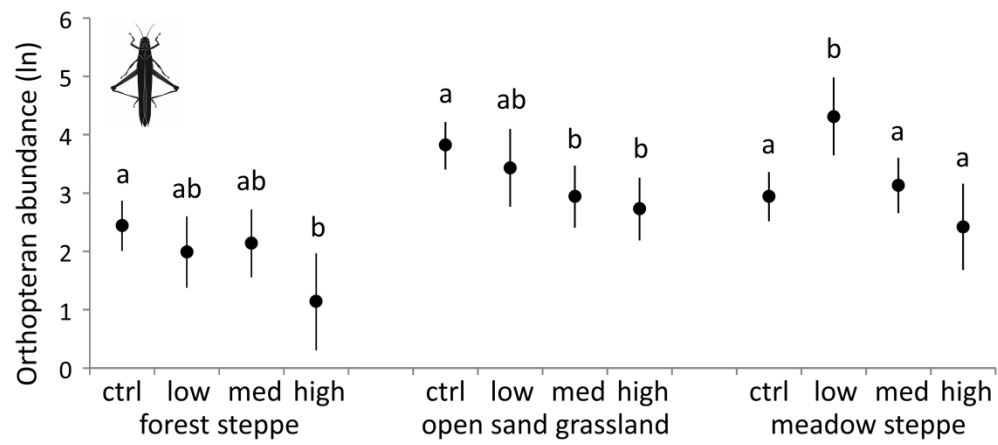
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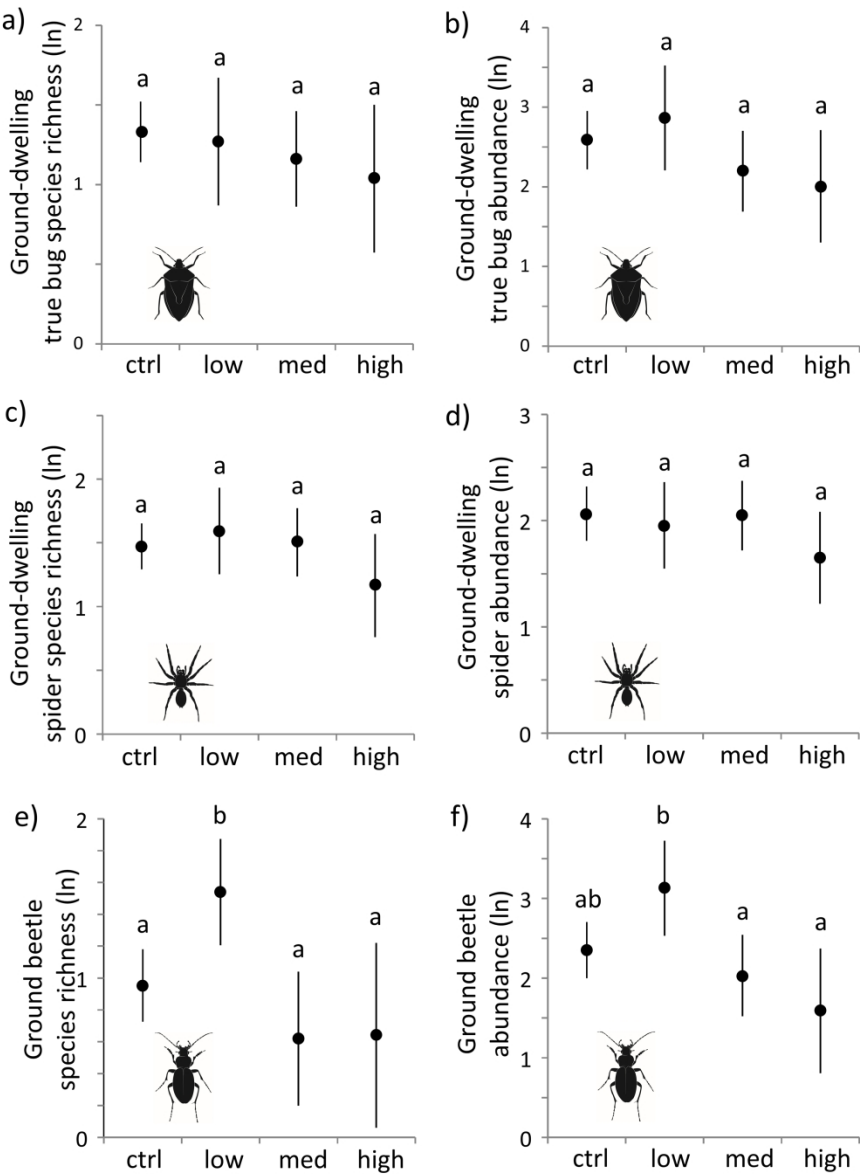
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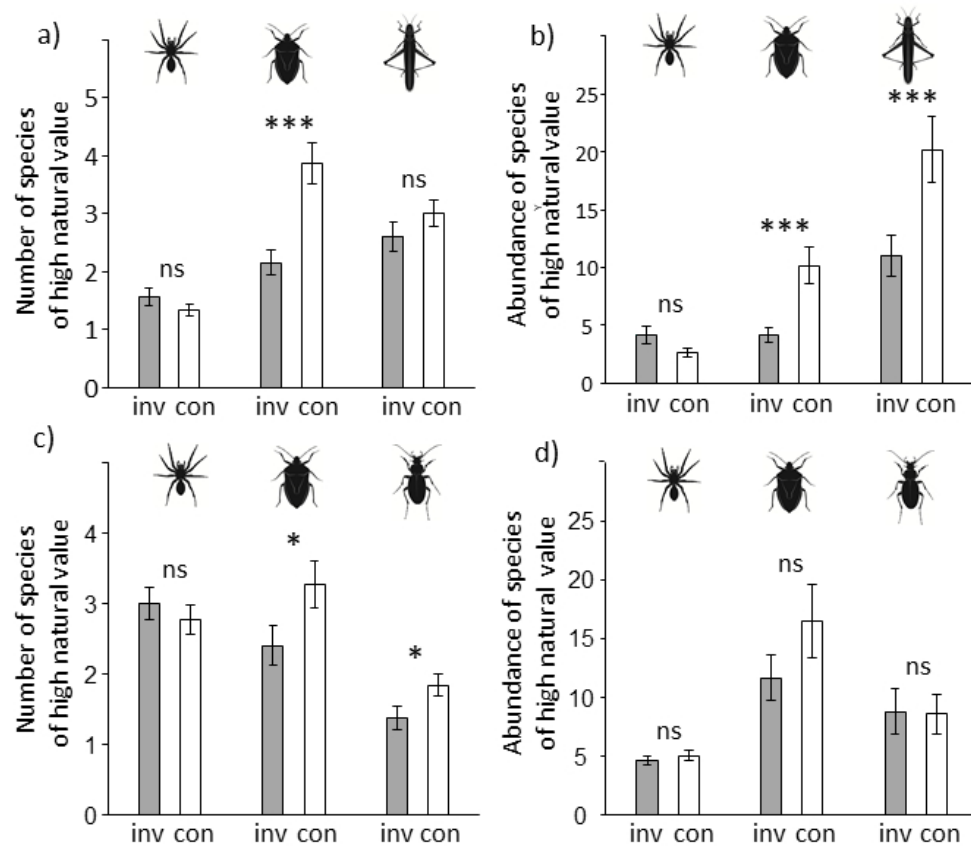
159x217mm (600 x 600 DPI)



159x71mm (600 x 600 DPI)



159x214mm (600 x 600 DPI)



180x157mm (96 x 96 DPI)

	Variance %	F	P
ORTHOPTERA			
invasion	6.97	4.123	< 0.001
habitat	33.46	9.894	0.028
invasion × habitat	19.03	5.626	0.004
HETEROPTERA			
invasion	11.84	5.527	< 0.001
habitat	22.68	5.295	< 0.001
invasion × habitat	14.19	3.311	< 0.001
ARANEAE			
invasion	4.98	1.801	0.149
habitat	24.24	4.392	< 0.001
invasion × habitat	4.68	0.849	0.568
HETEROPTERA			
invasion	22.63	0.480	0.799
habitat	22.63	3.800	0.003
invasion × habitat	4.54	0.762	0.600
ARANEAE			
invasion	1.10	0.385	0.952
habitat	27.35	4.790	< 0.001
invasion × habitat	3.40	0.599	0.904
CARABIDAE			
invasion	0.94	0.373	0.831
habitat	37.16	7.393	< 0.001
invasion × habitat	1.62	0.323	0.949

Species	Group	Forest steppe		Open sand grassland		Meadow steppe	
		Inv	Ctrl	Inv	Ctrl	Inv	Ctrl
<i>Calliptamus italicus</i>	Orth					×	
<i>Roeseliana roeselii</i>	Orth					×	
<i>Berytinus geniculatus</i> *	Het					×	
<i>Berytinus minor</i>	Het					×	
<i>Argiope bruennichi</i>	Ara					×	
<i>Euryopsis saukea</i>	Ara	×		×			
<i>Stenobothrus nigromaculatus</i> *	Orth						×
<i>Dolycoris baccarum</i>	Het						×
<i>Lasiacantha gracilis</i>	Het						×
<i>Polymerus unifasciatus</i>	Het						×
<i>Cheiracanthium pennyi</i>	Ara						×
<i>Oncochila scapularis</i> *	Het				×		×
<i>Stenobothrus fischeri</i> *	Orth				×		
<i>Aelia rostrata</i>	Het				×		
<i>Dicranocephalus albipes</i> *	Het				×		
<i>Trigonotylus caelestialium</i>	Het				×		
<i>Runcinia grammica</i>	Ara				×		
<i>Calliptamus barbarus</i> *	Orth		×		×		
<i>Chorosoma gracile</i> *	Het		×		×		
<i>Eurygaster dilaticollis</i> *	Het		×		×		
<i>Phimodera humeralis</i> *	Het		×		×		
<i>Trigonotylus pulchellus</i> *	Het		×		×		
<i>Chlamydatus saltitans</i>	Het		×				
<i>Europiella artemisiae</i>	Het		×				
<i>Emblethis ciliatus</i> *	Het				×		
<i>Sciocoris deltocephalus</i> *	Het	×	×		×		
<i>Hogna radiata</i>	Ara						×
<i>Syntomus truncatellus</i>	Car						×
<i>Harpalus servus</i> *	Car	×	×	×			
<i>Harpalus picipennis</i> *	Car	×				×	×

	Species richness ^P			Abundance ^{nb}		
	χ^2	df	P	χ^2	df	P
ORTHOPTERA						
invasion	4.51	3	0.211	39.2	3	< 0.001
habitat	44.81	2	> 0.001	33.02	2	< 0.001
invasion × habitat	8.18	6	0.225	36.41	6	< 0.001
HETEROPTERA						
invasion	20.61	3	> 0.001	32.37	3	< 0.001
habitat	2.54	2	0.281	4.44	2	0.108
invasion × habitat	5.25	6	0.511	10.03	6	0.123
ARANEAE						
invasion	1.87	3	0.598	8.163	3	0.043
habitat	8.15	2	0.017	3.534	2	0.171
invasion × habitat	2.97	6	0.812	11.49	6	0.074
HETEROPTERA						
invasion	3.41	3	0.332	2.83	3	0.418
habitat	9.19	2	0.01	5.45	2	0.065
invasion × habitat	7.6	6	0.268	0.98	6	0.986
ARANEAE						
invasion	1.85	3	0.604	4.36	3	0.225
habitat	34.12	2	> 0.001	57.44	2	< 0.001
invasion × habitat	4.56	6	0.6	2.91	6	0.821
CARABIDAE						
invasion	14.54	3	0.002	11.84	3	0.007
habitat	12.27	2	0.002	20.163	2	< 0.001
invasion × habitat	9.03	6	0.172	3.146	6	0.79