



## Plant invasion and fragmentation indirectly and contrastingly affect native plants and grassland arthropods<sup>☆</sup>

Róbert Gallé<sup>a,b,c,\*</sup>, Csaba Tölgyesi<sup>c,d</sup>, Ágota Réka Szabó<sup>a,b,e</sup>, Dávid Korányi<sup>a,b</sup>, Zoltán Bártori<sup>c,d</sup>, Alida Hábcenyus<sup>c,d</sup>, Edina Török<sup>a,b</sup>, Kitti Révész<sup>a,b</sup>, Attila Torma<sup>a,d</sup>, Nikolett Gallé-Szpisjak<sup>a</sup>, Tamás Lakatos<sup>a,e</sup>, Péter Batáry<sup>a,b</sup>

<sup>a</sup> 'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány út 2-4, 2163 Vácrátót, Hungary

<sup>b</sup> National Laboratory for Healthy Security, Centre for Ecological Research, Alkotmány út 2-4, 2163 Vácrátót, Hungary

<sup>c</sup> MTA-SZTE 'Momentum' Applied Ecology Research Group, Közép fasor 52, 6726 Szeged, Hungary

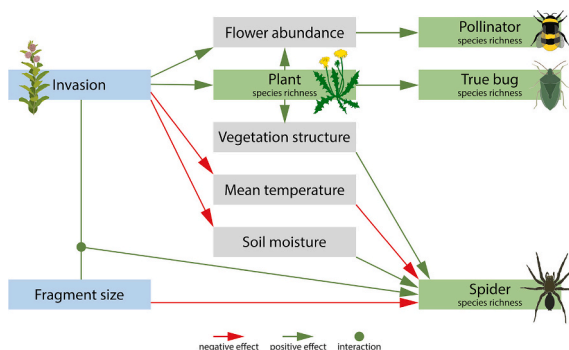
<sup>d</sup> Department of Ecology, University of Szeged, Közép fasor 52, 6726 Szeged, Hungary

<sup>e</sup> Doctoral School of Biology, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/C, 1117 Budapest, Hungary

### HIGHLIGHTS

- Invasion, fragmentation are global change drivers with negative effect on diversity.
- We studied their direct and indirect effects on plants and arthropods.
- The impact of invasion was stronger on generalists than on grassland specialists.
- Invasion positively affected generalists therefore homogenises communities.
- Revealing the direct and indirect effects is essential for understanding invasion.

### GRAPHICAL ABSTRACT



### ARTICLE INFO

Editor: Paulo Pereira

#### Keywords:

Forest-steppe  
Grassland  
Milkweed  
Pollinators  
True bugs  
Species richness  
Spiders  
Vegetation

### ABSTRACT

Plant invasion and habitat fragmentation have a detrimental effect on biodiversity in nearly all types of ecosystems. We compared the direct and indirect effects of the invasion of the common milkweed (*Asclepias syriaca*) on biodiversity patterns in different-sized Hungarian forest-steppe fragments. We assessed vegetation structure, measured temperature and soil moisture, and studied organisms with different ecological roles in invaded and non-invaded sites of fragments: plants, bees, butterflies, flower-visiting wasps, flies, true bugs, and spiders. Temperature and soil moisture were lower in invaded than in non-invaded area. Milkweed had a positive effect on plant species richness and flower abundance. In contrast, we mainly found indirect effects of invasion on arthropods through alteration of physical habitat characteristics and food resources. Pollinators were positively affected by native flowers, thus, milkweed indirectly supported pollinators. Similarly, we found higher species richness of herbivores in invaded sites than control sites, as species richness of true bugs also increased with

<sup>☆</sup> The data supporting the results will be archived in Zenodo repository when the manuscript will be accepted.

\* Corresponding author at: 'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány út 2-4, H-2163 Vácrátót, Hungary.

E-mail address: [galle.robert@ecolres.hu](mailto:galle.robert@ecolres.hu) (R. Gallé).

<https://doi.org/10.1016/j.scitotenv.2023.166199>

Received 23 February 2023; Received in revised form 8 August 2023; Accepted 8 August 2023

Available online 10 August 2023

0048-9697/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

increasing plant species richness. Predators were positively affected by complex vegetation structure, higher soil moisture and lower temperature. Furthermore, increasing fragment size had a strong negative effect on spider species richness of non-invaded sites, but no effect in invaded sites. Especially, grassland specialist spiders were more sensitive to fragment size than generalists, whereas generalist spider species rather profited from invasion. Although milkweed invades natural areas, we did not identify strong negative effects of its presence on the diversity of the grassland biota. However, the supportive effect of milkweed on a few generalist species homogenises the communities. The rate of invasion might increase with increasing fragmentation, therefore we recommend eliminating invasive plants from small habitat fragments to preserve the native biota. Focusing also on generalist species and revealing the indirect effects of invasions are essential for understanding the invasion mechanisms and would support restoration efforts.

## 1. Introduction

Invasive plants are established in nearly all types of terrestrial habitats (Simberloff et al., 2013) and even a single invasive plant species may have a fundamental impact on an ecosystem (Chapin III et al., 2000). They may form dense stands and impede native plant species by altering nutrient and water availability (Callaway and Aschehoug, 2000), and change habitat complexity (Pearson, 2009). Plant invasions can change vegetation, bare ground cover, and average vegetation height (Litt et al., 2014). In addition, invaded areas may differ in soil properties and microclimate compared to natural areas (Wolkovich et al., 2009). Invasive plant species are generally larger and grow faster than native species (van Kleunen et al., 2010). The large biomass and the rapid growth of invasive plants increase the evapotranspiration rate and, therefore, decrease soil moisture (Wolf et al., 2004). Invasive plants may change the rate of atmospheric N-fixation (Castro-Díez et al., 2014), increase shade and reduce temperatures, thereby altering native seed germination (McKinney and Goodell, 2010).

Besides biological invasions, land-use change and the associated loss and fragmentation of the remaining natural habitats are also among the most important processes resulting in biodiversity decline. The area of our focal ecosystem, namely natural grasslands, has declined considerably throughout the world, particularly in Europe, since the mid-20th century (Foley et al., 2011). The spatial distribution of organisms in fragmented landscapes is influenced by numerous local (e.g., biotic invasion of a habitat) and landscape-scale factors (e.g., fragment size) and presumably also by their complex interactions (Turner et al., 2005). Therefore, simultaneous studies of fragmentation and invasion would reveal novel information on their interacting effects and could aid effective nature conservation actions (Mazor et al., 2018).

Changes in habitat structure, soil and microclimate conditions induced by invasion and/or fragmentation alter habitat quality for the native flora, and through bottom-up mechanisms, higher trophic levels, and modify biotic interactions (van Hengstum et al., 2014; Pehle and Schirmel, 2015). Such changes may profoundly impact on arthropods, which play an important role in nearly all ecosystems. Arthropods are among the main primer consumers, predators and have a crucial role in pollination. Their relatively high species richness makes arthropods suitable model organisms to study the effects of plant invasion and habitat fragmentation (Schowalter, 2022). Generally, plant invasion and fragmentation negatively affect arthropod abundance and diversity (Lindenmayer and Fischer, 2006; Jeschke and Heger, 2018). However, the ecological effects of both processes can vary, even having a positive impact in some cases (Litt et al., 2014; van Hengstum et al., 2014; Gallé et al., 2022c). Furthermore, fragmentation may have interacting effects (either positive or negative) with biological invasion and other components of global environmental change (Bestion et al., 2019).

Our study focused on the direct and indirect effects of habitat fragmentation and plant invasion on the native vegetation and the arthropod fauna in the grassland component of Hungarian forest-steppe fragments. Natural forest-steppe are a mosaic of grasslands and forests in the transition of the temperate forest and steppe biomes (Erdős et al., 2018). The different habitat conditions of the two components result in structurally diverse vegetation with a high species richness of plants and

arthropods (Gallé et al., 2022b) and are recognised as important biodiversity hotspots (Dengler et al., 2014). During the past centuries, the majority of natural mosaic of forest-steppes was transformed into forest plantations of exotic species and arable fields, resulting in a fragmented landscape structure in Central-Europe (Bíró et al., 2013). Besides habitat quality, fragment size and landscape-scale parameters are important determinants of the forest-steppe biota (Gallé et al., 2022a, 2022b). The main elements of the current landscape matrix, i.e. plantation forests and arable fields, are regularly disturbed by forestry management and agriculture, enhancing their invasibility by the North American common milkweed (*Asclepias syriaca*) (Szilassi et al., 2019). Therefore, the remaining relatively small forest-steppe fragments face a high invasive propagule pressure from the surrounding disturbed habitats (Chytrý et al., 2008).

Milkweed causes serious conservation problems in Central Europe by invading large natural, semi-natural areas (e.g. Botta-Dukát and Balogh, 2008). Milkweed is a tall and fast-growing plant with rapid clonal spread (Kelemen et al., 2016). Beekeepers introduced it to Europe in the 17th century (Bukovinszky et al., 2014) and it has become one of the most abundant invasive plants in Central European lowlands (Sztár et al., 2018). It persists in dense populations and forms a novel ecosystem (Bakacsy and Bagi, 2020; Csécséris et al., 2011). However, its adverse effects are not always straightforward. It seems to have a minor impact on plant species richness per se, however it changes community composition by having a negative effect on grassland plant species (Kelemen et al., 2016). Milkweed invasion affects arthropods in various ways, and this effect is not necessarily negative for all arthropods. For example, dry milkweed stems may serve as nesting sites for certain ant species, altering abundance and community structure (Somogyi et al., 2017). Milkweed invasion may not change pollinator species richness; however, it offers a dense nectar resource for a set of species. Therefore, it may increase the abundance of pollinators (Szigeti et al., 2020). Milkweed also affects the community composition of spiders (Gallé et al., 2015). Ingle et al. (2019) found a negative effect of milkweed on the functional diversity of spiders in plantation forests and no evidence of the impact of milkweed on species richness and abundance. The mechanistic explanation of the above phenomena remains unclear.

Here, we aimed to further our mechanistic understanding of the combined effects of milkweed invasion and habitat fragmentation on native biodiversity. We focused on organisms with different ecological roles (1) plants as primary producers, (2) bees and hoverflies as pollinators, (3) herbivory true bugs, and (4) the predatory group of spiders. We underpinned our study with a conceptual model of the potential relationships between habitat fragment size, milkweed invasion, physical characteristics (soil and microclimate attributes), vegetation properties and species richness of arthropods (Fig. 1). We hypothesised that milkweed invasion positively affects arthropod species richness, abundance and generalist arthropods by modifying habitat structure, providing more web-attaching points for spiders, and offering supplementary food for pollinators and herbivores. Furthermore, milkweed invasion indirectly affects diversity and abundance via altering physical habitat parameters by creating a shaded microhabitat with lower temperature extremities.

## 2. Materials and methods

### 2.1. Study sites and sampling design

We carried out our study in the southern part of the Great Hungarian Plain. This region has a continental climate with a Mediterranean influence. The mean annual temperature is 11 °C, and the mean annual precipitation is 550–600 mm. The natural vegetation is forest-steppe formed on coarse-grained calcareous sand. Forest-steppes are composed of relatively small deciduous forests and grassland patches, resulting in a structurally and microclimatically fine-scale mosaic ecosystem (Erdős et al., 2018). Common woody species in the natural forests include *Populus alba* and *Crataegus monogyna*, while the steppe grasslands are dominated by perennial grasses, such as *Festuca vaginata* and *Stipa pennata* (Gallé et al., 2022a). In our study region, relatively small forest-steppe fragments remained in a matrix of forest plantation monocultures composed mainly of *Pinus sylvestris* and *P. nigra*, which are not native to the region (Gallé et al., 2022b). Large areas of the study region was used as pastures until the end of the 18th century. Significant afforestation started in the 19th century and was completed in the 20th century (Molnár et al., 2012). Parallel with the above land-use change, *A. syriaca* invaded the degraded habitats and spread to the natural and semi-natural habitats (Follak et al., 2021).

We selected 30 forest-steppe fragments based on the ecosystem map of Hungary (Tanács et al., 2021) and measured their size using Quantum GIS 3.6.1 software (Quantum GIS Development Team, 2019) and satellite images. Fragments were located around four villages (Bócsa, Pirtó, Soltvadkert-Selymes and Kéleshalom, Fig. 2). Fragment size ranged between 0.20 and 8.71 ha ( $2.47 \pm 0.38$ , mean  $\pm$  SEM). The proportion of woody vegetation was similar across fragments (i.e. 10–30 %). We exclusively sampled the grassland component of the fragments. The grassland of every forest-steppe fragment was invaded by milkweed in an at least  $25 \times 25$  m area, and all forest-steppe fragments had at least a  $25 \times 25$  m area without milkweed stems.

We established two  $5 \times 5$  m sampling sites in each of the grasslands: (1) invaded sites:  $8.57 \pm 0.32$  milkweed stems per  $m^2$  (milkweed percentage cover:  $18.04 \pm 1.05$ ) and (2) control sites: without milkweed. We selected the non-invaded control sites in a close vicinity of the invaded sites with habitat characteristics matching as closely as possible to reduce the a priori differences in invaded and control sites. Both

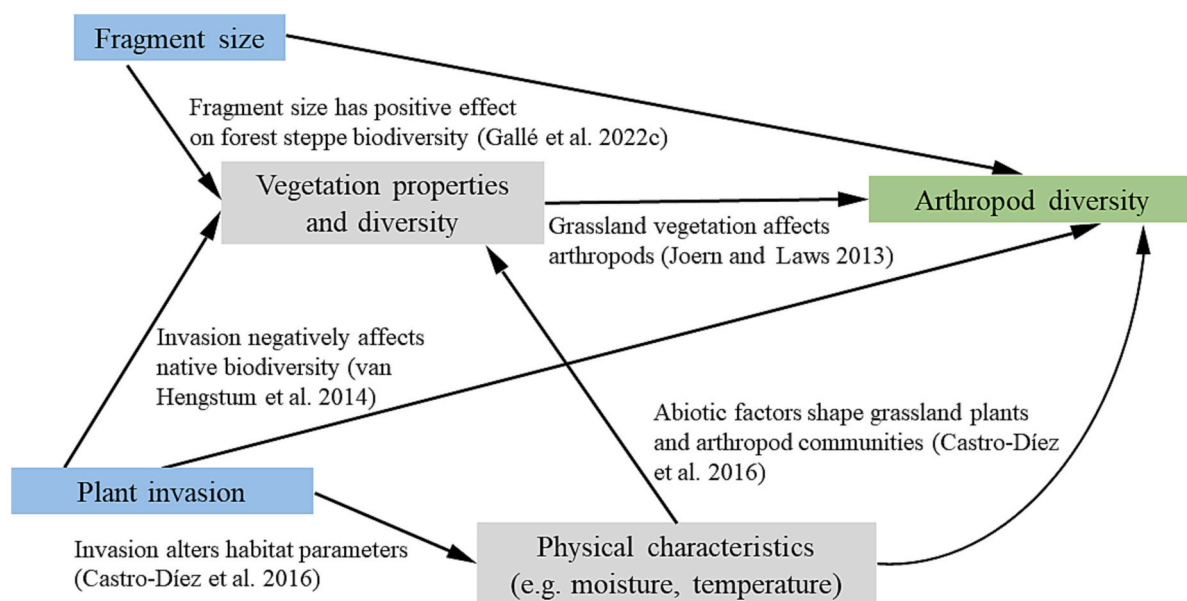
invaded and control sites were in the central part of the fragment at least 20 m from the edge of the fragments.

In each sampling site, we measured soil volumetric moisture content in the upper 20 cm at 10 random points in each invaded and control site in four occasions in late June and early July 2021, with no rainfall in the preceding three days with a Field Scout TDR 350 soil moisture meter (resolution: 0.1 V/V% of water). We obtained 2400 soil moisture data values (30 forest-steppe fragments  $\times$  2 sampling sites  $\times$  10 measurements  $\times$  4 temporal replicates), and averaged the data per site. We assessed the air temperature using data loggers (Optin ADL TH3–32) by installing one logger in the centre of each site and recorded microclimatic data every 20 min (60 data loggers) for six days between 6th and 12th July 2021. We averaged temperature data per site.

We recorded all vascular plant species in each of the  $5 \times 5$  m sampling sites and estimated their percentage cover visually (ranging between 0.1 and 100 %) in June 2021 (30 forest-steppe fragments  $\times$  2 sites = 60 plots). We summarised the coverage of insect pollinated plants to assess food resources for pollinators using literature data (Klotz et al., 2002). We assessed the vegetation structure in four  $2 \times 2$  m plots (30 forest-steppe fragments  $\times$  2 sites  $\times$  4 plots = 240 plots). We recorded the percentage cover of bare ground, vegetation cover at ground level, 10 cm and 40 cm above the ground and the average height of the vegetation. We averaged the data within each sampling site resulting in 60 statistical samples (Fig. 2).

We used pitfall traps to collect ground-dwelling arthropods (spiders and true bugs). We employed four traps in each sampling site (30 forest-steppe fragments  $\times$  2 sites  $\times$  4 traps = 240 traps). Traps were placed in the four corners of the sampling sites in a quadrat ( $5 \times 5$  m). Traps were 500-ml white plastic cups, 8.5 cm in diameter. We fitted the traps with transparent plastic funnels to reduce vertebrate bycatches and increase trapping efficiency (Császár et al., 2018). We filled them with 50 % propylene-glycol and water solution containing a few drops of detergent to preserve the sample. We placed a plastic roof above each trap to prevent the dilution of the preservative. Traps were open for 18 days between 9th and 27th July 2021. We pooled the species of pitfall traps within each sampling site resulting in 60 statistical samples (Fig. 2).

Finally, we surveyed the pollinators (bees, butterflies, flower-visiting wasps, flies) using the transect walk method. A pair of observers walked along a 50 m-long zig-zag transect for 15 min at each site and recorded all insects actively pollinating the flowers. Transects extended a few



**Fig. 1.** Conceptual path model for the factors influencing native biodiversity under plant invasion. Exogenous variables are in blue boxes, grey boxes represent habitat characteristics, and diversity is in green box.

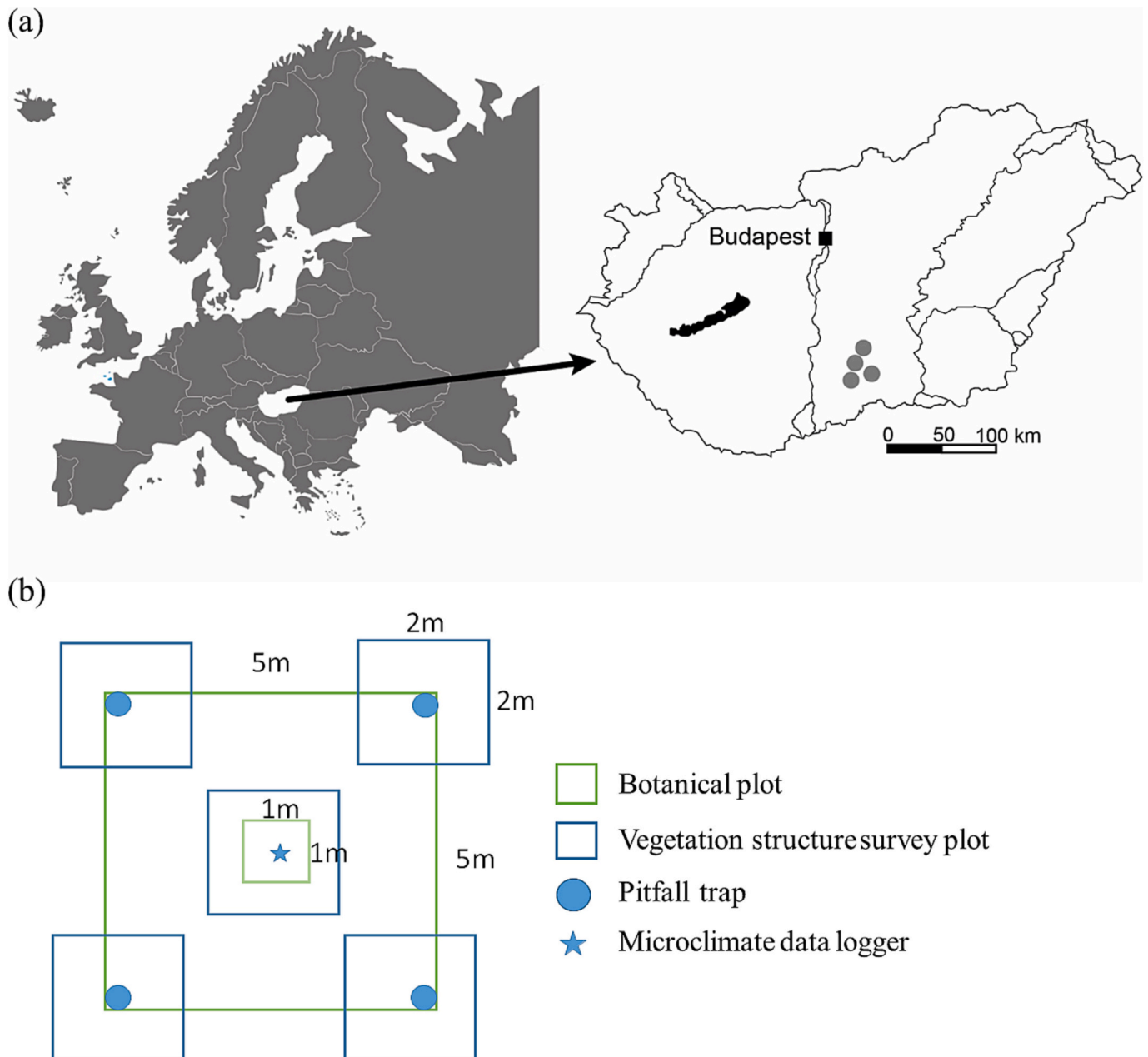


Fig. 2. Study region and sampling design. (a) Location sampling sites (b) arrangement of sampling units.

meters beyond our  $5 \times 5$  m sampling sites. Still, the surveyed area was the same microhabitat. We collected all flower-visiting insects we could not identify in the field and preserved them in 70 % ethanol for later identification. Transect counts were performed between 9:30 a.m. and 6:00 p.m. under suitable weather conditions (calm and sunny weather with a breeze or transient clouds at most). We surveyed pollinators during the peak flowering of *A. syriaca* (28th June–2nd July 2021). Szigeti et al. (2020) found the highest activity of pollinators and the strongest effect of milkweed in this period.

We assigned all recorded plant and arthropod species according to their habitat preference: (1) grassland specialist species (preference for natural, semi-natural open habitats) and (2) non-grassland plants (generalists and species with a preference for forest habitats), according to literature data (Appendix A).

## 2.2. Data analyses

Since the structural parameters of the vegetation were highly correlated, we performed a PCA analysis. We used the values of the first axis as a structural measure of vegetation (hereafter vegetation structure). Vegetation structure was positively correlated with vegetation cover at ground level (Pearson's  $r = 0.897$ ,  $p < 0.001$ ), 10 cm ( $r = 0.927$ ,  $p < 0.001$ ) and 40 cm ( $r = 0.812$ ,  $p < 0.001$ ), and with vegetation height ( $r = 0.564$ ,  $p < 0.001$ ), whereas the correlation was negative with the bare ground ( $r = -0.598$ ,  $p < 0.001$ ). We ranged soil moisture, air temperature, the log-transformed fragment size and vegetation structure between 0 and 1 to account for the different scales of the variables.

We performed a path analysis to evaluate the relationship between fragment size, presence of milkweed (exogeneous variables), temperature, soil moisture, vegetation structure, species richness of plants, species richness and abundance of pollinators (hoverflies and wild bees), true bugs and spiders (endogeneous variables) using the R package



“piecewiseSEM,” (Lefcheck, 2016). More specifically, we applied a piecewise structural equation modelling approach that makes it possible to identify the indirect pathways. We used Poisson and Gaussian error terms and included random effects. We tested the hypotheses that fragment size and milkweed presence directly impact plant and arthropod species richness and abundance. Milkweed also affect pollinators, true bugs and spiders indirectly by altering air temperature, soil moisture and vegetation properties (structure and species richness).

First, we constructed a model for the species richness of plants and all three invertebrate groups (Appendix B). We tested the effect of fragment size, presence of milkweed and their interaction on the species richness of plants and arthropods. We also included the indirect effect of milkweed on plants and arthropods via habitat parameters, soil moisture, mean temperature and vegetation structure. Furthermore, we also tested the impact of plant species richness on true bugs, vegetation structure on spiders and floral resources on pollinators. We always had “village” and “fragment identity” as nested random variables in our models to account for the potential spatial autocorrelation. Then we used a manual backward selection procedure based on Akaike’s information criterion (AIC) until we reached the best model (i.e., the model with the lowest AIC value, Lin et al., 2017). We ran the same model for grassland species and habitat generalists separately. Lastly, we ran a similar model for abundance data. In this model, we used quasipoisson error term as we detected overdispersion of abundance data.

### 3. Results

We recorded 114 plant species and 2538 (1748 excluding honeybees) specimens of 107 pollinator species. Furthermore, we collected 2812 true bugs of 74 species and 1272 adult spiders of 66 species (Appendix A). Soil moisture and air temperature were lower in invaded than in control sites. We found higher flower abundance in invaded than in control sites. Plant and arthropod species richness increased with milkweed presence (Appendix C).

We discriminated the direct and indirect causal effects of milkweed invasion and fragment size on physical habitat properties and the species richness of plants and arthropods (Fig. 3). After the backward selection procedure, our final models were statistically supported (total species richness: Fisher’s C = 70.47, df = 64,  $p = 0.27$ ; grassland species: Fisher’s C = 41.04, df = 44,  $p = 0.59$ ; habitat generalists: Fisher’s C = 55.71, df = 54,  $p = 0.41$ ).

Invasion supported the plant species richness and the amount of flowers, at the same time it decreased soil temperature and moisture. Nevertheless, plant species richness increased the complexity of the vegetation and the amount of flowers, positively affecting true bug and

pollinator richness, respectively. Spiders were positively affected by vegetation structure and soil moisture. Furthermore, mean temperature and forest-steppe fragment size had a negative effect on the species richness of spiders (Fig. 3). Fragment size had a strong negative impact on the species richness of spiders in the control sites, however, fragment size had no impact in invaded sites (separately plotted in Fig. 4a).

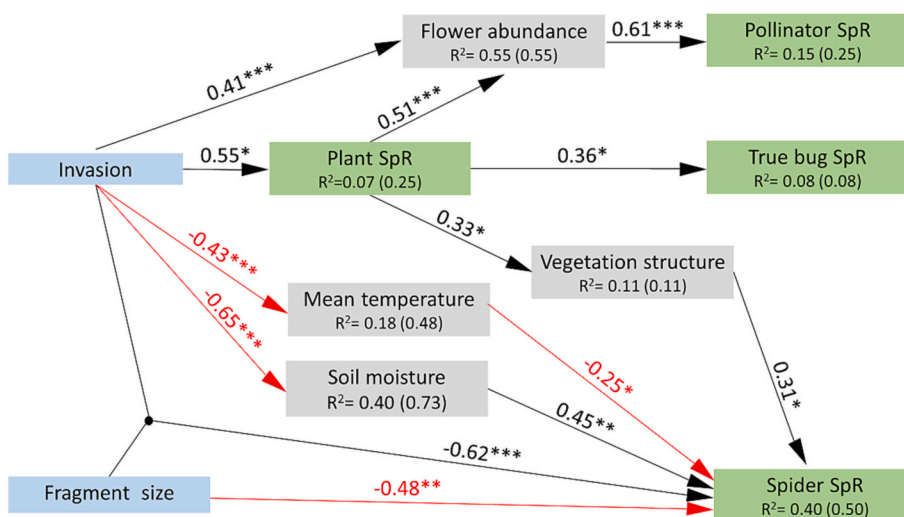
Grassland species richness was less affected by our focal parameters than total species richness. The mean temperature negatively affected grassland spiders, which is an indirect effect of invasion (Fig. 5), whereas fragment size positively affected grassland spider species richness in invaded areas. However, this effect was not detectable on control sites (Fig. 4b).

Habitat generalists were strongly affected by microhabitat characteristics. Invasion supported generalist plants, true bugs, spiders and the amount of flowers. Generalist plants positively affected generalist true bugs, flower abundance, and vegetation structure. Flower abundance positively, mean temperature negatively affected generalist pollinators. Generalist spiders were further supported by vegetation structure (Fig. 6).

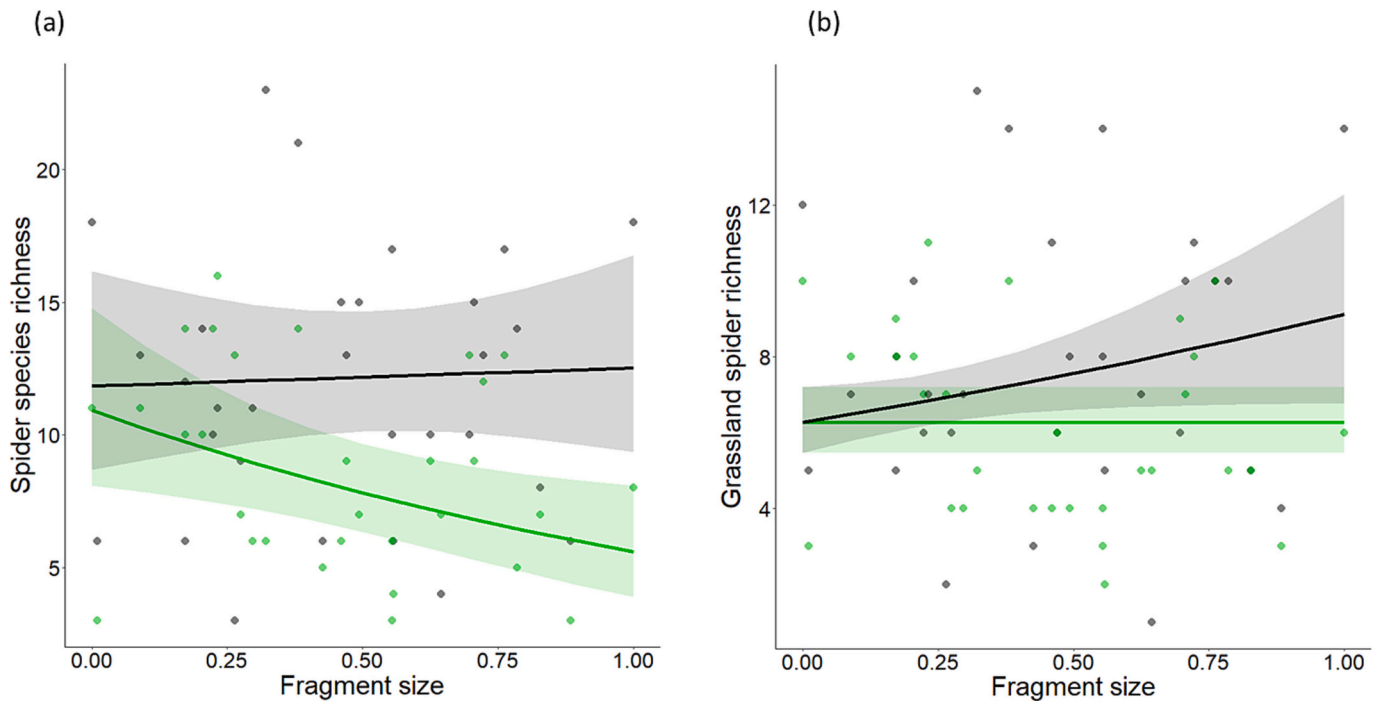
Abundances of arthropods were affected by both microhabitat characteristics and fragment size. Invasion and plant species richness supported flower abundance and indirectly pollinator abundance (Fig. 7a). The effect of fragment size on pollinator abundance was modified by the presence of the invasive plants, we found positive fragment size effect for non-invaded sites; however, this effect was negative for invaded sites (Fig. 7b). Invasion negatively affected mean temperature and true bug abundances in uninvaded sites, however, this effect was positive for invaded sites (Fig. 7c). Plant species richness had a positive effect on vegetation structure, furthermore, mean temperature negatively affected spider abundances.

### 4. Discussion

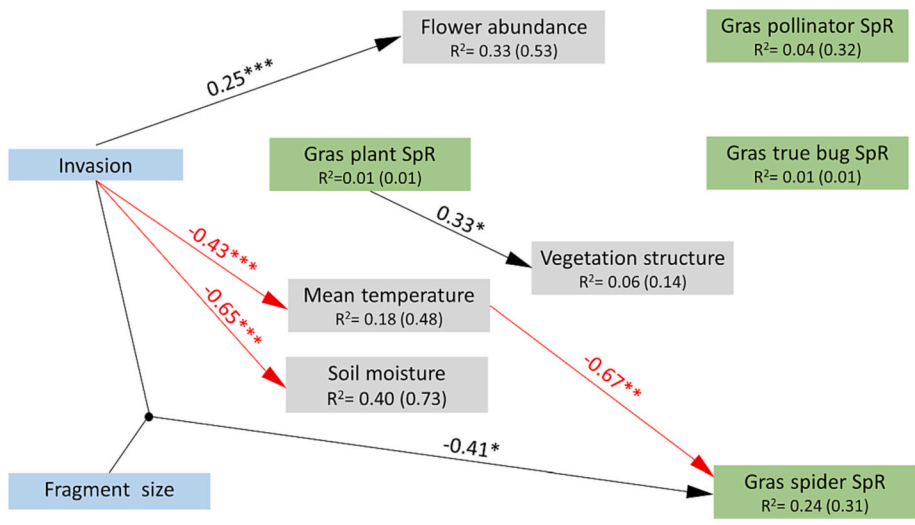
We found that plant invasion was a more important determinant of species diversity than fragmentation. The presence of the invasive plant species had a positive direct effect on plant species richness. In contrast, the effects were primarily indirect on the species richness of pollinator, herbivore, and predator arthropods through the alteration of physical habitat characteristics, i.e., soil moisture, temperature, and vegetation properties. We also found that the size of habitat fragment modified the effect of invasion on our predatory group, namely spiders. In general, we found stronger direct and indirect impacts of invasion on habitat generalist species than on grassland species.



**Fig. 3.** Path analysis for total arthropod and plant species richness. The final model includes all pathways after model simplification based on AIC. Exogenous variables are in blue boxes, grey boxes represent habitat characteristics, and diversity measures are in green boxes (SpR: species richness). Marginal (conditional) R-squared values for individual models are given with response variables. Black arrows show positive effects, and red arrows show negative effects. Dot indicates interaction effect. Values on arrows are estimated regression coefficients. Significance levels: \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .



**Fig. 4.** Interacting effect of milkweed invasion and fragment size on (a) spider species richness and (b) species richness of grassland spiders. Ranged values of log-transformed fragment size are plotted. Black dots show invaded sites and green dots are non-invaded sites. We indicated model fit and 95 % confidence intervals in black for invaded sites and green for non-invaded sites.



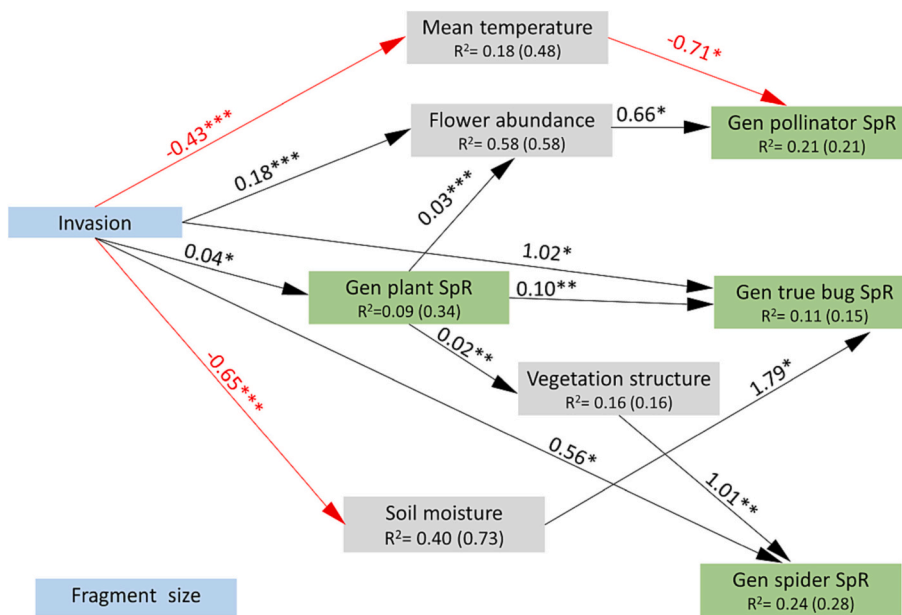
**Fig. 5.** Path-analysis for grassland specialist arthropod and plant species richness. Exogenous variables are in blue boxes, grey boxes represent habitat characteristics, and diversity measures are in green boxes (Gras: grassland; SpR: species richness). Marginal (conditional) R-squared values for individual models are given with response variables. Black arrows show positive effects, red arrows negative effects. Dot indicates an interaction effect. Only significant effects are plotted. Values on arrows are estimated regression coefficients. Significance levels: \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

**4.1. Milkweed modifies soil moisture and temperature**

Milkweed reduced available soil moisture below its canopy more than native vegetation, presumably due to high transpiration rates of milkweed and the structured and dense vegetation at the invaded sites (Te Beest et al., 2015). This is in accordance with observations that species efficiently utilising soil moisture are particularly successful invaders in dry areas (Kelemen et al., 2016). We found the negative impact of milkweed on soil moisture under shallow soil moisture conditions, although the average water content of the soil was below 1 % even in the control sites (Appendix C). Presumably, the desiccating effect of milkweed is pronounced during wet springs, a few months before our survey took place.

The temperature was lower in invaded sites than in non-invaded

areas. The broad leaves of the tall milkweed stems cast shade on the soil surface, resulting in a lower daily maximum temperature of invaded areas than intact open sandy grasslands. The leaf litter of milkweed may further insulate the soil surface and moderate day temperatures (Wolkovich et al., 2009). Milkweed invasion had an indirect effect on spiders. The invasive plant created a drier and cooler microhabitat than non-invaded microhabitats, and these microclimatic differences affected spider species richness. Generalist pollinators and true-bugs were more sensitive to changes in microclimate than grassland species. The extreme (warm and dry) microclimate of sandy grasslands is an important environmental filter for the biota (Gallé et al., 2022b). Grassland arthropods are adapted to this hot and dry microclimate. Therefore, they are not sensitive to moderate changes in temperature and moisture conditions. In contrast, generalist species were supported by the



**Fig. 6.** Path-analysis for generalist arthropod and generalist plant species richness. Exogenous variables are in blue boxes, grey boxes represent habitat characteristics, and diversity measures are in green boxes (Gen: generalist; SpR: species richness). Marginal and (conditional) R-squared values for individual models are given with response variables. Black arrows show positive effects, red arrows negative effects. Dot indicates an interaction effect. Only significant effects are plotted. Values on arrows are estimated regression coefficients. Significance levels: \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ .

moderate microclimate under milkweed stems.

#### 4.2. Invasion supports plant diversity and changes native vegetation

The invasion had a positive effect on the species richness of plants. In contrast, the majority of Central European invaders negatively affect the species richness of the native vegetation (Hejda et al., 2009; Bradley et al., 2019). Likely, invasive plants taller than members of the invaded plant communities may reach a high cover and substantially affect the resident plants (Brabec and Pysek, 2000). The lack of negative impact of milkweed can be attributed to several factors. An invasive plant's effect correlates with its dominance in the community (Hejda et al., 2009). This plant has an extensive rhizome system and is tall and fast-growing, therefore, it might avoid competition with native species. Milkweed did not develop homogeneous stands in our studied grassland fragments, presumably because of the low moisture availability of our sites. However, milkweed could provide favourable conditions for generalist plant species. Milkweed overshadows ground through its canopy, and it may mitigate unfavourable abiotic conditions for the germination of generalist plant species (Sztár et al., 2018).

The milkweed did not affect all plant species equally. We identified a positive effect on generalist plants; however, we found no effect on grassland species. The changes in species diversity and composition of vegetation resulted in a higher flower abundance and a more complex vegetation structure in invaded sites than in non-invaded areas. Kelemen et al. (2016) showed that milkweed invasion favoured plant species with larger specific leaf areas (SLA) and seed mass. Species with high SLA values are characterised by high efficiency of photosynthesis, fast growth and higher transpiration rates, presumably contributing to the decline soil moisture. In contrast, low values of SLA is associated with dry and nutrient-poor conditions (Bergholz et al., 2021), indicating stress-tolerance of dry grassland species. Large-seeded plants can be primarily generalists (Denelle et al., 2020), they are less dependent on habitat properties in their early life stage, and they can germinate under shaded conditions (Valkó et al., 2022), supporting the wide habitat preference.

#### 4.3. Indirect effects of invasion on arthropods

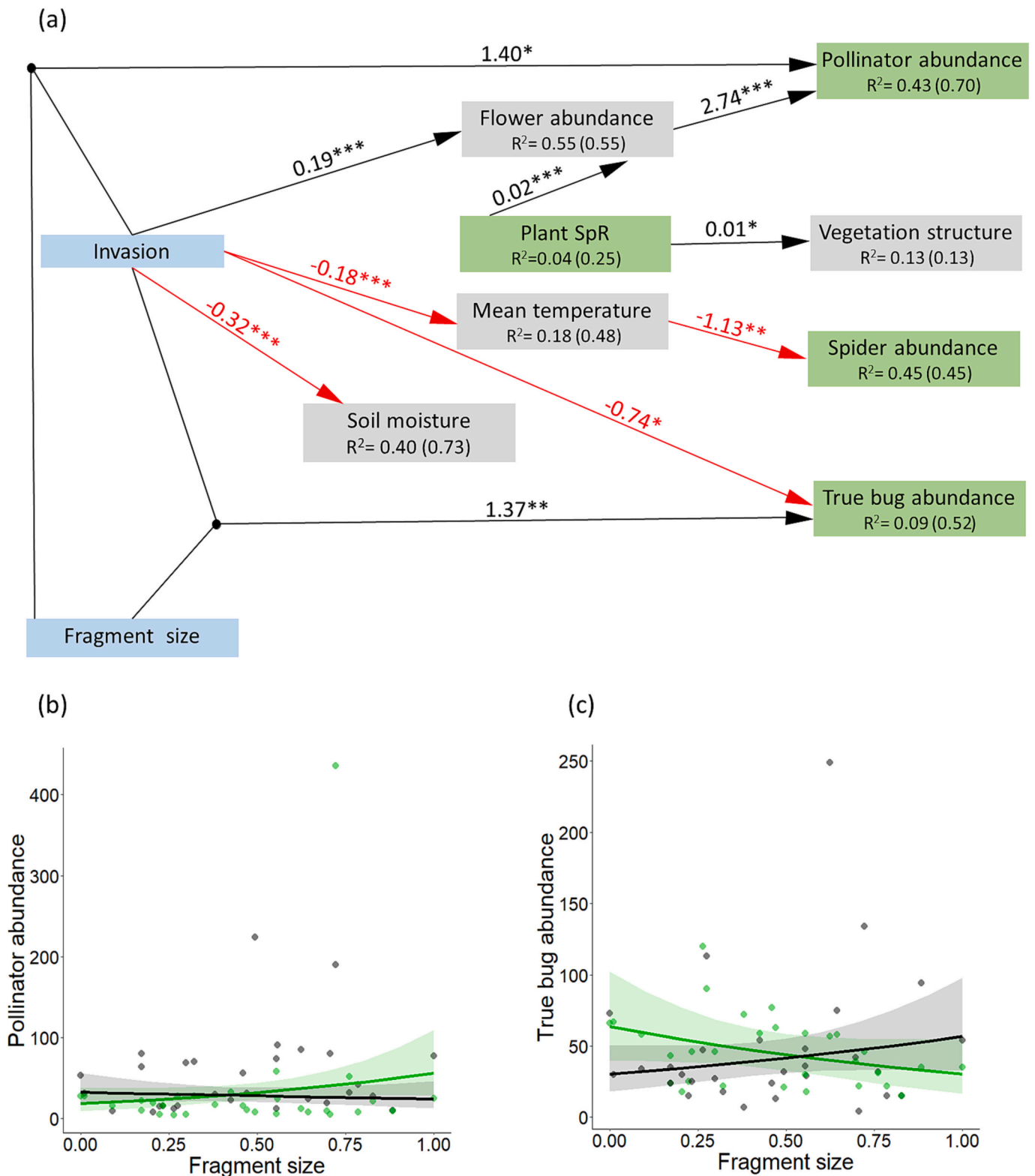
The relationship between the abundance of invasive species and the community response when the invasive species is at a lower trophic level

is mixed. The effect may cascade up to higher trophic levels. In general, invasive plants tend to remove resources or may replace food resources for native consumers rather than produce extra resources (Vilà et al., 2011; Bradley et al., 2019). Specialists rarely switch from natives to exotics with no close taxonomic relatives in the recipient community (Maron and Vila, 2007). We also found indirect effects of invasion in all three invertebrate groups. However, the effects were mainly positive, presumably due to the large milkweed biomass. The invasion resulted in changes in native vegetation by supporting habitat generalists, affecting herbivores and pollinators indirectly. Furthermore, it altered the vegetation structure and the milder microclimate, directly affecting habitat quality for predators (Pearson, 2009).

Pollinators are strongly connected to the nectar and pollen resources of flowers. Although milkweed flowers offer a large quantity of nectar, only a few common pollinator species, such as honeybee and bumblebees, may utilise this nectar due to the special structure of the flower (Szigeti et al., 2020). Our study did not show any significant direct effect of invasion on the species richness of pollinators. Although the response of different pollinator groups to milkweed invasion may differ (Kovács-Hostyánszki et al., 2022), pollinator diversity was clearly driven by the availability and diversity of native flowering resources.

The species richness of true bugs was significantly affected by the diversity of native vegetation. The majority of collected true bugs were grass-feeders (Torma et al., 2019). These species may benefit more from the presence of different generalist plant species rather than the larger plant biomass of invaded areas. In accordance with predictions of the enemy release hypothesis (Keane and Crawley, 2002), we found only a few mainly generalist true bug species that feed on milkweed. Therefore, similarly to pollinators, the invasion had mainly indirect effects on true bugs, as most species did not consume the milkweed resources directly.

Generally, the climate is among the prominent factors influencing arthropod species richness. For instance, Finch et al. (2008) identified a positive correlation between spider species richness with July temperature. However, we found a negative effect of mean temperature on spider species richness and generalist pollinators. The highest soil surface temperatures in our study ( $53.7 \text{ }^\circ\text{C} \pm 0.04$ , mean  $\pm$  SEM) were presumably well above the thermal maximum of many spider and pollinator species (not exceeding  $45 \text{ }^\circ\text{C}$  for spiders and  $50 \text{ }^\circ\text{C}$  for the majority of pollinators; Humphreys, 1974, Stork, 2012, Burdine and McCluney, 2019). Therefore, lower temperatures allow a higher locomotory activity of ground-dwelling spiders and flower-visiting flying



**Fig. 7.** Path analysis for arthropod and plant abundance. (a) the final model includes all pathways after model simplification based on AIC. Exogenous variables are in blue boxes, grey boxes represent habitat characteristics, and diversity measures are in green boxes (SpR: species richness). Marginal (conditional) R-squared values for individual models are given with response variables. Black arrows show positive effects, and red arrows show negative effects. Dot indicates interaction effect. Values on arrows are estimated regression coefficients. Significance levels: \*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ; (b) Interacting effect of milkweed invasion and fragment size on pollinator abundance; Ranged values of log-transformed fragment size are plotted. Black dots show invaded sites and green dots are non-invaded sites. We indicated model fit and 95 % confidence intervals in black for invaded sites and green for non-invaded sites. (c) Interacting effect of milkweed invasion and fragment size on true abundance. Variables displayed as above.



insects. Spiders also respond to changes in soil moisture (Perner and Malt, 2003). The moisture conditions of a habitat is a key driver of the distribution pattern of Central European spider species (Entling et al., 2007). The soil moisture content of our sampling sites did not exceed 1 % (Appendix C). Therefore, our focal grassland spiders are adapted to the moisture gradient's dry end. Even a small amount of available water might reduce the extreme character of arid habitats, supporting the colonisation of several species. Our results suggest that environmental filtering is a significant driver of arthropod species composition and richness.

Plant species richness affected spiders via the alteration of vegetation structure, and this effect was mainly driven by generalist species. The three-dimensional structure of the vegetation creates the physical habitat for arthropods (Pearson, 2009). Changes in vegetation and habitat architecture can result in bottom-up effects of invasive plants on higher trophic levels, such as spiders (Pehle and Schirmel, 2015). The influence of vegetation structure on spiders was previously documented in sandy grasslands (e.g. Carvalho et al., 2011). Structurally complex vegetation supports mainly generalist spider species by offering web attachment points for web builders and higher microhabitat heterogeneity for ground-dwelling species.

#### 4.4. Moderate effect of fragmentation

We found that fragment size modulated the effect of invasion on the species richness of spiders and the abundance of true bugs and pollinators. We found a negative effect of fragment size on the spider species richness on non-invaded sites and no effect on invaded sites. The study region comprises a mosaic of forest plantations and forest-steppe habitats, and forest plantations support many generalist and vegetation-dweller species that may colonise small fragments (Gallé et al., 2018, 2022c). The structurally complex milkweed microhabitats might enable many vegetation-dweller species to persist in larger habitats. However, they cannot colonise the non-invaded areas of large fragments. We found a similar pattern for true-bug abundances. Presumably, many true bug species with generalist feeding strategies persist in invaded areas of large fragments. Still, their abundance decreases in the absence of milkweed resulting in a decrease in total true bug abundances with increasing fragment size.

We found the opposite pattern for pollinator abundances, a positive effect of fragment size on non-invaded sites and a weak negative effect on invaded sites. Pollinators were the most mobile organisms in the present study. They forage on larger areas than true bugs and spiders and presumably use the whole fragment. Therefore pollinators were affected by fragment size; however, the high flower abundance of invaded sites might override this effect.

Generally, specialist species are more prone to fragmentation effects than generalists (Lindenmayer and Fischer, 2006). We also found that generalist spider species were less susceptible to fragment size than grassland species. In our study landscape of relatively well-connected habitat fragments, the effect of invasion was stronger than fragmentation effects.

#### 4.5. Implications for management

Fragmentation is considered as the driver of plant invasions. For example, habitat fragmentation increases the density of edges, which may facilitate the establishment of invasive plants (Didham et al., 2007). After the establishment and spread of milkweed in the last centuries, this invasive plant species has extant populations in the small forest steppe fragments of our study region. However, the fragments still preserve a large part of the native biota (Gallé et al., 2022b, 2022c), therefore they have a disproportional high conservation value despite their small size. The native biota seems to coexist with milkweed present in the study area for several decades, however, with increasing fragmentation, the rate of invasion might also increase, and the mostly indirect effects of

milkweed might escalate. This process will result in the alteration of physical habitat characteristics and a spread of generalist species, which in turn homogenises the communities. Therefore, we recommend focusing active restoration efforts on eliminating invasive plants from small habitat fragments to preserve the native biota and to maintain the high beta diversity of the landscapes.

## 5. Conclusions

Results of the studies addressing the effect of milkweed on native species of dry habitats are mixed. Besides some inevitably negative effects, the invasion of milkweed might even support a part of the native biota (Szítár et al., 2018). We found more substantial and generally positive effects on generalist species than on grassland specialist plants and arthropods. The supportive effect of milkweed on a few generalist species homogenises the communities. Therefore, further research should also focus on generalist species besides habitat specialists. Milkweed invasion might alter species interactions such as competition, pollination, and predation, and thereby affect the ecosystem functioning. The fast invasion process in small fragments might accelerate the ecosystem changes, therefore have a prompt effect on ecosystem functioning. Therefore, we emphasise that revealing the indirect effects of invasion and fragmentation is essential for understanding the mechanism of the effect of invasion and would support active restoration efforts.

### CRedit authorship contribution statement

**Róbert Gallé:** Conceptualization, Methodology, Data curation, Supervision, Formal analysis, Writing – original draft. **Csaba Tölgyesi:** Conceptualization, Resources, Writing – review & editing. **Ágota Réka Szabó:** Investigation, Writing – review & editing. **Dávid Korányi:** Investigation, Methodology, Writing – review & editing. **Zoltán Bátori:** Investigation, Supervision, Writing – review & editing. **Alida Hábczyus:** Investigation, Writing – review & editing. **Edina Török:** Investigation, Writing – review & editing. **Kitti Révész:** Investigation, Writing – review & editing. **Attila Torma:** Investigation, Writing – review & editing. **Nikolett Gallé-Szpisjak:** Investigation, Writing – review & editing. **Tamás Lakatos:** Investigation, Writing – review & editing. **Péter Batáry:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing.

### Declaration of competing interest

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

### Data availability

Data will be made available on request.

### Acknowledgement

This research was supported by the National Research, Development and Innovation Office within the framework of National Laboratory for Health Security (RRF 2.3.1-21-2021-00006) and NKFI-FK-131379. RG was supported by the Hungarian National Research, Development and Innovation Office (NKFI-FK-142926). The contribution of ZB was supported by the NKFI FK 142428 grant, by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences, and by the ÚNKP-22-5-SZTE-538 New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166199>.

## References

- Bakacsy, L., Bagi, I., 2020. Survival and regeneration ability of clonal common milkweed (*Asclepias syriaca* L.) after a single herbicide treatment in natural open sand grasslands. *Sci. Rep.-UK* 10, 1–10. <https://doi.org/10.1038/s41598-020-71202-8>.
- Bergholz, K., Kober, K., Jeltsch, F., Schmidt, K., Weiss, L., 2021. Trait means or variance—what determines plant species' local and regional occurrence in fragmented dry grasslands? *Ecol. Evol.* 11, 3357–3365. <https://doi.org/10.1002/ece3.7287>.
- Bestion, E., Cote, J., Jacob, S., Winandy, L., Legrand, D., 2019. Habitat fragmentation experiments on arthropods: what to do next? *Curr. Opin. Insect Sci.* 35, 117–122. <https://doi.org/10.1016/j.cois.2019.07.011>.
- Biró, M., Czúcz, B., Horváth, F., Révész, A., Csatári, B., Molnár, Z., 2013. Drivers of grassland loss in Hungary during the post-socialist transformation (1987–1999). *Landscape Ecol.* 28, 789–803. <https://doi.org/10.1007/s10980-012-9818-0>.
- Botta-Dukát, Z., Balogh, L., 2008. *The most Important Invasive Plants in Hungary*. Institute of Ecology and Botany. Hungarian Academy of Science, New Delhi, pp. 1–255.
- Brabec, J., Pyšek, P., 2000. Establishment and survival of three invasive taxa of the genus *Reynoutria* (Polygonaceae) in Mesic mown meadows: a field experimental study. *Folia Geobot.* 35, 27–42. <https://doi.org/10.1007/BF02803085>.
- Bradley, B.A., Laginhas, B.B., Whitlock, R., Allen, J.M., Bates, A.E., Bernatchez, G., Sorte, C.J., 2019. Disentangling the abundance–impact relationship for invasive species. *Proc. Natl. Acad. Sci.* 116, 9919–9924. <https://doi.org/10.1073/pnas.1818081116>.
- Bukovinsky, T., Gols, R., Agrawal, A.A., Roge, C., Bezemer, T.M., Biere, A., Harvey, J.A., 2014. Reciprocal interactions between native and introduced populations of common milkweed, *Asclepias syriaca*, and the specialist aphid, *Aphis nerii*. *Basic Appl. Ecol.* 15, 444–452. <https://doi.org/10.1016/j.baae.2014.07.004>.
- Burdine, J.D., McCluney, K.E., 2019. Differential sensitivity of bees to urbanisation-driven changes in body temperature and water content. *Sci. Rep.-UK* 9, 1–10. <https://doi.org/10.1038/s41598-018-38338-0>.
- Callaway, R.M., Aschehoug, E.T., 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290, 521–523. <https://doi.org/10.1126/science.290.5491.521>.
- Carvalho, J.C., Cardoso, P., Crespo, L.C., Henriques, S., Carvalho, R., Gomes, P., 2011. Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. *Divers. Distrib.* 17, 225–234. <https://doi.org/10.1111/j.1472-4642.2010.00731.x>.
- Castro-Díez, P., Godoy, O., Alonso, A., Gallardo, A., Saldaña, A., 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecol. Lett.* 17, 1–12. <https://doi.org/10.1111/ele.12197>.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Díaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242. <https://doi.org/10.1038/35012241>.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., Danihelka, J., 2008. Separating habitat invisibility by alien plants from the actual level of invasion. *Ecology* 89, 1541–1553. <https://doi.org/10.1890/07-0682.1>.
- Császár, P., Torma, A., Gallé-Szpisjak, N., Tölgyesi, C., Gallé, R., 2018. Efficiency of pitfall traps with funnels and/or roofs in capturing ground-dwelling arthropods. *Eur. J. Entomol.* 115, 15–24. <https://doi.org/10.14411/eje.2018.003>.
- Csécserits, A., Czúcz, B., Halassy, M., Kröel-Dulay, G., Rédei, T., Szabó, R., Török, K., 2011. Regeneration of sandy old-fields in the forest-steppe region of Hungary. *Plant Biosyst.* 145, 715–729. <https://doi.org/10.1080/11263504.2011.601340>.
- Denelle, P., Violle, C., DivGrass Consortium, Munoz, F., 2020. Generalist plants are more competitive and more functionally similar to each other than specialist plants: insights from network analyses. *J. Biogeogr.* 47, 1922–1933.
- Dengler, J., Janisová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. *Agric. Ecosyst. Environ.* 182, 1–14. <https://doi.org/10.1016/j.agee.2013.12.015>.
- Didham, R.K., Tylianakis, J.M., Gemmill, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* 22, 489–496. <https://doi.org/10.1016/j.tree.2007.07.001>.
- Entling, W., Schmidt, M.H., Bacher, S., Brandl, R., Nentwig, W., 2007. Niche properties of central European spiders: shading, moisture and the evolution of the habitat niche. *Glob. Ecol. Biogeogr.* 16, 440–448. <https://doi.org/10.1111/j.1466-8238.2006.00305.x>.
- Erdős, L., Kröel-Dulay, G., Bátor, Z., Kovács, B., Németh, C., Kiss, P.J., Tölgyesi, C., 2018. Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. *Biol. Conserv.* 226, 72–80. <https://doi.org/10.1016/j.biocon.2018.07.029>.
- Finch, O.D., Blick, T., Schuldt, A., 2008. Macroecological patterns of spider species richness across Europe. *Biodivers. Conserv.* 17, 2849–2868. <https://doi.org/10.1007/s10531-008-9400-x>.
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Zaks, D.P., 2011. Solutions for a cultivated planet. *Nature* 478, 337–342. <https://doi.org/10.1038/nature10452>.
- Follak, S., Bakacsy, L., Essl, F., Hochfellner, L., Lapin, K., Schwarz, M., Wolkowycy, D., 2021. Monograph of invasive plants in Europe N 6: *Asclepias syriaca* L. *Bot. Lett.* 168 (3), 422–451.
- Gallé, R., Erdélyi, N., Szpisjak, N., Tölgyesi, C., Maák, I., 2015. The effect of the invasive *Asclepias syriaca* on the ground-dwelling arthropod fauna. *Biologia* 70, 104–112. <https://doi.org/10.1515/biolog-2015-0011>.
- Gallé, R., Szabó, A., Császár, P., Torma, A., 2018. Spider assemblage structure and functional diversity patterns of natural forest steppes and exotic forest plantations. *For. Ecol. Manag.* 411, 234–239. <https://doi.org/10.1016/j.foreco.2018.01.040>.
- Gallé, R., Tölgyesi, C., Császár, P., Bátor, Z., Gallé-Szpisjak, N., Kaur, H., Batáry, P., 2022a. Landscape structure is a major driver of plant and arthropod diversity in natural European forest fragments. *Ecosphere* 13, e3905. <https://doi.org/10.1002/eecs2.3905>.
- Gallé, R., Tölgyesi, C., Torma, A., Bátor, Z., Lőrinczi, G., Szilassi, P., Batáry, P., 2022b. Matrix quality and habitat type drive the diversity pattern of forest-steppe fragments. *PECON* 20, 60–68. <https://doi.org/10.1016/j.pecon.2021.11.004>.
- Gallé, R., Korányi, D., Tölgyesi, C., Lakatos, T., Marcolin, F., Török, E., Batáry, P., 2022c. Landscape-scale connectivity and fragment size determine species composition of grassland fragments. *Basic Appl. Ecol.* 65, 39–49. <https://doi.org/10.1016/j.baae.2022.10.001>.
- Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393–403. <https://doi.org/10.1111/j.1365-2745.2009.01480.x>.
- Humphreys, W.F., 1974. Behavioural thermoregulation in a wolf spider. *Nature* 251, 502–503. <https://doi.org/10.1038/251502a0>.
- Ingle, K., Gallé-Szpisjak, N., Kaur, H., Gallé, R., 2019. Forest type interacts with milkweed invasion to affect spider communities. *Insect Conserv. Divers.* 12, 321–328. <https://doi.org/10.1111/icad.12346>.
- Jeschke, J.M., Heger, T., 2018. *Invasion Biology: Hypotheses and Evidence*, Vol. 9. CAB International, Wallingford, UK.
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0).
- Kelemen, A., Valkó, O., Kröel-Dulay, G., Deák, B., Török, P., Tóth, K., Tóthmérész, B., 2016. The invasion of common milkweed (*Asclepias syriaca*) in sandy old-fields – is it a threat to the native flora? *Appl. Veg. Sci.* 19, 218–224. <https://doi.org/10.1111/avsc.12225>.
- Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. - Schriftenreihe für Vegetationskunde 38. Bundesamt für Naturschutz, Bonn.
- Kovács-Hostyánszki, A., Szigeti, V., Miholcsa, Z., Sándor, D., Soltész, Z., Török, E., Fenesi, A., 2022. Threats and benefits of invasive alien plant species on pollinators. *Basic Appl. Ecol.* 64, 89–102. <https://doi.org/10.1016/j.baae.2022.07.003>.
- Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579. <https://doi.org/10.1111/2041-210X.12512>.
- Lin, L.C., Huang, P.H., Weng, L.J., 2017. Selecting path models in SEM: a comparison of model selection criteria. *Struct. Equ. Model.* 24, 855–869. <https://doi.org/10.1080/10705511.2017.1363652>.
- Lindenmayer, D.B., Fischer, J., 2006. *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press, Washington, DC.
- Litt, A.R., Cord, E.E., Fulbright, T.E., Schuster, G.L., 2014. Effects of invasive plants on arthropods. *Conserv. Biol.* 28, 1532–1549. <https://doi.org/10.1111/cobi.12350>.
- Maron, J., Vila, M., 2007. Exotic plants in an altered enemy landscape: effects on enemy resistance. In: Kelley, J., Tilmon, J. (Eds.), *Specialisation, Speciation and Radiation - The Evolutionary Biology of Herbivorous Insects*. University of California Press, pp. 280–295.
- Mazor, T., Doropoulos, C., Schwarzmueller, F., Gladish, D.W., Kumaran, N., Merkel, K., Gagic, V., 2018. Global mismatch of policy and research on drivers of biodiversity loss. *Nat. Ecol. Evol.* 2, 1071–1074. <https://doi.org/10.1038/s41559-018-0563-x>.
- McKinney, A.M., Goodell, K., 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol. Invasions* 12, 2751–2763. <https://doi.org/10.1007/s10530-009-9680-4>.
- Molnár, Zs, Biró, M., Bartha, S., Fekete, G., 2012. Past trends, present state and future prospects of Hungarian Forest-steppes. In: Werger, M.J.A., van Staalduinen, M.A. (Eds.), *Eurasian Steppes. Ecological Problems and Livelihoods in a Changing World*. Springer, Dordrecht, Heidelberg, New York, London, pp. 209–252.
- Pearson, D.E., 2009. Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. *Oecologia* 159, 549–558. <https://doi.org/10.1007/s00442-008-1241-5>.
- Pehle, A., Schirmel, J., 2015. Moss invasion in a dune ecosystem influences ground-dwelling arthropod community structure and reduces soil biological activity. *Biol. Invasions* 17, 3467–3477. <https://doi.org/10.1007/s10530-015-0971-7>.
- Perner, J., Malt, S., 2003. Assessment of changing agricultural land use: response of vegetation, ground-dwelling spiders and beetles to the conversion of arable land into grassland. *Agric. Ecosyst. Environ.* 98, 169–181. [https://doi.org/10.1016/S0167-8809\(03\)00079-3](https://doi.org/10.1016/S0167-8809(03)00079-3).
- Quantum GIS Development Team, 2019. Quantum GIS geographic information system. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
- Schwalter, T.D., 2022. *Insect ecology: an ecosystem approach*. Academic Press 349–411.
- Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Vilà, M., 2013. Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* 28, 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>.
- Somogyi, A.Á., Lőrinczi, G., Kovács, J., Maák, I.E., 2017. Structure of ant assemblages in planted poplar (*Populus alba*) forests and the effect of the common milkweed (*Asclepias syriaca*). *Acta Zool. Acad. Sci. Hung.* 63, 443–457. <https://doi.org/10.17109/AZH.63.4.443.2017>.

- Stork, R., 2012. Intraspecific variation in the thermal biology of *Rabidosa rabida* (Araneae: Lycosidae) (Walckenaer) from the mountains of Arkansas. *Environ. Entomol.* 41, 1631–1637. <https://doi.org/10.1603/EN12016>.
- Szigeti, V., Fenesi, A., Soltész, Z., Berki, B., Kovács-Hostyánszki, A., 2020. Neutral effect of an invasive plant species with specialised flower structure on native pollinator communities. *Biol. Invasions* 22, 3017–3030. <https://doi.org/10.1007/s10530-020-02305-6>.
- Szilassi, P., Szatmári, G., Pásztor, L., Árvai, M., Szatmári, J., Szitár, K., Papp, L., 2019. Understanding the environmental background of an invasive plant species (*Asclepias syriaca*) for the future: an application of LUCAS field photographs and machine learning algorithm methods. *Plants* 8, 593. <https://doi.org/10.3390/plants8120593>.
- Szitár, K., Kröel-Dulay, G., Török, K., 2018. Invasive *Asclepias syriaca* can have facilitative effects on native grass establishment in a water-stressed ecosystem. *Appl. Veg. Sci.* 21, 607–614. <https://doi.org/10.1111/avsc.12397>.
- Tanács, E., Belényesi, M., Lehoczki, R., Pataki, R., Petrik, O., Standovár, T., Maucha, G., 2021. Compiling a high-resolution country-level ecosystem map to support environmental policy: methodological challenges and solutions from Hungary. *Geocarto Int.* 1–24. <https://doi.org/10.1080/10106049.2021.2005158>.
- Te Beest, M., Esler, K.J., Richardson, D.M., 2015. Linking functional traits to impacts of invasive plant species: a case study. *Plant Ecol.* 216, 293–305. <https://doi.org/10.1007/s11258-014-0437-5>.
- Torma, A., Császár, P., Bozsó, M., Deák, B., Valkó, O., Kiss, O., Gallé, R., 2019. Species and functional diversity of arthropod assemblages (Araneae, Carabidae, Heteroptera and Orthoptera) in grazed and mown salt grasslands. *Agric. Ecosyst. Environ.* 273, 70–79. <https://doi.org/10.1016/j.agee.2018.12.004>.
- Turner, M.G., Gardner, R.H., O'Neill, R.V., 2005. *Landscape ecology. In: Theory and Practice.* Springer, New York.
- Valkó, O., Rádai, Z., Deák, B., 2022. Hay transfer is a nature-based and sustainable solution for restoring grassland biodiversity. *J. Environ. Manag.* 311, 114816. <https://doi.org/10.1016/j.jenvman.2022.114816>.
- van Hengstum, T., Hooftman, D.A.P., Oostermeijer, G.B., van Tienderen, P.H., 2014. Impact of plant invasions on local arthropod communities: a meta-analysis. *J. Ecol.* 102, 4–11. <https://doi.org/10.1111/1365-2745.12176>.
- van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13, 235–245. <https://doi.org/10.1111/j.1461-0248.2009.01418.x>.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>.
- Wolf, J.J., Beatty, S.W., Seastedt, T.R., 2004. Soil characteristics of Rocky Mountain National Park grasslands invaded by *Melilotus officinalis* and *M. alba*. *J. Biogeogr.* 31, 415–424. <https://doi.org/10.1046/j.0305-0270.2003.00983.x>.
- Wolkovich, E.M., Bolger, D.T., Holway, D.A., 2009. Complex responses to invasive grass litter by ground arthropods in a Mediterranean scrub ecosystem. *Oecologia* 161, 697–708. <https://doi.org/10.1007/s00442-009-1425-7>.