Beyond single invaders: Disentangling the effects of co-invading alien forbs on sandy old-fields

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Abstract

Aims

Invasive alien plants can severely impact ecosystem diversity and function. While individual species' effects are often studied, the interaction between multiple invasive species is less understood. This study examines how *Asclepias syriaca* and *Solidago* spp. (including *Solidago gigantea* and *S. canadensis*) influence taxonomic and functional diversity in sandy old-fields. The aims are to: (1) assess the individual and combined impacts of *Asclepias* and *Solidago* on resident plant diversity, and (2) determine whether interactions between these species alter their effects on the invaded community.

Location

Gödöllő Hills, Central Hungary.

Methods

I sampled 80 plots (2m × 2m) on sandy old-fields with varying levels of *Asclepias* and *Solidago* cover. Plant species cover was visually estimated, and trait data were obtained from databases. Species richness, community completeness, and community-weighted means (CWM) for plant traits, along with Rao functional diversity. Generalized linear and mixed models were used to evaluate the effect of invasive cover on resident diversity and traits, both with and without considering the invasives' traits in community indices.

Results

While *Asclepias* showed no significant effect, *Solidago* cover significantly reduced species richness and community completeness. When invasive species traits were excluded from the analysis, only the CWM and Rao diversity of the bud bank index were significantly related to *Solidago* cover. Including the invasives' traits revealed that their trait values influenced community indices significantly. *Asclepias* and *Solidago* cover were negatively correlated, but did not alter each other's effects.

Conclusions

Solidago has a stronger negative impact on resident species richness than *Asclepias*, which appears neutral. Trait-based mechanisms of reduced richness under *Solidago* dominance needs further study. The lack of interaction between these invaders suggests their individual impacts dominate over potential synergies or antagonisms.

Keywords

Asclepias, co-invasion, community diversity, competition, functional diversity, goldenrod, milkweed, *Solidago*, plant-plant interaction, plant traits

Introduction

Most alien plant invasions are known to reduce the diversity and functioning of the recipient communities (Livingstone et al. 2020). The effect of invasions are typically examined by seeking for correlation between the abundance of a focal alien species and a community-level index of diversity or ecological function (Barney et al. 2013, Bradley et al. 2019). Even though the colonization and the spread of multiple invasive species in the same community are relatively common, the interaction between their effects gained relatively little attention (but see Kuebbing et al. 2013, Tekiela & Barney 2017). Co-occurring invasive species may mitigate or facilitate each other's effect on the recipient community, either directly or indirectly (Reeb & Kuebbing 2024). Multi-species invasions (also called co-invasions) may need a different management approach, too; for which deep understanding of the interaction between invasive species is essential (Brandt et al. 2023).

The 'invasion meltdown' hypothesis (Simberloff & Von Holle 1999, Simberloff 2006) suggests that alien species facilitate the spread of other aliens in the invaded community, and their impact on the community or ecosystem thus accelerates. Braga et al. (2018) found a broad support for this hypothesis; however, the link with interspecific interactions was rarely justified. Kuebbing and Nuñez (2015) found neutral (additive) and negative (antagonistic) interaction between alien species the most common; on the contrary, several recent findings support synergistic effects between invasive species (Zenda et al. 2020, Zhang et al. 2020, Yu et al. 2023, Lone et al. 2024). The contradictory support for the type of interaction between the effects of alien species, as well as their variation in spatial scale, types of organism and ecosystem suggest that more case studies are necessary to find general rules (Ahmad et al. 2025).

The effects of invasive plants is highly context-dependent (Gonzalez-Moreno et al. 2014). Besides neglecting interactions between alien species, a caveat of examining them separately derives from the confounding effects of variation in site history, species pool and environmental background (Catford et al. 2021). Assessing how multiple invasive plants affect the same community offers an additional benefit by unifying the context of the study, thus fostering between-species comparisons.

Grasslands on sandy soils are among the habitats most threatened by alien plant invasions in Europe (Axmanová et al. 2021). Disturbed habitats, including ruderal vegetation and old-fields, are especially prone to colonization by alien plants (Pyšek et al. 2010). Along with large-scale changes in management driven by urbanization, the increasingly disturbed sandy areas have become hotspots for plant invasions worldwide (Chytrý et al. 2008, Lazaro-Lobo et al. 2020). In the Pannonian Ecoregion, several neophyte herbs contribute to the high level of invasion, including *Asclepias syriaca*, *Solidago gigantea*, *S. canadensis*, *Ambrosia artemisiifolia*, *Erigeron canadensis* and *E. annuus* (Botta-Dukát 2008, Botta-Dukát & Balogh 2008), while further arrivals have been expanding recently, e.g. *Gaillardia aristata* (Süle et al. 2023), *Sporobolus cryptandrus* (Kröel-Dulay et al. 2024), *S. neglectus* (Király 2016). Although, extensive cross-species comparisons estimated impacts of some of the above species on the diversity of the invaded communities (Hejda et al. 2009, Hejda & De Bello 2013, Fenesi et al. 2023), their combined effect has never been considered explicitly. *Asclepias syriaca* and *Solidago* spp. frequently colonize sandy old-fields and become dominant. Earlier studies found a negative effect of *Solidago* on the recipient community (Botta-Dukát & Dancza 2008, Pal et al. 2015), while there is no consensus about the effects of *Asclepias* (Kelemen et al. 2016, Szitár et al. 2018, Bakacsy 2019, Fenesi et al. 2023). Szitár et al. (2018) proposed even facilitative effects of *Asclepias* on grasses of water-stressed ecosystems.

Despite *Asclepias* and *Solidago* spp. are not close relatives phylogenetically, and they prefer slightly different habitats, their invasions on sandy old-fields might be viewed as similar phenomena: the colonisation by a functionally distinct, tall, perennial forb with effective below-ground clonal spreading (see below in more detail). Based on this functional similarity and the competitive exclusion hypothesis (Meszéna et al. 2006, Wang et al. 2019a), in the case of co-invasion, one might expect *Asclepias* and *Solidago* be competing with each other, thus indirectly facilitating the other species of the community; that is, their interaction effect should be negative (antagonistic).

In this study, I test how the diversity and trait composition of the recipient community are affected by the invasion of *Asclepias syriaca*, *Solidago gigantea* and *S. canadensis* (treated together as *Solidago*) on sandy old-fields in Central Hungary. My aims are (1) to examine the effect of *Asclepias* and *Solidago* on taxonomical and functional diversity of the same recipient communities, and (2) to test if they modify each other's effect.

Materials and Methods

Study area

The study was conducted in the Gödöllő Hills region of Central Hungary (Fig. 1) on sandy soils with moderate clay content (Pásztor et al. 2015, DoSoReMI.hu 2025). The climate is temperate, with mean annual temperature of 10–10.5 °C and 550–600 mm precipitation (Hungarian Meteorological Service 2024). The landscape is shaped by sand dunes and depressions, supporting subcontinental forest steppe vegetation, a mosaic of dry grasslands, open forests, and wetland patches (Zólyomi 1989). The most characteristic habitats are open and closed sand grasslands on dune tops and slopes, with dominant grasses such as *Festuca vaginata*, *Stipa borysthenica*, and *Koeleria glauca*, while less extreme sites support *Festuca rupicola*, *F. pseudovina*, and *Poa angustifolia*. Long-term human activity has fragmented the landscape, and recent urbanization near Budapest has intensified this trend, resulting in a mosaic of industrial zones, croplands, residential areas, and alien tree plantations (*Robinia pseudacacia*, *Populus*, *Pinus* spp.).

Four dry grassland sites were selected, sized 1100–4500 m^2 and ≤1.4 km apart, on flat sand ridges once cultivated but abandoned by 2002. They now support uncharacteristic successional vegetation, with the dominance of native grassland species (*Poa angustifolia*, *Stipa borysthenica*, *Teucrium chamaedrys*, *Carex stenophylla*) and alien species (*Asclepias syriaca*, *Solidago gigantea*). Mowing occurs irregularly, no more than once per year.

Site selection criteria included: (1) presence and varying density of *A. syriaca* and *S. gigantea*; (2) frequent co-occurrence of both at 2×2 m scale; (3) similar environmental and land-use history; (4) comparable species pools; and (5) absence of management or access constraints. Site 1 lies in a saddle between ridges, while sites 2–4 are on ridge plateaus. Elevation differences reach up to 14 m.

Aerial imagery shows all sites were cultivated in 1970. Site 1 was re-vegetated by 1990, ploughed again in 1992, and abandoned by 2002, when all four sites showed regenerating vegetation and expanding alien clones. Since then, sites remained largely unmanaged, except for occasional mowing likely motivated by legal requirements rather than forage use. Thus, all are 22–32-year-old, irregularly mown successional grasslands, with Site 1 adjacent to more natural sand grasslands and supporting a richer native flora. More information on the sites is available in the Appendices S1 and S2.

Focal alien species

The focal species are *Asclepias syriaca* (Asclepiadaceae), *Solidago gigantea* and *S. canadensis* (Asteraceae), and the latter two are considered together as *Solidago* due to their high morphological and functional similarity. *Asclepias* and *Solidago* share several traits that make them effective in spreading and competing with the species of the recipient communities. They are perennial herbs usually exceeding 1 m height. They develop a rich and hardy rhizome system that is highly efficient in clonal reproduction, uptake of water and nutrients, and regeneration after above-ground damage (Bagi 2008, Botta-Dukát & Dancza 2008). However, *Asclepias* has longer rhizomes with more distantly spaced above-ground shoots, thus its clones are sparser (Bagi 2008), usually not reaching higher cover than 50%, while the dense colonies of *Solidago* species can approach even 90%. All these species' leaf and root extracts have allelopathic effect. Their generative reproduction is also efficient due to flowers attractive to many pollinator groups and the large quantity of wind-dispersed fruit (Szigeti et al. 2020, Moroń et al. 2021). *Asclepias* blooms from June to August, *Solidago* from July to October. They are native to North America. Their large-scale invasion in Hungary started in the late 19th and the early 20th century (Bagi 2008, Botta-Dukát & Dancza 2008). By the end of the 20th century, *Asclepias* was documented as the most widespread invasive species on sandy areas of Hungary (Bagi 2008, Botta-Dukát 2008). Since then, observational data suggest that its spread continued on non-sandy soils, while recently spontaneous die-backs are experienced on the driest, formerly occupied, sandy habitats. *Solidago* spp. generally prefer wetter soils; however, they are also threatening dry grasslands if their deep root system is able to reach the ground water level. Their invasion were initiated from the more humid parts of the country but now they are common elsewhere in Hungary.

Vegetation sampling and trait data

In each site 20 plots of 2m×2m area were sampled between June and August 2022. Plots were located with the purpose of representing the range of cover values the focal invasive species reach, including patches where the two species co-occur or co-dominate. Hence, the study design applies a gradient approach instead of a 'control vs. treatment' view: a broadest possible range of potential values of the explanatory variables are sampled with the assumptions that higher cover of an invasive species affects the recipient community stronger. During the selection of sample plots, I tried to reduce spatial autocorrelation by avoiding plots with similar abundance composition (i.e. dominance by *Asclepias*, *Solidago* or other species) in close vicinity. In each plot the percentage covers of all vascular plant species as related to the plot area as 100% were visually estimated. The minimal summed cover of invasive species per plot was 0.01, the maximum was 93%. Species-specific cover tendencies and averages per site are available in the Appendix S1. Plant trait data for total height, specific leaf area, and seed mass were obtained from the PADAPT (Sonkoly et al. 2023), TRY (Kattge et al. 2020), LEDA (Kleyer et al. 2008), CLO-PLA (Klimešová et al. 2017), and Gyalus et al. (2022). These traits, as parts of the so-called leaf-height-seed (LHS) scheme, are considered a robust representation of major plant strategies (Westoby 1998, Laughlin et al. 2010). In addition, bud bank and clonality traits were involved according to Johansson et al. (2011) and E.-Vojtkó et al. (2016). Bud bank and clonality are similarly important dimensions of plant strategies, especially in avoiding and in regeneration after disturbance (Klimešová et al. 2016). As most grasslands and old-fields in the study area are maintained by humans or grazing animals, plant adaptation to disturbance regimes is key in shaping their vegetation, hence expectedly relevant here, too. The bud bank score is the rank sum of above-ground and below-ground bud bank scores, while the clonality score is the rank sum of lateral spread and the number of offsprings per parent in the CLO-PLA database. For *Hierochloe repens* trait data was scarcely available, thus the measurements of its close relative, *Hierochloe odorata* were used instead. There were data gaps also for the recently discovered endemic *Festuca pseudovaginata*, for which I used the average values of the functionally similar *F. vaginata*, *F. pseudovina* and *F. rupicola*.

In this study, I call 'resident' all species in the sample excluding *Asclepias syriaca*, *Solidago gigantea* and *S. canadensis*.

Community indices

To evaluate invasion effects, the following community indices were calculated for each plot:

- Species richness;
- Rao's quadratic entropy (RaoQ) for each trait and all traits combined, using modified Gower distances (De Bello et al. 2021);
- Community-weighted means (CWM) for each trait.

Because these indices are influenced by species pool properties (Kraft et al., 2011, Bennett et al. 2016), I calculated additional metrics to control for these effects:

- Community completeness, representing local richness relative to site-level species pool size (Pärtel et al. 2013)
- Standardized effect sizes (SES) of RaoQ and CWMs, obtained via randomization. Abundance values within each plot were permuted across all species recorded at the respective site, preserving species richness and abundance distribution. Observed values of community indices were compared against null distributions obtained from randomizations, and the results were probit-transformed to generate standardized effect sizes (Botta-Dukát 2018).

Community indices were calculated in two ways:

1) Excluding the focal invasives, focusing on changes within the resident species of the community, thus reflecting community assembly mechanisms under invasion pressure.
2) Including focal invasives, reflecting shifts in ecosystem properties in driven by invasion.

Statistical analysis

Generalized linear models (GLMs) and generalized linear mixed models (GLMMs) were fitted to assess relationships between focal alien cover and community indices. Site was included as a random effect in GLMMs (random intercept only). Four competing predictor structures were tested:

1. ASC: *Asclepias* cover only

2. SOL: *Solidago* cover only

3. SUM: Combined *Asclepias* + *Solidago* cover

4. INT: Additive and interactive effects of both invaders

The SUM model tested whether total invasive abundance, rather than species identity, was the key driver. The INT model tested for interactions (sensu Duncan & Kefford 2021) interpreted as synergistic or antagonistic effects.

GLMMs were used when the site as random factor improved the model fit significantly; otherwise, GLMs were preferred for simplicity and power. For each response variable, both model types were fitted, and the model with the lower Akaike Information Criterion (AIC) value was kept as a final model. Significant effects of model terms were tested using Wald tests. In the INT model, only the interaction term was interpreted to avoid redundancy with ASC and SOL models.

Response distributions were Poisson (for species richness) or Gaussian (for other indices). Holm's method (Holm 1979) was used to adjust p-values for multiple testing.

Finally, Pearson correlation between *Asclepias* and *Solidago* cover values was calculated as a basic measure of their co-occurrence.

All calculations were done using the R software environment using the gawdis (de Bello et al. 2021), vegan (Oksanen et al. 2022), glmmTMB (Brooks et al. 2017), fundiversity (Grenié & Gruson 2024) packages. A detailed description of data analysis methods is available in Appendix S3. I declare having used ChatGPT (OpenAI, 2024) to assist with language improvement, formatting, and R programming. The final content was reviewed and edited by the author.

Results

Asclepias and *Solidago* showed a negative linear correlation (r= -0.3198, p=0.0038; Fig. 2).

When *Asclepias* and *Solidago* were not considered during the calculation of community indices, significant relationships were found only in five models (Table 1). Species richness was negatively related with the SOL model (GLMM, z=-4.240, p=0.001; Fig. 3) and the SUM model (GLMM, z=-3.583, p=0.016; Fig. 3). SOL had a negative effect on community completeness (GLM, z=-4.784, p<0.001; Fig. 4), and a positive effect on the CWM of bud bank (GLM, z=3.345, p=0.041; Fig. 5).

When I included *Asclepias* and *Solidago* into the calculation of community indices, species richness had no significant predictor (Table 2). Community completeness decreased with the SOL model (GLM, z=-3.736, p=0.007). CWM of plant height increased with SOL (GLMM, z=8.211, p<0.001) and SUM (GLM, z=11.377, p<0.001) models. CWM of seed mass increased with the ASC (GLM, $z=5.383$, $p<0.001$) but decreased in response to the SOL model (GLMM, $z=-6.23$, $p<0.001$). CWM of bud bank score had a positive response to SOL (GLMM, $z=12.597$, $p<0.001$) and SUM (GLMM, $z=10.034$, $p<0.001$) models, while CWM of clonal score decreased with them (SOL: GLMM, $z=-6.272$, $p<0.001$; SUM: GLMM, $z=-6.693$, $p<0.001$). Rao diversity of seed mass increased with the ASC (GLM, $z=4.413$, $p<0.001$) but decreased with the SOL model (GLMM, $z=-4.745$, $p<0.001$). Rao diversity of the bud bank index increased with the SOL (GLMM, $z=7.048$, $p<0.001$) and SUM (GLMM, $z=5.114$, $p<0.001$) models. The INT model had no significant effect in any tests.

Discussion

Contrasting effects of Asclepias and Solidago on species richness and community completeness

I found contrasting relationship between the two invasive species and plot-level richness of resident species. This is in agreement with most earlier studies presenting a negative effect of invasive *Solidago* species (Ledger et al. 2015, Pal et al. 2015, Wang et al. 2021a), and also supports those claiming no negative effect of *Asclepias* on resident species richness (Szitár et al. 2014, 2018, Kelemen et al. 2016; but see Fenesi et al. 2023). Moreover, plot-level species richness relative to species pool size, i.e. community completeness, of resident species also decreased with *Solidago* cover. In case of models fitted on species richness, GLMM models proved to be more parsimonious, while when the response variable was community completeness, GLM acquired lower AIC values. GLMMs include the site as random factor to account for site-specific patterns of species richness, while community completeness relates observed plot-level species richness to the number of species at the site unobserved in specific plots. Hence, controlling for site-specific effects seems to be a straightforward tool in the modelling of species richness as a function of invasive cover (Bennett et al. 2016). This can be done either by using random factors in the model, or by choosing a measure of richness standardized by the species pool of the site. The importance of site-specificity is a sign of idiosyncrasy, a common barrier in invasion research (Elliott-Graves 2016). Local sites vary in species pool due to differences in environmental background and history (Cornell & Harrison 2014). However, species pool determines the community-level response to invasion; therefore, site-specificity must be controlled when searching for generalities in biological invasions (Bennett et al. 2016).

Earlier studies mostly found unclear (Kelemen et al. 2016), or sometimes even positive effect (Szitár et al. 2018) of *Asclepias* dominance on species richness. Although, its establishment on the scarcely vegetated sandy grasslands or old-fields is conspicuous even from a distance due to its prominent height and biomass, *Asclepias* rarely reaches a cover over 50% at the scale of the sample plots. The looser spacing of above-ground stems is due to the longer rhizomes typically produced on less favourable habitats (Bagi 2008, Follak et al. 2021), and this dominance may not be enough to outcompete resident species. Moreover, a low or moderate cover of *Asclepias* may even buffer the effect of drought, a major stress factor on open, sandy habitats. The nurse effect was already documented by Szitár et al. (2018) in the establishment of natural dominant grasses of sandy grasslands. The effect of *Solidago* and *Asclepias* covers summed (that is, SUM models) were weaker than *Solidago* alone but stronger than *Asclepias*, also pointing at their contrasting behaviour.

Trait responses of resident species to invasion

The decreased local richness in the resident community with increasing dominance of *Solidago* is commonly attributed to its competitive ability (Pal et al. 2015). However, competition may act through different mechanisms that are scarcely explored yet in the context of *Solidago* invasion (but see Wang et al. 2018, 2019b, 2021b). Regarding *Asclepias*, Kelemen et al. (2016) reported trait-level response of resident plants to *Asclepias* cover despite no relationship with total species richness, while Fenesi et al. (2023) found decreasing species richness and increasing Rao diversity among the rest of the community with increasing *Asclepias* cover. Surprisingly, I found limited evidence of trait responses to invasion. When *Asclepias* and *Solidago* were excluded from the calculation of CWM and Rao diversity, the only significant response to any model was the increasing CWM of bud bank to *Solidago* cover and to the summed cover of both invasive species. The bud bank is essential for plant regeneration and individual-level persistence (Klimešová & Klimeš 2007), which suggests that these ecological functions are important for resident plants to survive on grasslands invaded by *Solidago*. Fig. 4 showed that with low *Solidago* cover, the SES of bud bank score ranged close to zero, while it increased significantly with *Solidago* cover. This and the relationship with species richness and completeness suggest that species with more developed bud bank are more likely to co-exist with *Solidago*. Re-sprouting ability is a key trait under biomass removal (Latzel et al. 2008, Herben et al. 2017), thus mowing of the sites may also modulate the effect of traits in community assembly; even if the sampling plot size and the dominance of invaders vary on a finer scale than on which mowing is carried out (sites are mown uniformly). Nevertheless, bud bank can be correlated to reproductive traits or some specific forms of vegetative growth, that I did not involve in the analysis, but might play proximal role in competition.

Together with the above significant relationships, the overall effect of *Solidago* on the trait composition and diversity of the resident species insufficiently explains why species richness and community completeness decrease with *Solidago* cover. I suggest two non-exclusive hypotheses on the reasons behind the weak explanatory power of trait-based models on community response to *Solidago* invasion. According to a deterministic explanation, decreasing richness/completeness is driven by a trait-based mechanism but not involving the traits I considered in this study. I selected traits that are most commonly included in studies dealing with community assembly. Among them, height is known as an important competitive trait for plants (Klimešová et al. 2008, Violle et al. 2009), including Pannonian sand grasslands (Lhotsky et al. 2016). Plant height of native species also responded to the invasion of *S. canadensis* according to Wang et al. (2021b). High SLA is also considered a successful strategy for plants of the recipient community to thrive under the invasion of alien species (Kelemen et al. 2016, Loiola et al. 2018, Wang et al. 2021b). Of course, the availability of measurements also played a role in selecting traits (Sonkoly et al. 2023). Other traits could respond more specifically to *Solidago* invasion, e.g. root traits related to nutrient uptake (Garbowski et al. 2020) or relationships with soil biota (Liao et al. 2015). This is reasonable, because *Solidago* invasion causes fundamental changes in soil properties and biota (Zhang et al. 2009, Wang et al. 2018b). Unfortunately, such trait data are not available in sufficient coverage for the Pannonian flora. According to a stochastic explanation, species resisting *Solidago* invasion do not obey any regularity; they are assembled randomly from the habitat-specific species pool. Such a pattern could be expected, if *Solidago* outcompetes all species with similar efficiency; therefore, increased *Solidago* cover simply reduces the area of the plot suitable for existence of any other vascular plant. Higher *Solidago* cover allows fewer individuals of other species to grow in the plot, and under stochastic assembly, these individuals will represent fewer species. This mechanism can be reinforced by the stage of succession on the study sites. The sites are mainly in the phases of early colonization after a major disturbance (e.g. after ploughing), when random processes have a strong impact on community assembly of sandy old-fields on fine spatial scales (Török et al. 2018, Halassy et al. 2019, Csecserits et al. 2021). That is, community assembly might be stochastic on the sites anyway, not just as a response to *Solidago* invasion. In case of more natural or midsuccessional grasslands, the community response to invasion might show a tighter link with changes in trait composition or diversity (Kelemen et al. 2016, Bakacsy 2019).

Invasions altering community functionality – the mass ratio hypothesis

When I considered *Asclepias* and *Solidago* during the calculation of plot-level CWM and RaoQ, I found much more significant effects. One may argue this is trivial, since the covers of *Asclepias* and *Solidago* contributed to both the predictors and the dependent variables of the models thus involving circularity. However, the randomization procedure embodied the same level of circularity; therefore, its effect was partialled out from the SES values of the raw impact measures. Instead, I argue that the higher number of significant relationships is due to that both species bear rare trait syndromes within the species pool; thus, their increased contribution in a community affect both the mean trait value and the variation around it. These relationships can be explained by the mass ratio hypothesis (Grime 1998).

One manifestation of the mass ratio hypothesis is the increased plant height CWM and RaoQ with the SOL and SUM models, but only when the focal species were included in the calculation. *Solidago* and *Asclepias* are among the tallest plants on sandy grasslands, and their increasing contribution to the total cover of the communities naturally increases the CWM of plant height. The Rao diversity of plant height also increases with increasing cover of tall plants, if shorter plants are not excluded selectively.

Seed mass showed a strikingly different response to *Asclepias* and *Solidago* cover. While CWM and RaoQ of seed mass increased with *Asclepias* cover, they decreased with *Solidago* cover. The mass ratio hypothesis offers a parsimonious explanation here, too. *Asclepias* seeds are among the heaviest ones in the species pool (SES = +1.44), while *Solidago* seeds are moderately light (*S. gigantea*: SES = -0.694, *S. canadensis*: SES = -0.739). Hence, increased cover of *Asclepias* increases the mean seed mass of the community, and also the variation around it, if light-seeded species are not filtered out. In contrast, the dominance of light-seeded *Solidago* naturally decreases the CWM of seed mass due to its increased contribution in the community.

Interspecific relationship between Asclepias and Solidago

Asclepias and *Solidago* covers were negatively correlated. This is not surprising as they share several resource acquisitive traits (height, extensive belowground organs, leaves distributed evenly along the stem, similar leaf types, slightly shifted but overlapping phenology; Bagi

2008, Botta-Dukát & Dancza 2008) suggesting interspecific competition when getting in close contact. The negative correlation between any pair of species reaching high cover percentage is also a mathematical constraint due to limited space. Notably, I detected no significant interaction effect of *Solidago* and *Asclepias* cover; that is, the invasion of the two species affect the recipient community independently (i.e., additively) as they do not change each other's effect. More specifically, *Solidago* is a strong competitor acting negatively on species richness and completeness of the community of resident species, and also on *Asclepias*. In contrast, *Asclepias* seems largely indifferent towards other species.

Broader implications for interpretation and management

There is a methodological difference between this study and the predecessors detecting eventual relationship between *Asclepias* or *Solidago* dominance and trait composition or diversity of native species in the recipient community. I used a permutation method in which random communities were assembled for each site from the site-level species pool in many repeats to generate null distributions of CWM and RaoQ (Götzenberger et al. 2016, Botta-Dukát & Czúcz 2016), and then the observed values were transformed to standardized effect sizes. These SES values were used as dependent variables in the models instead of the raw index values. It is a rather 'strict' approach in the sense that structural biases in the data set due to plot-level or site-level species richness, site-level species pool, as well as the abundance distribution within plots are controlled. Earlier studies did not apply such permutation techniques to reduce these potential sources of bias but used raw CWM or functional diversity values as dependent variables without randomizations. As in similar cases (e.g. Kraft et al. 2011), some of the earlier conclusions might lose support, if validated against stricter null hypotheses.

Fenesi et al. (2023) recently emphasized difficulties in finding general patterns in the relationship of community indices and invasive cover. Similarly, one must be careful when extrapolating the relationships (or the lack of them) found here outside the studied system: the Pannonian disturbed sandy old-fields. The species pool of this vegetation type is strongly filtered: it comprises species tolerating drought attributable to warm summers and low water retention capacity of the soil. Moreover, early successional and disturbance tolerant species are also overrepresented in the species pool compared to the entire Hungarian flora due to the history of the sites (Csecserits et al. 2021). It is possible that among such harsh conditions, the species pool is already strongly filtered leaving little room for invasive species to further reduce diversity. Bearing in mind the possible facilitative effects of invasive plants on sandy grasslands (Szitár et al. 2018), the more articulate examination of the relationship between community indices and invasive cover is necessary, including possible non-linear and density-dependent effects (Fenesi et al. 2023). Besides the shape of the impact function, site history and the effects of species pool complicates generalization.

Managing co-invasions may need a different perspective from single-species invasions (Brandt et al. 2023). However, in the case of *Asclepias* and *Solidago*, the interaction effect is not validated. Moreover, similar methods proved to be useful measures against the invasion of both species, e.g. long-term mowing and herbicide application (see Bakacsy & Bagi 2020, Berki et al. 2023 for *Asclepias*, and Nagy et al. 2022, Perera et al. 2022, Świerszcz et al. 2024 for *Solidago*); therefore, no differentiation in management seems necessary on co-invaded stands.

Conclusions

While *Solidago* reduces plot-level species richness and community completeness of resident species, *Asclepias* has no significant effect on these properties. I found generally weak evidence of *Asclepias syriaca* and *Solidago* spp. affecting the trait composition and diversity of the accompanying resident species. However, in accordance with the mass ratio hypothesis, increased cover of invasive species proportionately contributes and changes the community-level trait properties. I found no evidence of *Asclepias* and *Solidago* changing each other’s effect.

Data availability

The community data and the trait data table will be uploaded to the Dryad repository upon acceptance of the manuscript.

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Figure 1. The map of the study sites

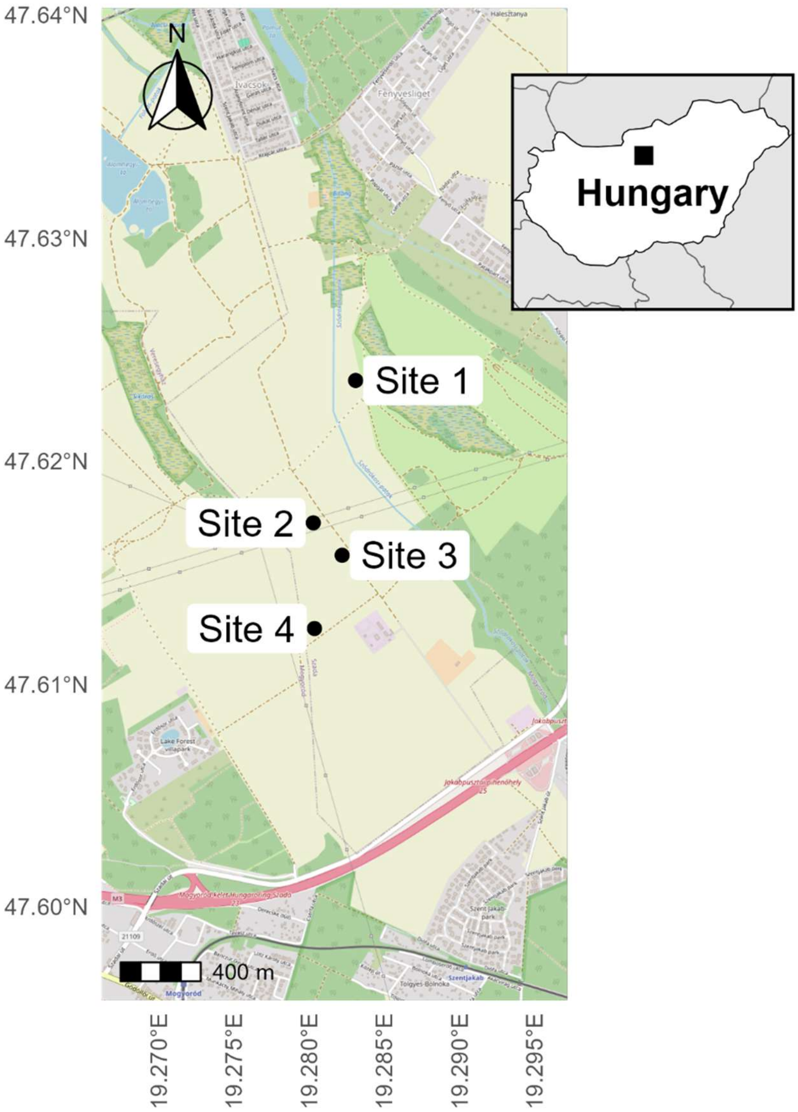

Figure 2. Correlation of *Asclepias* cover and *Solidago* cover. The solid line is fitted with a major axis linear regression. Dashed lines show the 2.5%-97.5% confidence interval. The Pearson's correlation coefficient is r=-0.3198 (p=0.0038).

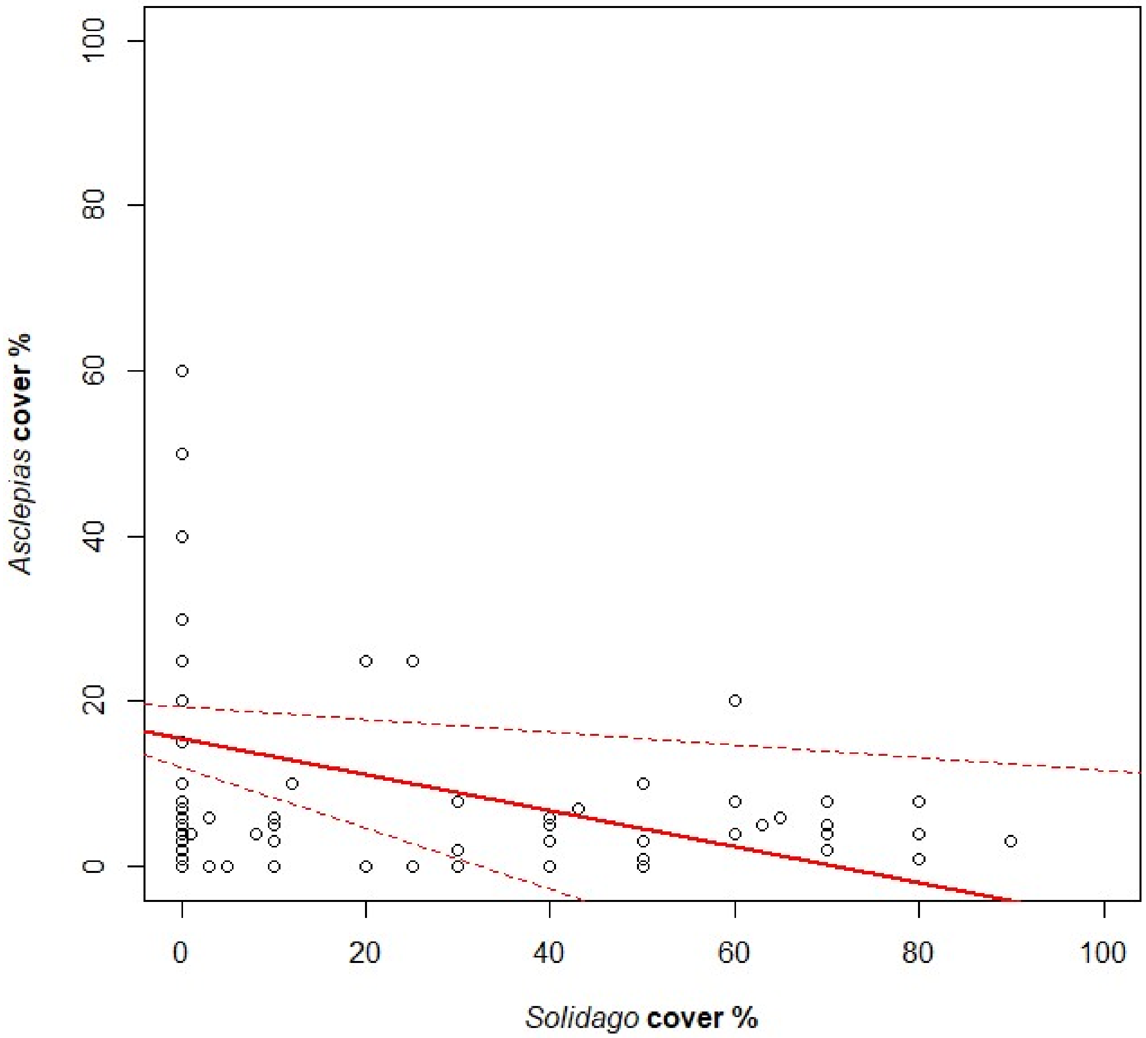

Figure 3. Relationship of species richness with *Asclepias* (A; ASC model), *Solidago* (B; SOL model) and *Asclepias* + *Solidago* (C; SUM model) cover percentage. For significant relationships (Wald test, $p<0.05$), trend lines are fitted for each site, based on a GLMM with site as random factor.

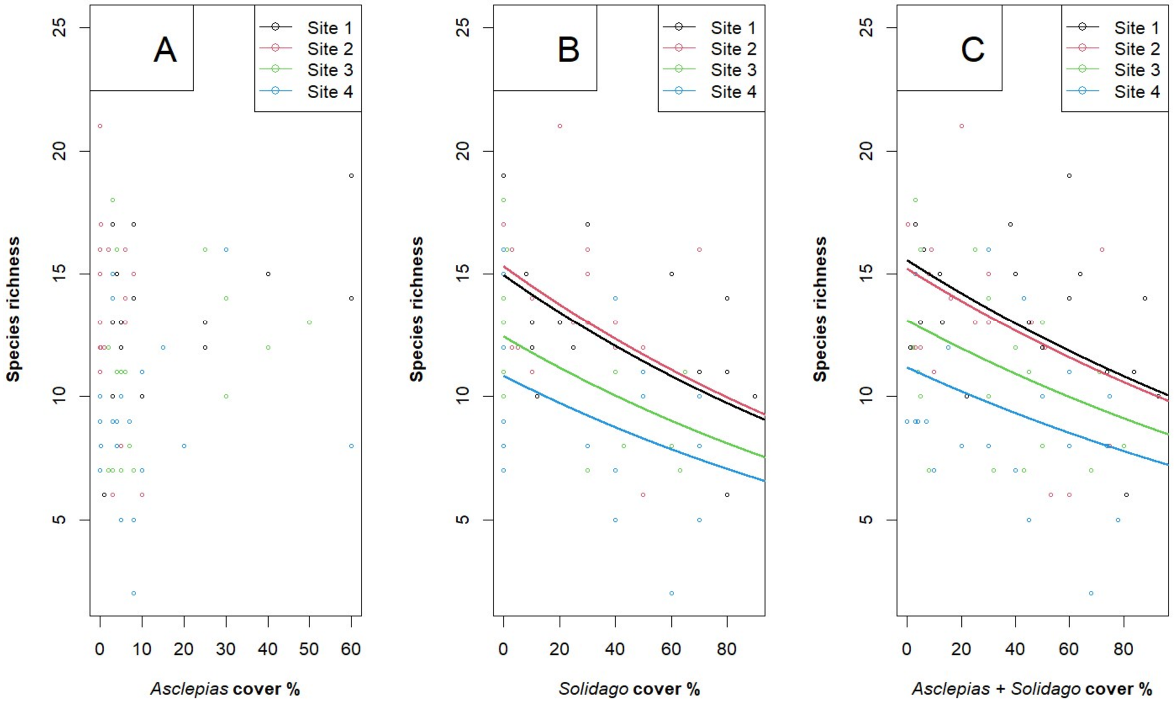

Figure 4. Relationship of community completeness with *Asclepias* (A; ASC model), *Solidago* (B; SOL model) and *Asclepias* + *Solidago* (C; SUM model) cover percentage. Points of different colours indicate different study sites. For significant relationships (Wald test, $p<0.05$), a trend line is fitted based on a GLM with plots from all sites pooled.

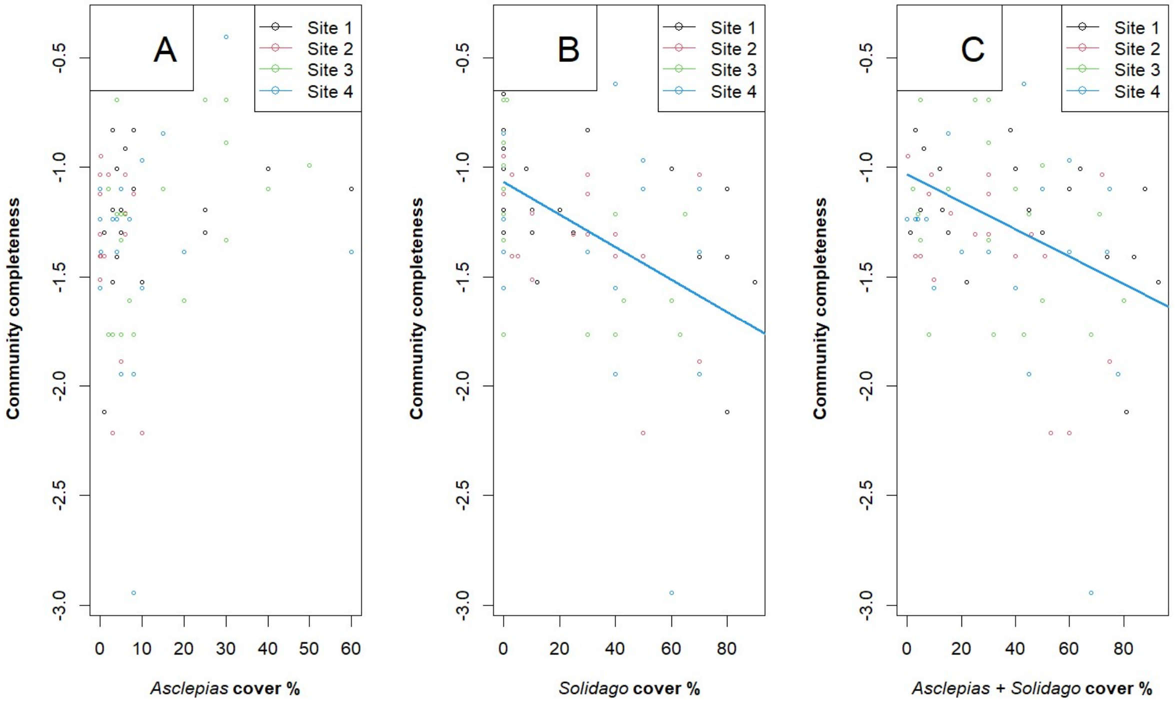

Figure 5. Relationship of standardized effect size (SES) of the community-weighted mean (CWM) of the bud bank index with *Asclepias* (A; ASC model), *Solidago* (B; SOL model) and *Asclepias* + *Solidago* (C; SUM model) cover percentage. Trait values of *Asclepias* and *Solidago* are not considered in the calculation of bud bank index. Points of different colours indicate different study sites. For significant relationships (Wald test, *p*<0.05), a trend line is fitted based on a GLM with plots from all sites pooled.

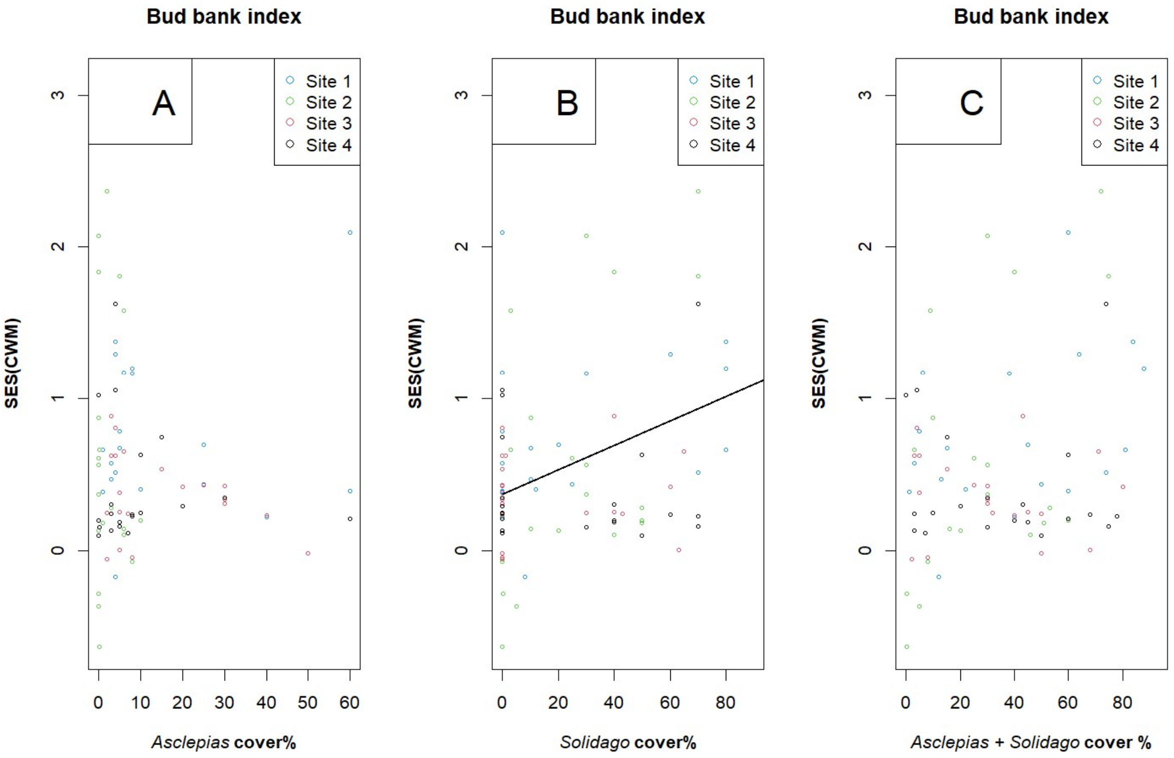

Table 1. Wald test results of models and model terms (columns) related to community indices as response variables (rows). The occurrence and trait values of *Asclepias syriaca* and *Solidago* ssp. are not considered in the calculation of CWM- and RaoQ-based the response variables. Bold numbers indicate significant effect. *Italics* indicate GLMM, normal font indicate GLM. CWM = community-weighted mean, SLA = specific leaf area, RaoQ = Rao's functional diversity.

	ASC		SOL		SUM		INT	
	z	*p*	*z*	*p*	*z*	*p*	*z*	*p*
species richness	1.583^{M}	1	**-4.240**^{M}	**0.001**	**-3.583**^{M}	**0.016**	-0.901^{M}	1
community completeness	1.744	1	**-4.784**	**<0.001**	**-3.723**	**0.01**	-1.007	1
CWM-height	0.906	1	0.710	1	1.226	1	-0.208	1
CWM-SLA	-0.841^{M}	1	-0.817^{M}	1	-1.282^{M}	1	0.338^{M}	1
CWM-seedmass	-1.89^{M}	1	-0.820^{M}	1	-1.855^{M}	1	0.882^{M}	1
CWM-buds	-0.388	1	**3.345**	**0.041**	3.217	0.063	-1.789	1
CWM-clonal	-0.62^{M}	1	-1.049^{M}	1	-1.419^{M}	1	-0.306^{M}	1
RaoQ-all traits	-0.725^{M}	1	-0.533^{M}	1	-0.934^{M}	1	-0.318^{M}	1
RaoQ-height	-0.898^{M}	1	-1.844^{M}	1	-2.418^{M}	0.687	-0.045^{M}	1
RaoQ-SLA	1.088	1	-1.158^{M}	1	-0.776^{M}	1	-0.812^{M}	1
RaoQ-seedmass	-1.611^{M}	1	0.143^{M}	1	-0.677^{M}	1	0.364^{M}	1
RaoQ-buds	-0.744^{M}	1	2.826^{M}	0.217	2.525^{M}	0.521	-1.507^{M}	1
RaoQ-clonal	0.053^{M}	1	-0.334^{M}	1	-0.32^{M}	1	-1.124^{M}	1

Table 2. Wald test results of models and model terms (columns) related to community indices as response variables (rows). The occurrence and trait values of *Asclepias syriaca* and *Solidago* ssp. are considered in the calculation of CWM- and RaoQ-based response variables. Bold numbers indicate significant effects. GLMM models are indicated as “^{M}” next to the respective *z*-values, other models are GLMs. CWM = community-weighted mean, SLA = specific leaf area, RaoQ = Rao’s functional diversity.

	ASC		SOL		SUM		INT	
	z	*p*	*z*	*p*	*z*	*p*	*z*	*p*
species richness	1.042^{M}	1	-3.039^{M}	0.093	-2.613^{M}	0.314	-0.488^{M}	1
community completeness	1.586	1	**-3.736**	**0.007**	-2.857	0.158	-0.493	1
CWM-height	1.872	1	**8.211**^{M}	**<0.001**	**11.377**	**<0.001**	0.375	1
CWM-SLA	-0.306^{M}	1	2.429^{M}	0.515	2.329^{M}	0.656	-0.983^{M}	1
CWM-seedmass	**5.383**	**<0.001**	**-6.23**^{M}	**<0.001**	-2.97^{M}	0.113	1.368^{M}	1
CWM-buds	-1.498	1	**12.597**^{M}	**<0.001**	**10.034**^{M}	**<0.001**	-0.792^{M}	1
CWM-clonal	-0.008^{M}	1	**-6.272**^{M}	**<0.001**	**-6.693**^{M}	**<0.001**	-0.589^{M}	1
RaoQ-all traits	-0.714	1	-0.937	1	-1.36	1	-0.917	1
RaoQ-height	0.183^{M}	1	0.141^{M}	1	0.244^{M}	1	-1.567^{M}	1
RaoQ-SLA	0.728	1	-1.167^{M}	1	-1.131^{M}	1	-1.591^{M}	1
RaoQ-seedmass	**4.413**	**<0.001**	**-4.745**^{M}	**<0.001**	-2.024	1	1.873^{M}	1
RaoQ-buds	-2.654^{M}	0.286	**7.048**^{M}	**<0.001**	**5.114**^{M}	**<0.001**	-0.725^{M}	1
RaoQ-clonal	-1.024	1	-1.013	1	-1.612	1	-0.337	1