1 **Beyond single invaders: Disentangling the effects of co-invading alien herbs on sandy**

2 **old-fields**

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15

16 **Abstract**

17 *Aims*

18 Invasive alien plants can severely impact ecosystem diversity and function. While individual

19 species' effects are often studied, the interaction between multiple invasive species is less

20 understood. This study examines how *Asclepias syriaca* and *Solidago* spp. (including

21 *Solidago gigantea* and *S. canadensis*) influence taxonomic and functional diversity in sandy

22 old-fields. The aims are to: (1) assess the individual and combined impacts of *Asclepias* and

23 *Solidago* on resident plant diversity, and (2) determine whether interactions between these

24 species alter their effects on the invaded community.

25 *Location*

26 Gödöllő Hills, Central Hungary.

27 *Methods*

28 I sampled 80 plots (2m × 2m) with varying levels of *Asclepia*s and *Solidago* cover. Plant

29 species cover was visually estimated, and trait data were obtained from databases. Species

30 richness, community completeness, and community-weighted means (CWM) for traits like

31 plant height and seed mass were calculated, along with Rao functional diversity. Generalized

32 linear and mixed models were used to evaluate the effect of invasive cover on resident

33 diversity and traits, both with and without considering the invasives' traits in community

34 metrics.

35 *Results*

36 *Solidago* cover significantly reduced species richness and community completeness, while

37 *Asclepias* showed no significant effect. When invasive species traits were excluded from the

38 analysis, only the CWM and Rao diversity of the bud bank score were significantly related to

39 *Solidago* cover. Including the invasives' traits revealed that their trait values influenced

40 community metrics significantly. *Asclepias* and *Solidago* cover were negatively correlated,

41 but did not alter each other's effects.

42 *Conclusions*

43 *Solidago* has a stronger negative impact on resident species richness than *Asclepias*, which

44 appears neutral. The lack of interaction between these invaders suggests their individual

45 impacts dominate over potential synergies or antagonisms.

46 **Introduction**

47 Invasions of alien plants are known to reduce the diversity and functioning of the recipient

48 communities (Livingstone et al. 2020). The effect of invasions are typically examined by

49 seeking for correlation between the abundance of a focal alien species and a community-level

50 index of diversity or ecological function (Barney et al. 2013, Bradley et al. 2019). Even

51 though the colonization and the spread of multiple invasive species in the same community

52 are relatively common, the interaction between their effects gained relatively little attention

53 (but see Kuebbing et al. 2013, Tekiela & Barney 2017). Co-occurring invasive species may

54 mitigate or facilitate each other's effect on the recipient community, either directly or

55 indirectly (Reeb & Kuebbing 2024). Multi-species invasions (also called co-invasions) may

56 need a different management approach, too; for which deep understanding of the interaction

57 between invasive species is essential (Brandt et al. 2023).

58 The 'invasion meltdown' hypothesis (Simberloff & Von Holle 1999, Simberloff 2006)

59 suggests that alien species facilitate the spread of other aliens in the invaded community, and

60 their impact on the community or ecosystem thus accelerates. Kuebbing and Nuñez (2015)

61 found neutral and negative interaction between alien species the most common; on the

62 contrary, several recent findings support synergistic effects between invasive species (Zenda

63 et al. 2020, Zhang et al. 2020, Yu et al. 2023). The contradictory support for the sign of

64 interaction between the effects of alien species, as well as their variation in spatial scale, types

65 of organism and ecosystem suggest that more case studies are necessary to find general rules

66 (Braga et al. 2018).

67 The effect on invasive plants is highly context-dependent (Gonzalez-Moreno et al. 2014).

68 Besides neglecting interactions between alien species, a caveat of examining them separately

69 derives from the confounding effects of variation in site history, species pool and

70 environmental background (Catford et al. 2021). Assessing how multiple invasive plants

71 affect the same community offers an additional benefit by unifying the context of the study,

72 thus fostering between-species comparisons.

73 Herbaceous vegetation on sandy soils are among the habitats most threatened by alien plant

74 invasions in Europe (Axmannová et al. 2021). Disturbed habitats, including ruderal vegetation

75 and old-fields, are especially prone to colonization by alien plants (Pyšek et al. 2010). Along

76 with large-scale changes in management driven by urbanization, the increasingly disturbed

77 sandy areas have become hotspots for plant invasions worldwide (Chytrý et al. 2008, Lazaro-

78 Lobo et al. 2020). In the Pannonian Ecoregion, several neophyte herbs contribute to the high

79 level of invasion, including *Asclepias syriaca*, *Solidago gigantea*, *S. canadensis*, *Ambrosia*

80 *artemisiifolia*, *Erigeron canadensis* and *E. annuus* (Botta-Dukát 2008, Botta-Dukát & Balogh

81 2008), while further arrivals have been expanding recently, e.g. *Gaillardia aristata* (Süle et al.

82 2023), *Sporobolus cryptandrus* (Török et al. 2021), *S. neglectus* (Király 2016). Although,

83 extensive cross-species comparisons estimated impacts of some of the above species on the

84 diversity of the invaded communities (Hejda et al. 2009, Hejda & De Bello 2013, Fenesi et al.

85 2023), their combined effect has never been considered explicitly. *Asclepias syriaca* and

86 *Solidago* spp. frequently colonize sandy old-fields and become dominant. Earlier studies

87 found a negative effect of *Solidago* on the recipient community (Botta-Dukát & Dancza 2008,

88 Pal et al. 2015), while there is no consensus about the effects of *Asclepias* (Kelemen et al.

89 2016, Szitár et al. 2018, Fenesi et al. 2023). Szitár et al. (2018) proposed even facilitative

90   effects of *Asclepias* on grasses of water-stressed ecosystems. It is, therefore, an open question,

91   whether *Asclepias* modifies the negative effects of *Solidago* in case of a co-invasion.

92   In this study, I test how the diversity and trait composition of the recipient community are

93   affected by the invasion of *Asclepias syriaca*, *Solidago gigantea* and *S. canadensis* (treated

94   together as *Solidago*) on sandy old-fields in Central Hungary. My aims are (1) to examine the

95   effect of *Asclepias* and *Solidago* on taxonomical and functional diversity of the same recipient

96   communities, and (2) to test if they modify each other's effect.

97

Materials and Methods

99   *Study area*

100   The study area is located in the Gödöllő Hills geographical region in Central Hungary. The

101   soil is sandy with a moderate clay content. The climate is temperate with mean annual

102   temperature is 10 to 10.5 °C and the total annual precipitation is 550 to 600 mm (Hungarian

103   Meteorological Service 2024) The landscape is structured by sand dunes, hills and

104   depressions. The climatically and edaphically adapted natural vegetation of the study area was

105   subcontinental forest steppe comprising a mosaic of dry grasslands and open forests (Zólyomi

106   1989), with wetlands in the depressions. The most significant semi-natural habitats still

107   present in the region are open and closed sand grasslands that are located in the tops or the

108   southerly slopes of the sand dunes. Driest stands are dominated by *Festuca vaginata*, *Stipa*

109   *borysthenica*, *Koeleria glauca*, while among less extreme conditions, *Festuca rupicola*, *F.*

110   *pseudovina*, *Poa angustifolia* are more typical. Characteristic grassland species are *Fumana*

111   *procumbens*, *Alkanna tinctoria*, *Onosma arenaria* and *Centaurea arenaria*. However, due to

112   the long-lasting human activity in the area, all semi-natural vegetation types exist in reduced

113   and isolated patches. Landscape alteration has become especially intensive in the last few

114   decades along with the increasing urbanization at the city outskirts of Budapest. Now the

115   region is characterized by a mixture of large-scale industrial constructions, agricultural

116   intensification, extending residential areas, and recreational use by the increased population,

117   all connected to the economic development of the agglomeration around Budapest. A

118   significant area is covered by ruderal vegetation, successional old-fields, agricultural land,

119   and tree plantations (mostly of alien species, e.g. *Robinia pseudacacia*, *Populus* spp., *Pinus*

120   spp.).

121 Four sites were selected on grasslands. All of them were agricultural land in the past, and are

122 under regeneration by native plants of sandy grasslands (most common dominants: *Poa*

123 *angustifolia*, *Stipa borysthenica*, *Teucrium chamaedrys*, *Carex stenophylla*), and typical alien

124 species of the region (*Asclepias syriaca*, *Solidago gigantea*, *S. canadensis*). The sites are

125 mown irregularly but not more often than once a year.

126 *Focal alien species*

127 The focal species are *Asclepias syriaca* (Asclepiadaceae), *Solidago gigantea* and *S.*

128 *canadensis* (Asteraceae), and the latter two are considered together as *Solidago* due to their

129 high morphological and functional similarity. Notably, the non-native, European populations

130 of *Solidago* raise taxonomical problems, too (Weber 1998, 2000). *Asclepias* and *Solidago*

131 share several traits that make them effective in spreading and competing with resident species.

132 They are perennial herbs reaching approximately 1 m height. They develop a rich and hardy

133 stolon system that is highly efficient in clonal reproduction, uptake of water and nutrients, and

134 regeneration after above-ground damage. However, *Asclepias* has longer stolons with more

135 distantly spaced above-ground shoots, thus its clones are sparser, usually not reaching higher

136 cover than 50%, while the dense colonies of *Solidago* species can approach even 90%. All

137 these species' leaf and root extracts have allelopathic effect. Their generative reproduction is

138 also efficient due to flowers attractive to many pollinator groups and the large quantity of

139 wind-dispersed fruit. *Asclepias* blooms from June to August, *Solidago* from July to October.

140 They are native to North America. Their large-scale invasion in Hungary started in the late

141 19th and the early 20th century (Bagi 2008, Botta-Dukát & Dancza 2008). By the end of the

142 20th century, *Asclepias* was documented as the most widespread invasive species on sandy

143 areas of Hungary (Bagi 2008, Botta-Dukát 2008). Since then, observational data suggest that

144 its spread continued on non-sandy soils, while recently spontaneous die-backs are experienced

145 on the driest, formerly occupied, sandy habitats. *Solidago* spp. generally prefer wetter soils;

146 however, they are also threatening dry grasslands if their deep root system is able to reach the

147 ground water level. Their invasion were initiated from the more humid parts of the country

148 but now they are common elsewhere in Hungary.

149 *Vegetation sampling and trait data*

150 In each site 20 plots of 2m×2m area were sampled between June and August 2022. Plots were

151 located with the purpose of representing the range of cover values the focal invasive species

152 reach, including patches where the two species co-occur or co-dominate. In each plot the

percentage covers of all vascular plant species were visually estimated. 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), Gyalus et al. (2022) and unpublished data. 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 in some form by humans or 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*.

Data analysis

I calculated the following indices of diversity and trait composition for each plot as impact metrics of *Asclepias* and *Solidago* invasion:

- Species richness
- Rao quadratic diversity (RaoQ) calculated for each trait separately and all traits combined. For all cases, between-species trait dissimilarity was calculated using the modified Gower index by De Bello et al. (2021).
- Community-weighted means for each trait, with and without *Asclepias* and *Solidago*.

All impact metrics were calculated without and with considering the abundance and the trait values of *Asclepias* and *Solidago*. When the focal species is not considered, variation in impact metrics reflects how the resident species respond to the invasion. In contrast, taking the focal species into account reflects levels of community-level attributes as contributors of ecosystem processes regardless species identities.

185   The above indices are 'absolute' in terms they describe which values are observed in the

186   plots. However, the number and the properties of species theoretically able to penetrate into a

187   local community (also called the species pool) can profoundly influence these observed

188   values, and neglecting the effect of species pool can provide misleading conclusions (Kraft et

189   al. 2011). Controlling for species pool effects makes the observed values more comparable

190   and may provide insight into ecological mechanisms behind index values. Therefore, I also

191   calculated the following indices:

192   -   Community completeness – The size of the species pool has a well-known influence

193   on local richness (Cornell & Harrison 2014). Partel et al. (2013) suggested the

194   community completeness index to quantify the relationship between observed richness

195   and species pool size. Community completeness provides an improved understanding

196   of invasion processes (Bennett et al. 2016). Here I considered the total number of

197   species in the respective site as the size of species pool for each plot.

198   -   Standardized effect size (SES) of RaoQ and CWM. For each plot each index value

199   was re-calculated after randomly permuting abundance percentages in the plot across

200   all species in the site. These null-communities represented the hypothetical random

201   assembly of species from the species pool. It is notable that null-communities have the

202   same species richness and abundance distribution as the original communities; that is,

203   the null-hypothesis applied here includes the observed species occurrence matrix as a

204   constraint. This provides SES values independent from species richness and

205   abundance distribution. I calculated the proportion of randomized values lower than

206   the observed index value. Then, this probability was probit-transformed, thus resulting

207   in the respective quantile of the standard normal distribution. This method accounts

208   for eventual asymmetry in the distribution of index values of the random communities

209   (Botta-Dukát 2018). I used these SES values instead of the raw CWM and Rao

210   diversity values throughout the analyses.

211   I fitted generalized linear models (GLM) and generalized linear mixed models (GLMM) using

212   the site as random factor to find relationships of diversity indices and CWMs with the cover

213   of focal invasive species. In more detail, I considered as dependent variables the species

214   richness, community completeness, SES(RaoQ) for each trait and all traits combined, and

215   SES(CWM) for each trait. For trait-based indices, variants both with and without involving

216   *Asclepias* and *Solidago* were considered. Model with the invasives are expected to represent

217   how the recipient community as a whole changes due to the increasing contribution of

218   *Asclepias* or *Solidago*, while models without invasives target questions about community

219   assembly. I fitted four models:

220   1. ASC: In this model the only predictor is the cover of *Asclepias*: Y ~ [*Asclepias* cover]

221   2. SOL: Here the only main effect is the cover of *Solidago*: Y ~ [*Solidago* cover]

222   3. SUM: In this model the only main effect is the summed cover of *Asclepias* and *Solidago*: Y

223   ~ [*Asclepias* cover + *Solidago* cover]

224   4. INT: This model contains only the interaction term of percentage cover of *Asclepias*, and

225   that of *Solidago*: Y ~ [*Asclepias* cover] * [*Solidago* cover]

226   The error distribution was Poisson for the species richness and Gaussian for all the others. For

227   each pair of GLM and GLMM models using the same set of variables with and without

228   random factor, Akaike information criterion (AIC) was used to select the more parsimonious

229   model. Then, the model with the lower AIC of each pair (either GLM or GLMM) was

230   evaluated using Wald tests to test for significant effects of model terms. Although the main

231   effects (*Asclepias* cover, *Solidago* cover) are also tested in the INT model implicitly, I paid

232   attention only to the significance of the interaction term, since the others can be better tested

233   in the ASC and SOL models. In case one invasive species changes the effect of the other, the

234   interaction term should be significant. The SUM model was involved with the aim of sorting

235   out whether the identity or the absolute quantity of the invasive species plays significant role.

236   *p*-values were corrected using the sequential adjustment method by Holm (1979).

237   I tested the association between *Asclepias* and *Solidago* using Pearson's linear correlation

238   calculated on their cover percentages.

239   All calculations were done using the R software environment using the gawdis (de Bello et al.

240   2021), vegan (Oksanen et al. 2022), glmmTMB (Brooks et al. 2017), fundiversity (Grenié &

241   Gruson 2024) packages.

242   **Results**

243   *Asclepias* and *Solidago* showed a negative linear correlation (r= -0.3198, p=0.0038; Fig. 1).

244   When *Asclepias* and *Solidago* were not considered during the calculation of impact metrics,

245   significant relationships were found only in five models. The SOL model had a significant

246   negative effect on species richness (GLMM, z=-4.240, p=0.001; Fig. 2) and community

247   completeness (GLM, z=-4.784, p<0.001; Fig. 3), and a positive effect on the CWM of bud

248 bank (GLM, z=3.345, p=0.041; Fig. 4). The SUM model had similar but weaker relationship

249 with species richness (GLMM, z=-3.583, p=0.016; Fig. 2) and community completeness

250 (GLM, z=-3.723, p=0.01; Fig. 3).

251 When I included *Asclepias* and *Solidago* into the calculation of impact metrics, the

252 community completeness, the CWM of the clonal index, the CWM and the Rao diversity of

253 seed mass were negatively related with the SOL model. In contrast, the CWM of plant height,

254 as well as the CWM and the Rao diversity of the bud bank index increased with the SOL

255 model. Both the CWM and the Rao diversity of seed mass increased with the ASC model.

256 The CWM and the Rao diversity of bud bank, as well as the CWM of plant height increased

257 with the SUM model, while the CWM of the clonal index showed a negative dependence. The

258 INT model was not significant in any tests.

259

260 **Discussion**

261 I found contrasting relationship between the two invasive species and plot-level richness of

262 resident species. This is in agreement with most earlier studies presenting a negative effect of

263 invasive *Solidago* (Ledger et al. 2015, Pal et al. 2015, Wang et al. 2021a), and also supports

264 those claiming no negative effect of *Asclepias* on resident species richness (Szitár et al. 2014,

265 2018, Kelemen et al. 2016; but see Fenesi et al. 2023). Moreover, plot-level species richness

266 relative to species pool size, i.e. community completeness, of resident species also decreased

267 with *Solidago* cover. In case of models fitted on species richness, GLMM models proved to

268 be more parsimonious, while when the response variable was community completeness, GLM

269 acquired lower AIC values. GLMMs include the site as random factor to account for site-

270 specific patterns of species richness, while community completeness relates observed plot-

271 level species richness to the number of species at the site unobserved in the each plot. Hence,

272 controlling for site-specific effects seems to be a straightforward tool in the modelling of

273 species richness as a function of invasive cover (Bennett et al. 2016). This can be done either

274 by using random factors in the model, or by choosing a measure of richness standardized by

275 the species pool of the site. The importance of site-specificity is a sign of idiosyncrasy, a

276 common barrier in invasion research (Elliott-Graves 2016). Local sites vary in species pool

277 due to differences in environmental background and history (Cornell & Harrison 2014).

278 However, species pool determines the community-level response to invasion; therefore, site-

279 specificity must be controlled when searching for generalities in biological invasions (Bennett
280 et al. 2016).

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

293 The decreased local richness in the resident community with increasing dominance of
294 *Solidago* is commonly attributed to its competitive ability (Pal et al. 2015). However,
295 competition may act through different mechanisms that are scarcely explored yet in the
296 context of *Solidago* invasion (but see Wang et al. 2018, 2019, 2021b). Regarding *Asclepias*,
297 Kelemen et al. (2016) reported trait-level response of resident plants to *Asclepias* cover
298 despite no relationship with total species richness, while Fenesi et al. (2023) found decreasing
299 species richness and increasing Rao diversity among the rest of the community with
300 increasing *Asclepias* cover. Surprisingly, I found limited evidence of trait responses to
301 invasion. When *Asclepias* and *Solidago* were excluded from the calculation of CWM and Rao
302 diversity, the only significant response to any model was the increasing CWM of bud bank to
303 *Solidago* cover and to the summed cover of both invasive species. The bud bank is essential
304 for plant regeneration and individual-level persistence (Klimešová & Klimeš 2007), which
305 suggests that these ecological functions are important for resident plants to survive on
306 grasslands invaded by *Solidago*. Fig. 4 showed that with low *Solidago* cover, the SES of bud
307 bank score ranged close to zero, while it increased significantly with *Solidago* cover. This and
308 the relationship with species richness and completeness suggest that species with more
309 developed bud bank are more likely to co-exist with *Solidago*. Re-sprouting ability is a key
310 trait under biomass removal (Latzel et al. 2008, Herben et al. 2017), thus mowing of the sites
311 may also modulate the effect of traits in community assembly; even if the sampling plot size

312 and the dominance of invaders vary on a finer scale than on which mowing is carried out

313 (sites are mown uniformly). Nevertheless, bud bank can be correlated to reproductive traits or

314 some specific forms of vegetative growth, that I did not involve in the analysis, but might play

315 proximal role in competition.

316 Together with the above significant relationships, the overall effect of *Solidago* on the trait

317 composition and diversity of the resident species insufficiently explains why species richness

318 and community completeness decrease with *Solidago* cover. I suggest two non-exclusive

319 hypotheses on the reasons behind the weak explanatory power of trait-based models on

320 community response to *Solidago* invasion. According to a deterministic explanation,

321 decreasing richness/completeness is driven by a trait-based mechanism but not involving the

322 traits I considered in this study. I selected traits that are most commonly included in studies

323 dealing with community assembly. Among them, height is known as an important competitive

324 trait for plants (Klimešová et al. 2008, Violle et al. 2009), including Pannonian sand

325 grasslands (Lhotsky et al. 2016). Plant height of native species also responded to the invasion

326 of *S. canadensis* according to Wang et al. (2021b). High SLA is also considered a successful

327 strategy for plants of the recipient community to thrive under the invasion of alien species

328 (Kelemen et al. 2016, Loiola et al. 2018, Wang et al. 2021b). Of course, the availability of

329 measurements also played a role in selecting traits (Sonkoly et al. 2023). Other traits could

330 respond more specifically to *Solidago* invasion, e.g. root traits related to nutrient uptake

331 (Garbowski et al. 2020) or relationships with soil biota (Liao et al. 2015). This is reasonable,

332 because *Solidago* invasion causes fundamental changes in soil properties and biota (Zhang et

333 al. 2009, Wang et al. 2018b). Unfortunately, such trait data are not available in sufficient

334 coverage for the Pannonian flora. According to a stochastic explanation, species resisting

335 *Solidago* invasion do not obey any regularity; they are assembled randomly from the habitat-

336 specific species pool. Such a pattern could be expected, if *Solidago* outcompetes all species

337 with similar efficiency; therefore, increased *Solidago* cover simply reduces the area of the plot

338 suitable for existence of any other vascular plant. Higher *Solidago* cover allows fewer

339 individuals of other species to grow in the plot, and under stochastic assembly, these

340 individuals will represent fewer species. This mechanism can be reinforced by the stage of

341 succession on the study sites. The sites are mainly in the phases of early colonization after a

342 major disturbance (e.g. after ploughing), when random processes have a strong impact on

343 community assembly of sandy old-fields on fine spatial scales (Török et al. 2018, Halassy et

344 al. 2019, Csecserits et al. 2021). That is, community assembly might be stochastic on the sites

345 anyway, not just as a response to *Solidago* invasion.

346 When I considered *Asclepias* and *Solidago* during the calculation of plot-level CWM and

347 RaoQ, I found much more significant effects. One may argue this is trivial, since the covers of

348 *Asclepias* and *Solidago* contributed to both the predictors and the dependent variables of the

349 models thus involving circularity. However, the randomization procedure embodied the same

350 level of circularity; therefore, its effect was partialled out from the SES values of the raw

351 impact measures. Instead, I argue that the higher number of significant relationships is due to

352 that both species bear rare trait syndromes within the species pool; thus, their increased

353 contribution in a community affect both the mean trait value and the variation around it.

354 These relationships can be explained by the mass ratio hypothesis (Grime 1998).

355 One manifestation of the mass ratio hypothesis is the increased plant height CWM and RaoQ

356 with the SOL and SUM models, but only when the focal species were included in the

357 calculation. *Solidago* and *Asclepias* are among the tallest plants on sandy grasslands, and their

358 increasing contribution to the total cover of the communities naturally increases the CWM of

359 plant height. The Rao diversity of plant height also increases with increasing cover of tall

360 plants, if shorter plants are not excluded selectively.

361 Seed mass showed a strikingly different response to *Asclepias* and *Solidago* cover. While

362 CWM and RaoQ of seed mass increased with *Asclepias* cover, they decreased with *Solidago*

363 cover. The mass ratio hypothesis offers a parsimonious explanation here, too. *Asclepias* seeds

364 are among the heaviest ones in the species pool (SES = +1.44), while *Solidago* seeds are

365 moderately light (*S. gigantea*: SES = -0.694, *S. canadensis*: SES = -0.739). Hence, increased

366 cover of *Asclepias* increases the mean seed mass of the community, and also the variation

367 around it, if light-seeded species are not filtered out. In contrast, the dominance of light-

368 seeded *Solidago* naturally decreases the CWM of seed mass due to its increased contribution

369 in the community.

370 *Asclepias* and *Solidago* covers were negatively correlated. This is not surprising as they share

371 several resource acquisitive traits (height, extensive belowground organs, leaves distributed

372 evenly along the stem, similar leaf types, slightly shifted but overlapping phenology; Bagi

373 2008, Botta-Dukát & Dancza 2008) suggesting interspecific competition when getting in

374 close contact. The negative correlation between any pair of species reaching high cover

375 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 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.

Fenesi et al. (2023) recently emphasized difficulties in finding general patterns in the relationship of impact metrics 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 sand grasslands and 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 impact metrics 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.

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 metrics. 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.

409

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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666   Figure 1. Correlation of Asclepias cover and Solidago cover. The trend line is fitted with a

667   major axis linear regression.
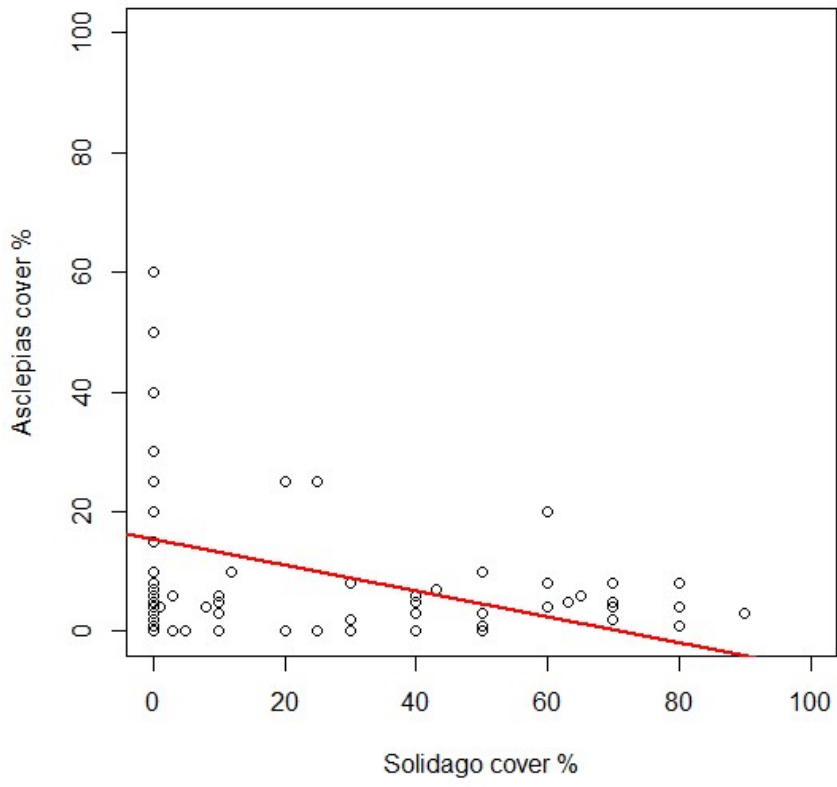
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671   Figure 2. Relationship of species richness with *Solidago* (left), *Asclepias* (centre) and

672   *Solidago + Asclepias* (right) cover percentage. Lines of different colours denote fixed slope

673   and random intercept model fits of individual sites from the GLMM models where the site

674   was a random factor. Solid lines: p<0.05, dashed lines: not significant.
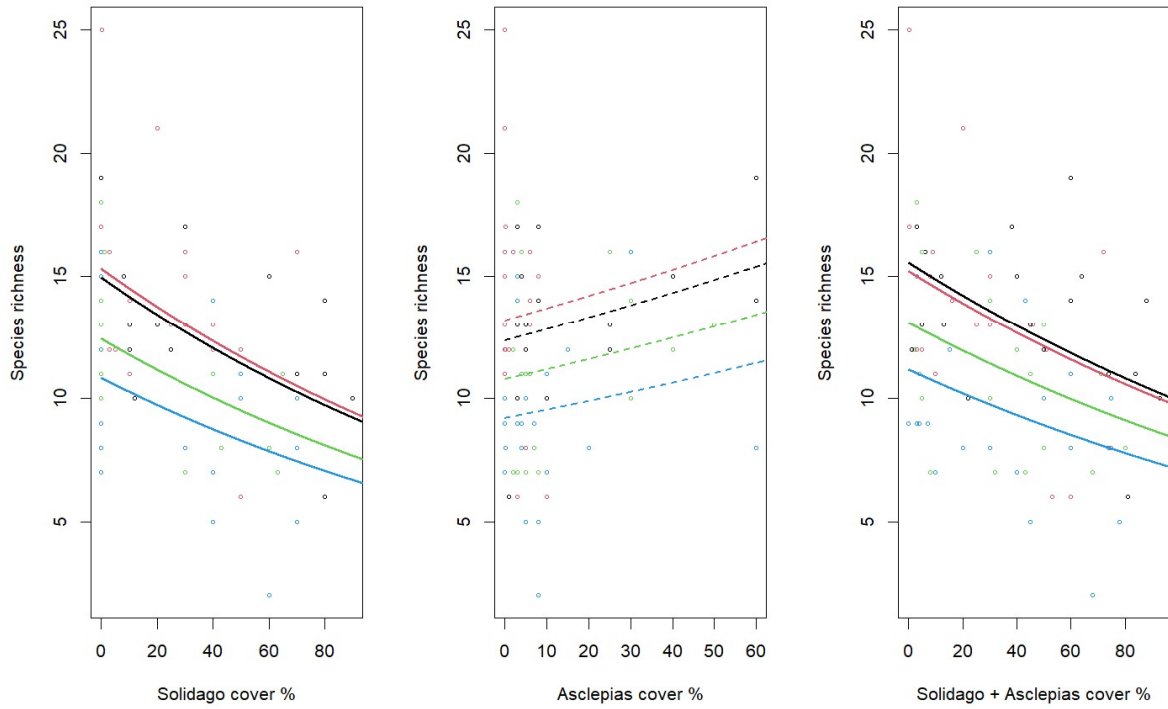
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677   Figure 3. Relationship of community completeness with *Solidago* (left), *Asclepias* (centre)

678   and *Solidago + Asclepias* (right) cover percentage. Point of different colours correspond with

679   study sites. The trend line is fitted with a GLM with plots from all sites pooled. Solid lines:

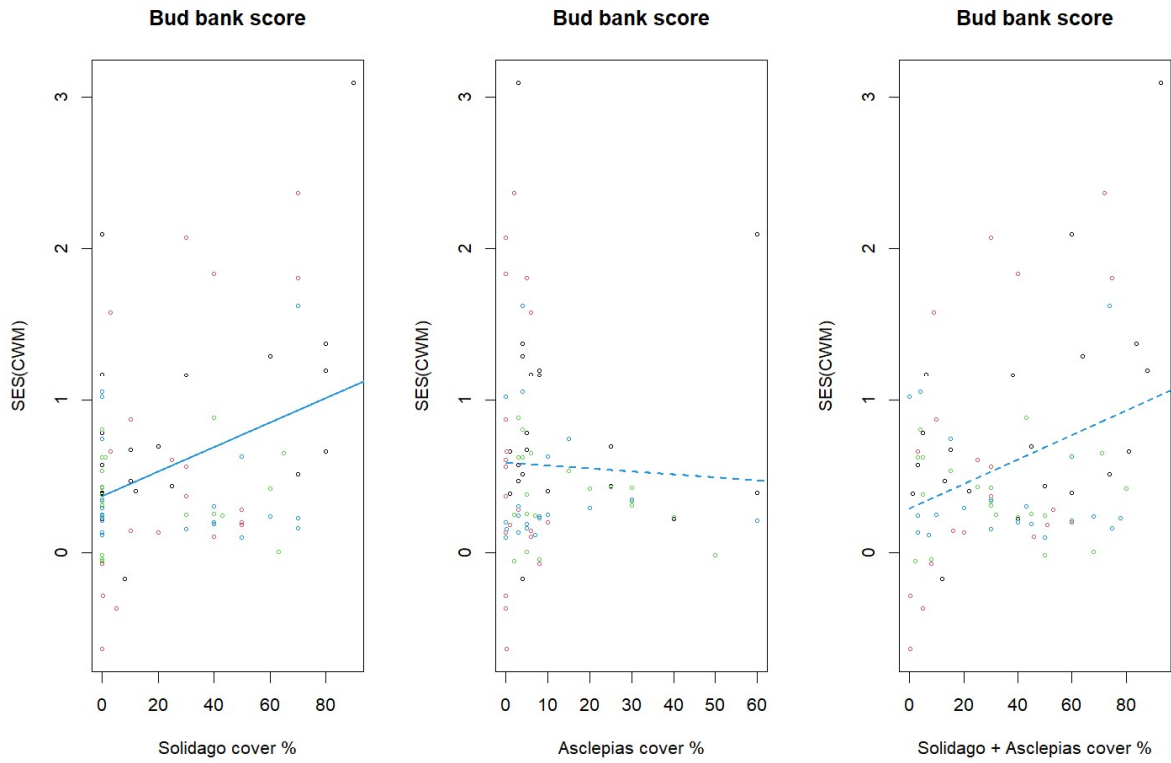680   p<0.05, dashed lines: not significant.

681
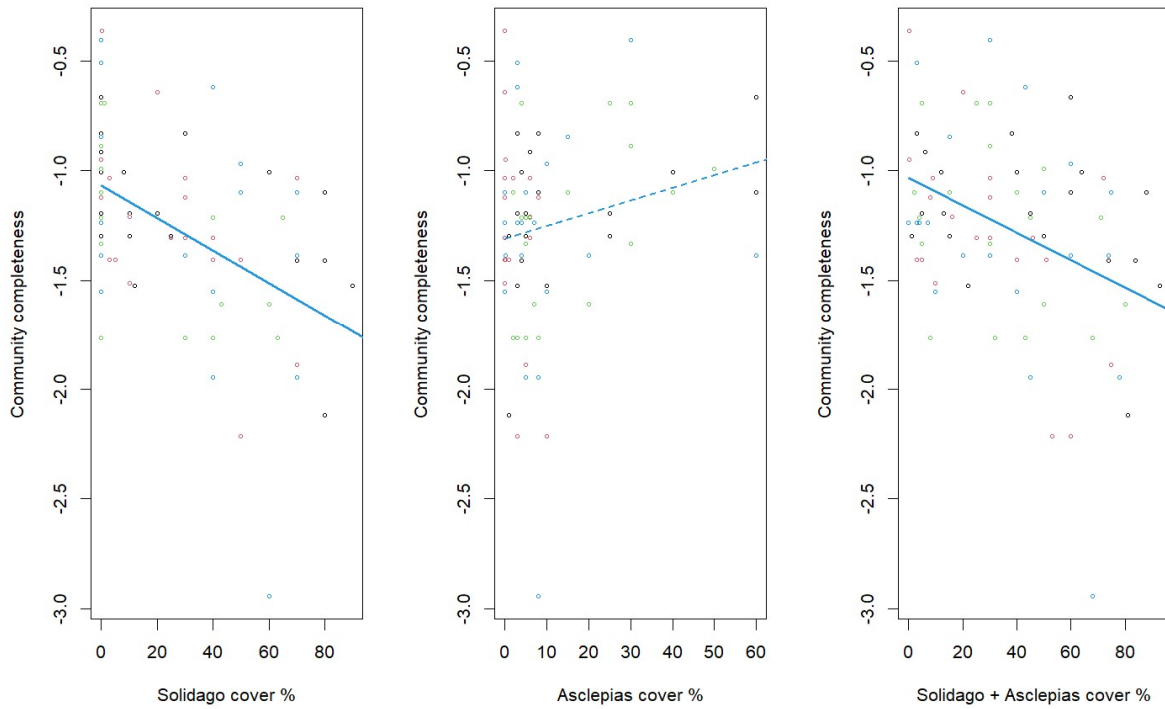
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685 Figure 4. Relationship of standardized effect size of the CWM of the bud bank index with

686 *Solidago* (left), *Asclepias* (centre) and *Solidago + Asclepias* (right) cover percentage. The

687 trend line is fitted with a GLM. Solid lines: $p<0.05$, dashed lines: not significant.

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691   Table 1. Wald test results of models and model terms (columns) related to impact metrics as

692   response variables (rows). The occurrence and trait values of *Asclepias syriaca* and *Solidago*

693   ssp. are not considered in the calculation of CWM- and RaoQ-based the response variables.

694   Bold numbers indicate significant effect. *Italics* indicate GLMM, normal font indicate GLM.

	INT		ASC		SOL		SUM	
	z	*p*	*z*	*p*	*z*	*p*	*z*	*p*
species richness	*-0.901*	*1*	*1.583*	*1*	***-4.240***	***0.001***	**-3.583**	**0.016**
community completeness	-1.007	1	1.744	1	**-4.784**	**<0.001**	**-3.723**	**0.01**
RaoQ-all traits	*-0.318*	*1*	*-0.725*	*1*	*-0.533*	*1*	*-0.934*	*1*
CWM-height	-0.208	1	0.906	1	0.71	1	1.226	1
CWM-SLA	*0.338*	*1*	*-0.841*	*1*	*-0.817*	*1*	*-1.282*	*1*
CWM-seedmass	*0.882*	*1*	*-1.89*	*1*	*-0.82*	*1*	*-1.855*	*1*
CWM-buds	-1.789	1	-0.388	1	**3.345**	**0.041**	3.217	0.063
CWM-clonal	*-0.306*	*1*	*-0.62*	*1*	*-1.049*	*1*	*-1.419*	*1*
RaoQ-height	*-0.045*	*1*	*-0.898*	*1*	*-1.844*	*1*	*-2.418*	0.687
RaoQ-SLA	*-0.812*	*1*	1.088	1	*-1.158*	*1*	*-0.776*	*1*
RaoQ-seedmass	*0.364*	*1*	*-1.611*	*1*	*0.143*	*1*	*-0.677*	*1*
RaoQ-buds	*-1.507*	*1*	*-0.744*	*1*	*2.826*	*0.217*	*2.525*	*0.521*
RaoQ-clonal	*-1.124*	*1*	*0.053*	*1*	*-0.334*	*1*	*-0.32*	*1*

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696

697 Table 2. Wald test results of models and model terms (columns) related to impact metrics as
698 response variables (rows). The occurrence and trait values of *Asclepias syriaca* and *Solidago*
699 ssp. are considered in the calculation of CWM- and RaoQ-based the response variables. Bold
700 numbers indicate significant effect. *Italics* indicate GLMM, normal font indicate GLM

	INT		ASC		SOL		SUM	
	SES	*p*	*SES*	*p*	*SES*	*p*	*SES*	*p*
species richness	*-0,488*	*1*	*1,042*	*1*	*-3,039*	*0,093*	*-2,613*	*0,314*
community completeness	-0,493	1	1,586	1	**-3,736**	**0,007**	-2,857	0,158
RaoQ-traits	-0,917	1	-0,714	1	-0,937	1	-1,36	1
CWM-height	0,375	1	1,872	1	*8,211*	*<0.001*	**11,377**	**<0.001**
CWM-SLA	*-0,983*	*1*	*-0,306*	*1*	*2,429*	*0,515*	*2,329*	*0,656*
CWM-seedmass	*1,368*	*1*	**5,383**	**<0.001**	*-6,23*	*<0.001*	*-2,97*	*0,113*
CWM-buds	*-0,792*	*1*	*-1,498*	*1*	*12,597*	*<0.001*	*10,034*	*<0.001*
CWM-clonal	*-0,589*	*1*	*-0,008*	*1*	*-6,272*	*<0.001*	*-6,693*	*<0.001*
RaoQ-height	*-1,567*	*1*	*0,183*	*1*	*0,141*	*1*	*0,244*	*1*
RaoQ-SLA	*-1,591*	*1*	*0,728*	*1*	*-1,167*	*1*	*-1,131*	*1*
RaoQ-seedmass	*1,873*	*1*	**4,413**	**<0.001**	*-4,745*	*<0.001*	*-2,024*	*1*
RaoQ-buds	*-0,725*	*1*	*-2,654*	*0,286*	*7,048*	*<0.001*	*5,114*	*<0.001*
RaoQ-clonal	-0,337	1	-1,024	1	-1,013	1	-1,612	1

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