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Similarity in Persistence Traits Is Important for CoExistence With Perennial Invasive *Asclepias syriaca* but Not Annual Invasive *Conyza canadensis*

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Keywords: *Asclepias syriaca* | *Conyza canadensis* | functional traits | Hungary | old-field | plant invasion | sandy grassland | trait similarity

ABSTRACT

Questions: What is the position of the two selected invasive alien species in the regional trait space? Does the probability of occurrence of a species depend on the interaction of its similarity to and the cover of the selected invasive species, *Asclepias syriaca* and *Conyza canadensis*?

Location: Hungary, Kiskunság, sandy grasslands.

Methods: We used data from a stratified random grassland survey (plot size: 25 m^2, $n = 161$). Our analysis focused on the two most common invasive species of studied habitats: clonal perennial *A. syriaca* and annual *C. canadensis*. Trait similarity between species was measured by weighted Gower distance using three sets of traits: (1) 12 traits covering all aspects of life history, (2) traits related to reproduction and (3) traits related to persistence. Calculated similarities were used to describe the position of the two focal invasive species in the trait space generated by all species. We fitted generalised mixed-effects models with the presence/absence of all species except *A. syriaca* and *C. canadensis* as dependent variables and trait similarity to, and cover of invasive species as predictors.

Results: We found that both invasive species were in the trait range of the regional species pool. *C. canadensis* was closer to the centre of regional trait space than *A. syriaca*. Similarity to *A. syriaca* and its cover interacted to influence the occurrence of the rest of the species: Where the cover of *A. syriaca* was higher, similar species occurred with a higher probability. We found no such effect of similarity in the case of *C. canadensis*.

Conclusions: These results suggest that for perennial invasive species *A. syriaca*, trait similarity may influence the composition of co-occurring species. In contrast, the results of annual *C. canadensis* suggest a more random assembly.

Abbreviations: LDMC, leaf dry matter content; SLA, specific leaf area.

Nomenclature: Király et al. (2009).

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1 | Introduction

Invasion ecology should be conceptually embedded in the framework of community ecology (Shea and Chesson 2002; Gurevitch et al. 2011), where the role of traits is often described by the metaphor of two filters: traits should allow each species to survive and reproduce in a given environment (abiotic or environmental filtering), and coexisting species should differ in traits related to population regulation to avoid competitive exclusion (biotic or limiting similarity filter) (Keddy 1992). It is generally assumed that abiotic filtering selects similar species; thus, the two filters counteract. The idea that these two opposing forces determine the success of invaders can be traced back to Darwin's main work (Darwin 1859). In the invasion biology literature, it is known as Darwin's naturalisation conundrum. In Bennett's (2019) interpretation: 'Successful invaders must be closely related to native species to possess the traits to tolerate that environment, but distantly related enough to possess traits allowing exploitation of underutilised niches, thereby minimising competition' (Figure 1a,b). Darwin wrote about (phylogenetic) relatedness; however, it is clear from the context that he always assumed that more closely related species share more similar traits. Since this assumption is not always fulfilled (Mayfield and Levine 2010), it is better to use trait differences instead of phylogenetic differences (Gallien and Carboni 2017).

The characteristics of successfully invading alien species can be described by functional traits (sensu Violle et al. 2007). Therefore, these are central factors in explaining the spread of invasive plants (Richardson and Pyšek 2006; Chytrý et al. 2008; Perkins et al. 2011). Using traits can lead to more comparable results across different ecosystems, indicate the mechanisms behind the success of invasive species and thus help understand the invasion process (Lemoine et al. 2016; Divíšek et al. 2018; Hulme and Bernard-Verdier 2018). The functional traits of invasive plants influence the invasiveness of alien species with respect to the trait distribution of native plant communities (as part of invasion resistance or habitat invasibility). The position of an invasive alien species in the trait space of the local species assemblage can give insights into the role of invasive alien species in the community and into the possible mechanism behind their success (Jones et al. 2010; Ordóñez et al. 2010; van Kleunen et al. 2010; Bennett 2019). Lemoine et al. (2016) pointed out that a species' position in the trait space may influence the occurrence frequency and local abundance of both native and alien species. This explains why invasive alien species are at the border of community trait

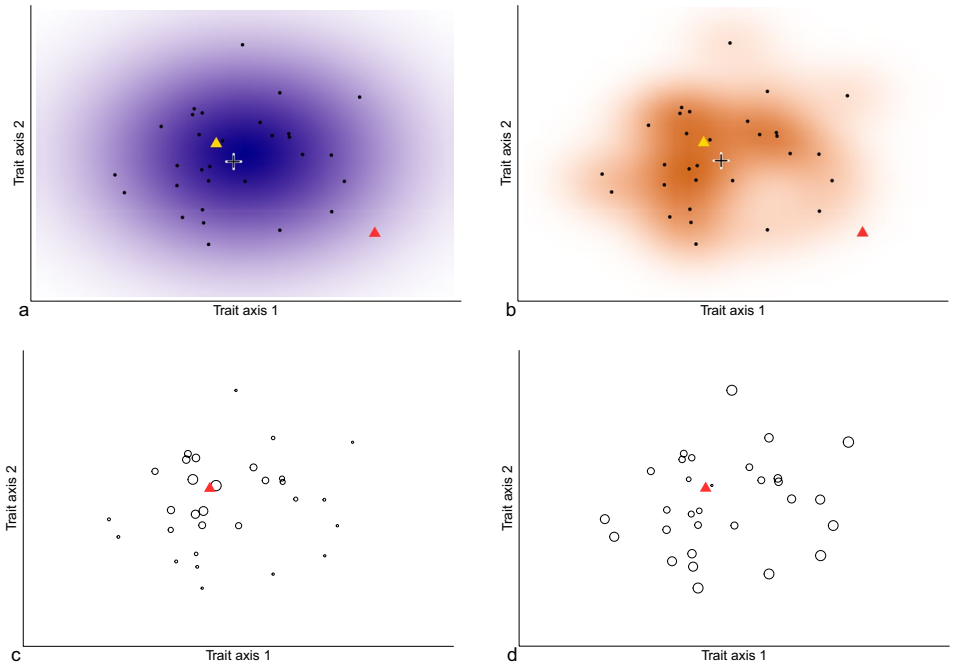

FIGURE 1 | Conceptual figures illustrating the tested hypotheses at the landscape (a and b) and local community (c and d) levels. Two trait axes represent the multidimensional trait space here; however, in the real data analyses, all axes were considered. Black dots and circles represent the resident species, while triangles denote the invasive ones. Cross in (a) and (b) shows the position of the centroid of the resident community. The intensity of the background colour indicates how well adapted a species is to the habitat (blue background) or how intense its competition with the resident community is (brown background). The species denoted by a yellow triangle is situated near the centroid; it is well adapted, but receives strong competition from the resident community. This trait combination can be successful if its good adaptation to the habitat can override the negative effects of strong competition. The species denoted by a red triangle is situated far from the centroid. It is not well adapted to the local conditions, but can succeed by avoiding the strong competition with the residents. The size of circles (c and d) indicates the probability of occurrence when the invasive species denoted by the red triangle is present. Species with high co-occurrence probability may be similar to the invasive species (c) or different from it (d). The former pattern suggests that adaptation to local conditions is the main driver of the trait pattern: Co-occurring species have to be similar. The latter pattern indicates the high importance of competition: The alien species invades communities whose species differ from it to avoid the strong competition from residents. Or the invader outcompeted the species similar to it, and only species that differ from the invader in their traits can co-occur with the invader.

space, while naturalised alien species are more similar to native ones (Divíšek et al. 2018; Loiola et al. 2018). However, little information is available on the traits of species that can coexist with dominant invasive species and the processes that drive coexistence.

Concerning the functional traits of a successful alien species and the processes of community assembly, the DNC can be formulated as the following two competing hypotheses: environmental filtering or limiting similarity. In the case of 'environmental filtering', certain traits are required for survival and reproduction in a given habitat, so the alien species must have similar traits to those of the native species (Bennett 2019). Alternatively, if 'limiting similarity' prevails in the assembly process, then the alien species must have different traits from the native species; otherwise, strong competition due to high niche overlap would hinder survival and spread (MacArthur and Levins 1967, Abrams 1983, Dawson et al. 2015, Figure 1b). The importance of environmental filtering and limiting similarity effects is influenced by several factors, including the scale of the study and the list of traits included in the analysis (Götzenberger et al. 2012). Plant individuals compete for resources primarily with their immediate neighbours; therefore, limiting similarity is more detectable at finer scales, while environmental filtering may act at coarser scales. That explains why studies comparing performance at regional and local scales have shown different mechanisms: environmental filtering at the large scale and limiting similarity at the local scale (e.g., Carboni et al. 2013, 2016; Gross et al. 2013).

Different mechanisms act through different plant traits, and different plant traits can differentially influence ecosystem processes, so studying individual traits or groups of plant traits can provide further insights into understanding community assembly and invasion processes (Thuiller et al. 2010; Bennett 2019; Hulme and Bernard-Verdier 2018). This suggests that different traits are linked to environmental filtering and limiting similarity. We can expect that environmental filtering acts mainly through persistence traits (e.g., leaf traits or clonality), while traits connected to reproduction (e.g., seed mass or flowering time) are better linked to dispersal and quick exploitation of new habitats.

Moreover, the success of non-woody perennial or annual species is determined by different traits (e.g., Fenesi and Botta-Dukát 2010). Perennial invasive species tend to invest more in persistence traits that ensure long-term survival in the community, often also resulting in a loss of diversity and a shift in the trait composition and functional diversity (Bartha et al. 2014; Nagy et al. 2020; Szymura et al. 2022). Perennial invasive species with guerrilla clonality are particularly problematic as they can effectively use the resources located in random distribution. This strategy can be successful in disturbed habitats or habitats with changing land use (Pyšek 1997; Song et al. 2013; You et al. 2014; Wang et al. 2017, 2019). On the contrary, short-living annual invasive species invest more in reproduction and can easily spread into recently disturbed habitats, like newly abandoned agricultural fields. Early arrival can determine the course of community assembly and also influence the invasion process (Halassy et al. 2023). However, native perennial species can effectively outcompete invasive annual species if appropriate conditions exist for their establishment (e.g., Kröel-Dulay et al. 2019).

In this research, we used a trait-based approach to study which species can coexist with the dominant invasive species and which processes drive the coexistence in dry sandy grasslands of the Kiskunság region. We investigated the position of two common invasive alien species, clonal perennial common milkweed (*Asclepias syriaca* L., from here: *A. syriaca*) and annual Canadian horseweed (*Conyza canadensis* (L.) Cronquist, from here: *C. canadensis*), in the regional trait space (Figure 1a,b). We studied the relationship between the co-occurrence with and similarity to the invasive species (*A. syriaca* or *C. canadensis*) (Figure 1c,d).

Our specific questions were: (1) Where are the two invasive species, *A. syriaca* and *C. canadensis*, located in the trait space of the dry grassland species pool of the Kiskunság region? (2) Does the probability of co-occurrence with the two invasive species depend on similarity to them in traits (based on the studied trait groups) and on the cover of the invasive species? We considered different sets of traits (persistence traits, reproductive traits and both groups of traits) for answering both questions. Based on Divíšek et al. (2018), we hypothesise that *A. syriaca*, as a dominant invasive species, is at the border of the trait space of the regional species pool for all sets of traits. While we hypothesise that *C. canadensis* is more integrated into the regional trait space, as it is a frequent species in the region, the cover of this species is rarely high.

2 | Materials and Methods

2.1 | Study Site and Field Sampling

We used the data of the Kiskun–LTER sampling site network [1]. The region is characterised by calcareous, nutrient-poor sandy soils and a dry climate. The network consists of 16 sampling sites with a size of 5 km × 5 km, established in 2007, which represent the variability in land use patterns of the region. In these sampling sites, we conducted a stratified random vegetation survey along the most dominant and typical habitats of the region; thus, these described the regional species pool well. A more detailed description of the sampling sites and sampled habitats can be found in Csecserits et al. 2016. In each sampling site, we sampled open and closed primary sand grasslands (namely grasslands that were not ploughed in the last 200 years) and secondary sandy grasslands (arable lands or vineyards abandoned between 1950 and 2006).

The studied primary sand grasslands (6260 Pannonic sand steppes in the EU Habitats Directive) are stress-dominated habitats (Lhotsky, Kovács, et al. 2016; Lhotsky, Csecserits, et al. 2016), and at the same time, are vulnerable to invasion (Botta-Dukát 2008). The open sand grassland (Eunis code: E 1.1, Chytrý et al. 2020) is characterised by a low cover of vascular plants 20%–80% cover of open soil surface or cryptogam layer. The dominant native grasses are *Festuca vaginata* and *Stipa borysthenica*. The closed grassland is characterised by a larger (70%–100%) cover of vascular plant species. The dominant native species of this vegetation type are *Festuca wagneri*, *Stipa capillata* and *Poa angustifolia*; however, *F. vaginata* and *S. borysthenica* can also be present (Csecserits et al. 2016, Eunis code: E 1.2, Chytrý et al. 2020). According to a recent survey in secondary

grasslands developing on abandoned arable fields or vineyards, they are similar in composition, but there are higher levels of invasion, mostly by *A. syriaca* (Csecserits et al. 2011, 2016, 2022).

The presence and visually estimated cover of each vascular plant species were recorded in 161 5 m × 5 m large plots between 2019 and 2021 (82 primary grassland and 79 secondary grassland plots). Thus, we could cover the regional species pool of the dominant dry grassland habitats. Vegetation types were considered during planning and sampling to represent the variation of vegetation, but they were not considered during the analysis, as we compared the invasive species with the rest of the local grassland species pool (from here, the rest of the species).

We found 254 plant species altogether. We excluded from further analysis the remnants of cultivation (e.g., *Vitis vinifera* and *Medicago sativa*), as these are not spontaneously established species. Shrubs and tree species were excluded from the analysis, as they are not characteristic of grasslands, exhibit substantial trait differences between juvenile and mature stages, and the database primarily provides trait information for mature individuals. We also excluded five species for which several trait values were missing. Consequently, 226 species were retained in the dataset.

2.2 | The Studied Invasive Species

The perennial common milkweed (*A. syriaca* L.) originated in North America and is invasive in Europe (Follak et al. 2021). It has guerrilla-type, creeping lateral rhizomes and, besides, has some deep-rooting branches which can grow even 1.5 m deep (Follak et al. 2021). The shoot of the plant contains milky sap. The flowers are compound; it is flowering from the end of June till the end of July. The pod contains many large seeds (7–10 mm long) with silky hairs. In Hungary, it is a widespread invasive species occurring both in primary and secondary habitats, like open sandy grasslands, abandoned arable lands or vineyards (Bagi 2008). *A. syriaca* can dominate abandoned fields even after several decades (Csecserits et al. 2016, 2022; Kelemen et al. 2016), and its control does not necessarily result in the restoration of natural vegetation (Berki et al. 2023).

The annual Canadian horseweed (*Conyza canadensis* (L.) Cronquist) also originates from North America (Thebaud and Abbott 1995; Weaver 2001; Bajwa et al. 2016). It is widely distributed in Hungary and is among the most frequent agricultural weeds (Novák et al. 2011). It germinates during autumn or winter, producing a basal rosette. During spring, it grows a shoot with many long, hairy leaves and many small white flowers. It produces small (1–2 mm long) seeds with pappus (Weaver 2001). While *A. syriaca* is considered the second most problematic invasive species in Hungary and is listed among the most important invasive plant species for Europe (Regulation [EU] 1143/2014), *C. canadensis* is only the 22nd in Hungary and has no European concern. Moreover, while 73 protected areas are impacted considerably by the invasion of *A. syriaca*, only three areas are impacted by *C. canadensis*, according to nature conservationists (Kézdy et al. 2018). The different views and opinions about the two species suggest that their performance differs in semi-natural habitats despite their wide distribution.

2.3 | Traits

To compare the traits of the two invasive species (*A. syriaca* and *C. canadensis*) with the traits of the rest of the species, we selected 12 functional traits, which are connected to ecosystem processes, such as reproduction, dispersal, vegetative growth and persistence (Westoby et al. 2002) (Table 1). Trait data were obtained mostly from regional databases containing our own measurements (Lhotsky, Csecserits, et al. 2016; Gyalus et al. 2022) or measurements from Hungary (Török et al. 2013, 2016; Sonkoly et al. 2023) and the Hungarian plant identification book (Király et al. 2009), and partly from international databases (LEDA: Kleyer et al. 2008, TRY: Kattge et al. 2020).

We considered three sets of traits in the analysis: (1) all 12 traits together, (2) vegetative traits, which are connected mainly to persistence (SLA, LDMC, life form, generative height minimum and maximum, lateral spread type and leaf distribution) and (3) reproduction traits, which are connected to sexual reproduction (seed mass, flowering start, flowering length, pollination type and dispersal type). Each subsequent analysis was done using each of these three trait sets.

3 | Data Analysis

The position of two focal invasive species in the trait space was characterised by two measures: (1) their distance from the centroid of the rest of the species and (2) the empirical cumulative distribution function of the distance (i.e., number of neighbours in trait space within a given radius) from the rest of the species. For this purpose, first, functional (trait) dissimilarity between each pair of species in the regional species list was calculated. The weighted version of Gower distance was used that allows giving equal importance to each trait irrespective of its variance and correlations among them (de Bello et al. 2021). Life form was used as a fuzzy trait, allowing multiple life forms (e.g., both annual and perennial). SLA, LDMC, seed mass and minimum and maximum generative height were log-transformed to achieve a normal distribution of these trait values in the dataset. To calculate the centroid, we transformed the weighted Gower distances into an Euclidean space by metric multidimensional scaling, and we calculated the centroid by averaging the coordinates along each axis (Legendre and Legendre 2012).

To answer the second question, namely to test whether the probabilities of species' presence are influenced by the dissimilarity of this species from the invader (*A. syriaca/C. canadensis*), the invader's cover and their interaction, we fitted a generalised linear mixed model. The presence/absence of the rest of the species was modelled by a binomial distribution with logit link. We supposed that environmental filtering and limiting similarity may act together, thus species should be similar enough to survive in the same environment, but dissimilar enough to lower the competition. Thus, avoidance of competition increases the dissimilarity, while struggling against the same environment decreases it. As a result of these two mechanisms, there can be an optimal dissimilarity when the probability of species presence is the highest. Therefore, we fitted a quadratic model for the dissimilarity (Botta-Dukát et al. 2022), including the interaction of the invader's cover with both the linear and quadratic

TABLE 1 | Functional traits of species used in the analysis and some basic information about these traits. Abbr: Abbreviation, Data completeness: Percentage of species for which we had data in the given trait. Min: Minimum value, Max: Maximum value. Data source: 1—LEDA, 2—own measurements published in Lhotsky, Csecserits, et al. (2016) and Gyalus et al. (2022), 3—Török et al. (2013), 4—Török et al. (2016), 5—Király et al. (2009) and 6—Sonkoly et al. (2023). For SLA and LDMC, we indicated the percentage of data origin. Regarding seed mass, both data sources contain seed measurements from Hungary.

Functional traits	Abbr.	Unit	Values of ordinal and categorical variables	Data source	Data completeness %	Min	Mean	Max	Connection with life cycle
Specific leaf area	SLA	mm^2/mg		1: 19%, 2: 80% 6: 1%	98.7	5.03	19.73	43	Persistence
Leaf dry matter content	LDMC	mg/g		1: 16%, 2: 83% 6: 1%	98.7	64.82	258.6	630.32	Persistence
Life form	LiF	Ordinal	Annual, biennial, perennial, geophyte and chamaephyte	5	100				Persistence
Generative height_min	GH_min	m		5	100	0.01	0.1991	1	Persistence
Generative height_max	GH_max	m		5	100	0.05	0.6613	3	Persistence
Lateral spread	LaS	Ordinal	No clonal, short clonal, long clonal	5	100				Persistence
Leaf distribution		Categorical	1: Rosette, 2: Semi-rosette, 3: Along the stem	5	100				Persistence
Seed mass	SM	g		3, 4	98.7	0.005	2.59	43.74	Reproduction
Start of flowering	FS	Month		5	100	2	5.38	8	Reproduction
Length of flowering	FL	Month		5	100	0.5	2.65	8	Reproduction
Pollination type	PT	Categorical	0: With insect, 1: Not obviously with insect	5	100				Reproduction
Dispersal type	DT	Categorical	1: Special organ for wind dispersal or small seed, 2: Different dispersal	5	100				Reproduction

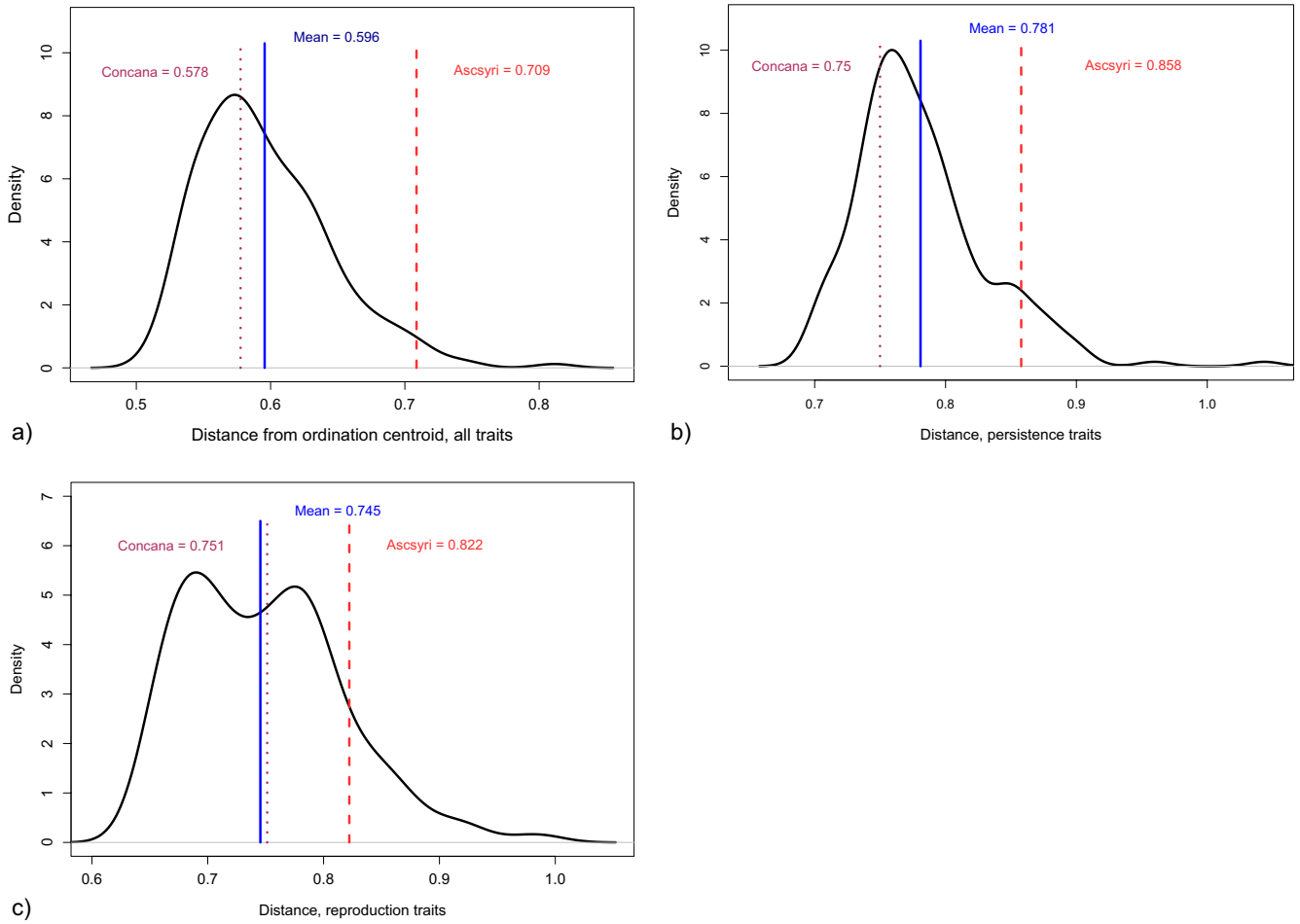

FIGURE 2 | The Kernel-density of the species distance from centroids of metric multidimensional scaling with the value of *Asclepias syriaca* (red) and *Conyza canadensis* (violet) and mean distance of 226 species from the centroid (blue), considering (a) all traits, (b) persistence traits and (c) reproduction traits.

terms of dissimilarity. In the quadratic model, the parameter of the quadratic term represents the tolerance width (i.e., speed of decay going away from the optimal dissimilarity), while the parameters of the linear and quadratic terms together determine the optimum. Including both interactions allows changing the optimum and tolerance width with changing invader cover independently from each other (Deák et al. 2024). The random part of the model was an analogue of ter-Braak's (2019) MLM3 model for handling two sources of non-independence of predictor: The same invader's covers were used for each native species and the same similarities to the invader used for each plot. The full model was:

$$\text{Presence} \sim \left(\text{dissim} + \text{I}\left(\text{dissim}^2\right)\right)^* \text{inv\_cover} + (1 + \text{inv\_cover}|\,\text{species}) + \left(1 + \text{dissim} + \text{I}\left(\text{dissim}^2\right)|\,\text{plot}\right)$$

where 'presence' means the probability of the given species occurrence in a given plot, 'dissim' means dissimilarity between the invasive alien species (*A. syriaca* or *C. canadensis*) and the focal plant species of the regional species pool, 'inv_cover' means the cover of invader (*A. syriaca* or *C. canadensis*) in percentage, 'species' means species identity and 'plot' means plot identity.

Non-significant interactions and quadratic terms were successively removed from the model to make the parameter estimates more robust. We built separate models for the three trait-based similarities and the two invasive species (*A. syriaca*/*C. canadensis*), resulting in six different models.

All statistical tests were performed in R version 4.1.3 (R Development Core Team 2022). We used the 'gawdis' function in the gawdis package (de Bello et al. 2021) to calculate the dissimilarity of species, the 'cmdscale' function to produce metric multidimensional scaling and the glmmTMB package (Brooks et al. 2017) for fitting GLMM models.

4 | Results

4.1 | Position in Trait-Space

We found that the two focal invasive species occupy different positions in trait space. In all three types of trait space (all traits, persistence trait and reproduction traits), *A. syriaca* is situated farther from the centroid (in other words, farther from a hypothetical species with average traits) than *C. canadensis* (Figure 2a–c). When considering all studied traits or traits

connected to persistence, *A. syriaca* occupies a position near the periphery of the regional trait space, being functionally more distinct than over 90% of the species (Figure 2a,b, Table 2). In contrast, when considering traits connected to reproduction, *A. syriaca* falls within the upper quartile of species (Figure 2c, Table 2).

On the other hand, *C. canadensis* is close to the centroid in all three types of trait space. Thus, *C. canadensis* is more similar to the centroid, based on either trait groups (Figure 2a–c, Table 2).

Considering the distance of the rest of the species to the two focal species, *C. canadensis* has more neighbours within medium distances than *A. syriaca* (Figure 3a–c). We list the similarity between the two studied invasive species and the rest of the species, indicating also the species most similar to the two invasive species in Appendix S1.

4.2 | Relationship Among Dissimilarity and Co-Occurrence

According to the fitted generalised linear mixed model, the probability of species' presence was influenced by the trait dissimilarity, the cover of *A. syriaca*, and their interaction when all traits or persistence traits were considered. Thus, the effect of

TABLE 2 | Distance of the two studied species from the ordination centroid and rank among the species (1: Closest) considering all traits (Dist_all), persistence traits (Dist_per) and c reproduction traits (Dist_rep). Number of species in the species pool: 226.

	Dist_all	Dist_per	Dist_rep
A. syriaca	0.709/220 (D1)	0.858/208 (D1)	0.822/196 (Q1)
C. canadensis	0.578/98 (Q3)	0.75/62 (Q3)	0.751/121 (Q2)

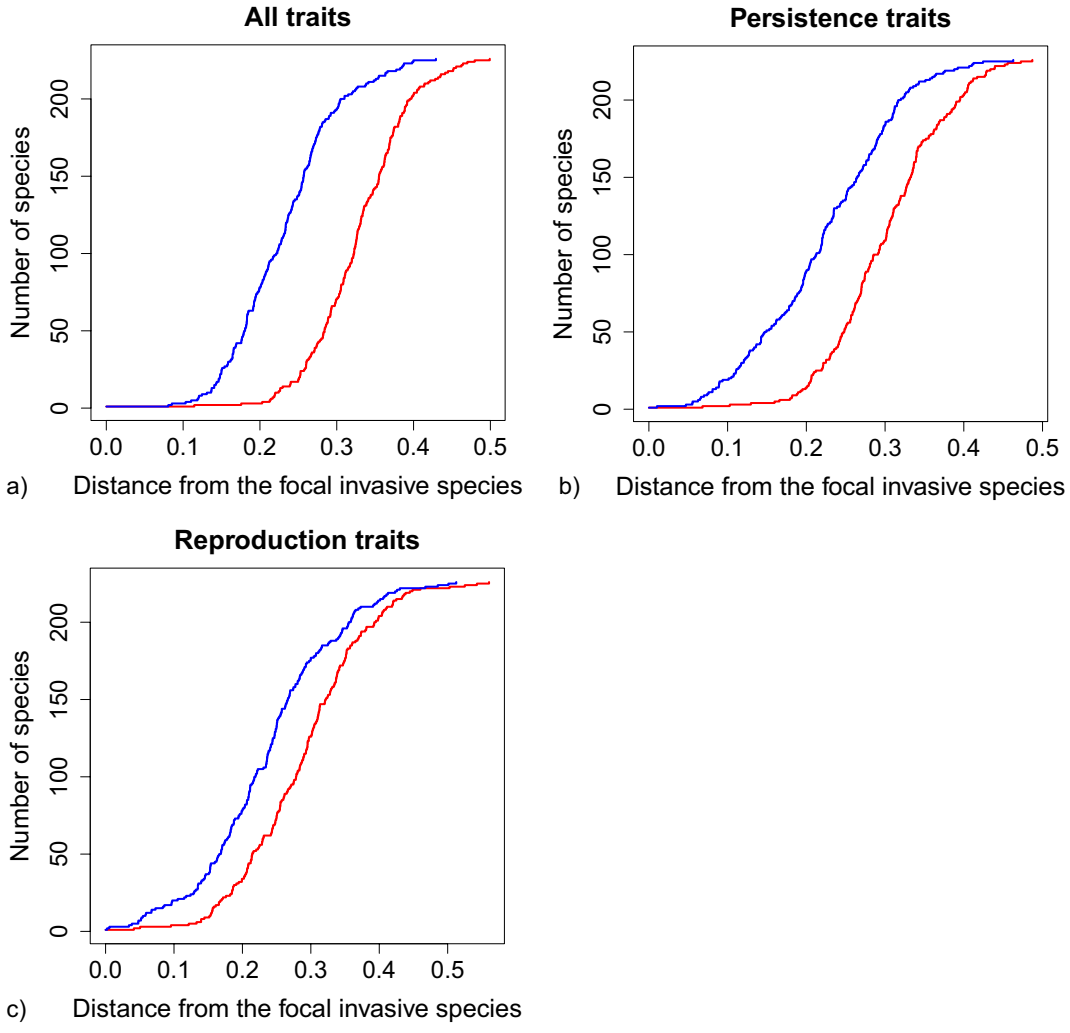

FIGURE 3 | Distance of remaining species to *C. canadensis* (blue) and *A. syriaca* (red) based on the metric multidimensional ordination considering (a) all traits, (b) persistence traits and (c) reproduction traits.

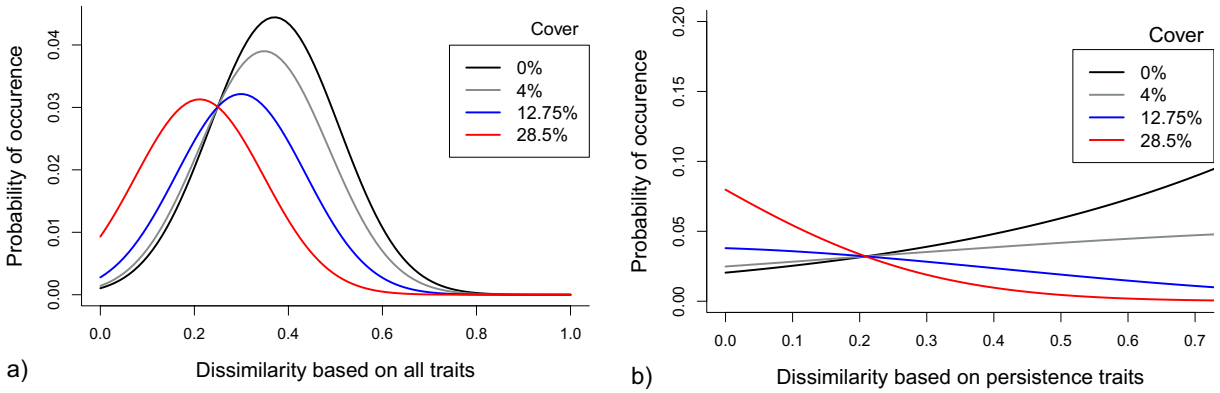

FIGURE 4 | The probability of species occurrence in the function of dissimilarity to *A. syriaca* in (a) all and (b) persistence traits. The different colours indicate different covers of *A. syriaca*; black: Absence, grey: 4% (median cover), blue: 12.75% (0.75 quantile of cover) and red: 28.5% (0.9 quantile of cover).

A. syriaca cover on the probability of occurrence of other species depends on their similarity to *A. syriaca* (Appendix S2). If a species is similar to *A. syriaca* (e.g., the dissimilarity is 0.1), the probability of its occurrence is higher at higher *A. syriaca* cover. At the same time, if a species is less similar to *A. syriaca* (e.g., the dissimilarity is 0.4), the probability of occurrence is higher if the *A. syriaca* cover is lower (Figure 4a,b). However, in the case of reproduction traits, the interaction was not significant (Appendix S2).

In the case of *C. canadensis*, there was no interaction between the species similarity and cover of *C. canadensis*—considering any of the three trait groups, only the cover of *C. canadensis* had a significant effect on the co-occurrence of the rest of the species (Appendix S2).

5 | Discussion

5.1 | Position in Trait-Space

Our study shows that the two dominant invasive species in the dry sandy grasslands of the Kiskunság region, *C. canadensis* and *A. syriaca*, fall within the trait range of the regional native species pool. However, their positions within this trait space differ markedly, suggesting distinct ecological strategies and potential impacts on native community assembly. *C. canadensis*, an annual species, is close to the regional trait centroid—implying functional similarity to a theoretical average species of the region. In contrast, *A. syriaca*, a perennial clonal species, is positioned at the periphery of the trait space, indicating greater functional distinctiveness.

The difference in position in the trait space between the two widespread invasive alien species suggests that different mechanisms may be responsible for their success. In the case of *C. canadensis*, the similarity to the regional species pool indicates that environmental filtering is an important mechanism for the establishment and high frequency of this species. This may explain why *C. canadensis* is considered a less problematic invader (Divíšek et al. 2018; Loiola et al. 2018; Kézdy et al. 2018). This mechanism selects among the alien species also in other grasslands, for example, in New Zealand mountain grasslands (Gross et al. 2013), European grasslands (Carboni et al. 2016) or a burned grassland (Pinto-Ledezma et al. 2020).

The position of *A. syriaca* at the edge of the regional trait space could be interpreted as a clue that limiting similarity can act even on this coarse scale, and its different trait composition is the reason behind the long-lasting success of *A. syriaca* in this region. Some other studies have also found that the distinct trait composition is the reason behind the success of invasive species (e.g., Mathakutha et al. 2019). It contradicts the interpretation that assumes that adaptedness to the local environment decreases monotonically with increasing distance from the centre in the trait space. This assumption does not hold if multiple trait combinations allow plants to survive and reproduce in the given environment (Marks and Lechowicz 2006; Pakgohar et al. 2024). It should be taken into account that 'evolution is contingent and imperfect' (Fridley and Sax 2014); thus, most competitive trait combinations may be missing from the native species pool. Tóth and BottaDukát (2008) proposed that some guilds, including tall herbs or herbs with guerrilla-type clonality, are underrepresented in the European flora ('unsaturated guilds'), thus, aliens belonging to these groups can easily invade habitats due to the lack of strong competition with natives belonging to the same guild. Following this logic, the border position of *A. syriaca* indicates that it filled a previously 'empty' niche (Divíšek et al. 2018; Bennett 2019).

However, *A. syriaca* is not situated totally out of the border of the trait space. One of the most similar native species in our regional species pool is *Calamagrostis epigeios*, a perennial clonal grass, with guerrilla-type clonality. This species can effectively spread in some grasslands; thus, sometimes *C. epigeios* is considered a native invasive species (Somodi et al. 2008; Házi et al. 2022; Axmanová et al. 2024). However, in most of the studied grasslands, it is not a problematic species, as this region is already too dry and nutrient-poor for it. These observations suggest that besides the studied traits, other traits could also be important for the local success of a species. Moreover, other factors not directly related to adaptedness and competitive ability (e.g., direct human dispersal) may also play an important role in the spreading of *A. syriaca*.

The selection of traits taken into account when evaluating the position of an alien species in the trait space of native species can be relevant to the results (Hulme and Bernard-Verdier 2018; Bennett 2019). For example, many studies use the SLA-height-seed mass triplet (e.g., Divíšek et al. 2018) to describe trait similarities. In our study, we used 12 traits to gain a more complex view of the position of species. Moreover, different traits may be important at different life stages (Heger 2001). The fact that we considered three different groups of traits helped us explore the possible processes and rules behind the observed patterns.

It is exciting that both invasive species are closer to the centre of the regional species pool when reproduction traits are taken into account. This suggests that their reproduction strategy is not novel to the region. According to recent hypotheses, appropriate and effective reproduction traits are important at the early stages of invasion and better-linked dispersal and quick exploitation of new habitats (Moodley et al. 2013). The traits describing persistence are more different from the native species pools in our case, especially in the case of *A. syriaca*, which is at the border of the trait space. Persistence traits are expected to be important at the later stage of invasion, namely in the case of already well-spread invasive species. The finding that the localisation of common invasive species in the trait space is different for traits connected to persistence or reproduction suggests these trait groups are under different rules (assembly processes). Reproductive traits are similar to those of native species in line with the environmental filtering hypothesis for both species, whereas differences in persistence traits suggest limiting similarity for *A. syriaca* only.

Although we involve as many traits as possible based on available data, there are some critical shortages: the traits we used do not cover the full trait spectrum of plant life. For example, there is less available information about the belowground traits (but see Guerrero-Ramírez et al. 2021). We could use only the lateral spread, and the three-level ordinated value of this trait could not describe the full complexity of the belowground part of plants. Some studies suggest a fine-scale niche separation between the species with different root traits (Luo et al. 2021; Semchenko et al. 2018; Zhou et al. 2024). Thus, the involvement of more traits connected to belowground traits could enhance our understanding. However, there is no detailed information about root traits for most of the species found in our study, so it is necessary to make measurements on belowground organs in this vegetation, too.

5.2 | Relationship Among Dissimilarity to and Co-Occurrence With the Invasive Species

Our result on the interaction between trait similarity and *A. syriaca* cover suggests a cover-dependent change in the filtering mechanisms. In the case of larger *A. syriaca* cover, an environmental filtering effect results in a selection for species more similar to *A. syriaca*. The large *A. syriaca* cover may indicate a specific environmental situation with a strong filtering effect working through persistence traits but not reproduction traits. As *A. syriaca* is a long-living perennial clonal species, once it becomes abundant, it can have a long-lasting effect on species assembly, especially during old-field succession. Some studies also found a connection between the similarity of invasive and the rest of the species and the probability of co-occurrence (Carboni et al. 2016; Rodrigues et al. 2024).

The relationship between trait similarity to and coexistence with *A. syriaca* indicates that this species might be able to drive community assembly once it reaches high cover, primarily through persistence traits, implying that environmental filtering is more important than limiting similarity during this process. Given the low abundance of *A. syriaca*, even dissimilar species may co-occur with this species. This suggests that lowering the amount of *A. syriaca* can help the long-term survival of a more diverse species assemblage. Thus, nature conservation actions should aim at reducing the abundance of *A. syriaca*, which is in many cases a more feasible goal than total eradication. On the other hand, the predominant assembly rule at the local scale, environmental filtering, implies that prevention or control of invasive *A. syriaca* is less likely to be achieved by sowing native species with similar plant traits.

In the case of *C. canadensis*, similarity to the invader does not affect the occurrence of the rest of the species considering any of the trait groups. *C. canadensis* was close to the centroid of the trait space; thus, it can be considered a less 'outstanding' species concerning the local species pool. It is a short-living, annual species, which is a common trait combination in our species assemblage and *C. canadensis* is confined to recently disturbed (early successional) habitats (Csecserits et al. 2016; Bajwa et al. 2016). Our results confirm that even if the cover of *C. canadensis* is large, no processes are selecting either for similar or dissimilar species, contrary to Wu et al.'s (2019) findings, who found that the effect of *C. canadensis* on native communities is dependent on its abundance. Thus, we can conclude that in our case, in such habitats (e.g., dry grasslands and old fields), the random processes are the dominants, similar to other studies (Schleicher et al. 2011; Marteinsdottir et al. 2018), or there is a parallel and equalising effect of the two opposite assembly processes—of the limiting similarity and environmental filtering. Our results support the experience of nature conservation experts that *C. canadensis* is not a driver of changes and therefore is not a real conservation problem (Kézdy et al. 2018).

These findings highlight the importance of considering trait dissimilarity and invasion intensity simultaneously when assessing the ecological impacts of alien species. Moreover, our results support previous work suggesting that functionally distinct invaders can exert stronger filtering effects on native communities (e.g., Funk et al. 2008; Carboni et al. 2016). Future studies should investigate whether these patterns persist across other ecosystems and for species with different life histories or invasion stages.

6 | Conclusions

Our contrasting results for the two species provide important lessons about their role in the system and, consequently, the management needs. Neither studied species was outside of the species trait space, indicating that invasive species are also selected by environmental filtering at the regional scale, as expected due to

the stressed environment. *C. canadensis* was well integrated in the regional trait space. Higher dissimilarity was observed for *A. syriaca*, which was close to the edge of the range of persistence traits and the full trait set considered, indicating the importance of limiting similarity for this species. The result that traits connected to reproduction or persistence show a different pattern suggests that they are affected by different processes.

We proved that perennial invasive species *A. syriaca* have a density-dependent influence on community composition. The co-occurrence of species similar to *A. syriaca* at high cover indicates that environmental filtering is the primary process once *A. syriaca* becomes abundant, while at lower cover dissimilar species can also coexist with the invader, which can be interpreted as a sign of limiting similarity, whereas results for annual *C. canadensis* are indicative of a more random assembly.

Overall, our results suggest that perennial *A. syriaca* exhibits a trait pattern typical of the successful invader described by Bennett (2019), in that it not only has a similar trait complex to the native species to tolerate the local environment, but also differs enough to exploit vacant niches and that it might also have a density-dependent effect on community assembly, thus highlighting it as a conservation priority invasive species. The annual *C. canadensis* follows a different strategy; it is better integrated into its environment and can be a successful invader because of good dispersal ability and a fast life cycle. Given that trait similarity does not influence co-occurrence with *C. canadensis*, we can assume that random processes explain community assembly, and thus it is a less significant invader from the nature conservation point of view.

Author Contributions

A.Cs. and Z.B.-D. conceived of the research idea; A.Cs., B.B., E.Cs., M.H., A.M. K.Sz. conducted the field survey; A.C. and Z.B.-D. performed the analysis A.Cs., Z.B.-D. and M.H. wrote the paper; and all authors revised and commented on the manuscript.

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Conflicts of Interest

Zoltán Botta-Dukát is Editor-in-Chief of the journal and co-author of this article. He was excluded from the peer review process and all editorial decisions related to the acceptance and publication of this article. Peer review was handled independently by the receiving Editor, Dr. Viktoria Wagner and handling Editor, Dr. Meelis Pärtel to minimise bias. The authors declare no conflicts of interest.

Data Availability Statement

Data are available at Zenodo (https://zenodo.org/). The reference number of data is: DOI https://doi.org/10.5281/zenodo.16411176 and of the R script is: DOI https://doi.org/10.5281/zenodo.17122418.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** The dissimilarity value of each species to the two studied invasive species, *Asclepias syriaca* and *Conyza canadensis*. **Appendix S2:** Summaries of final models.