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Research Article

Hidden fronts of invasion: Fine-scale boundaries reshape native plant communities

László Bakacsy[1]

1 *Department of Plant Biology, Institute of Biology, Faculty of Science and Informatics, University of Szeged, Szeged, H-6726, Hungary*
Corresponding author: László Bakacsy (bakacsy.laszlo@szte.hu)

Abstract

Invasion-driven ecological transitions remain underrepresented in fine-scale analyses, despite their central role in reshaping native vegetation. This study investigated how the invasive species *Asclepias syriaca* alters community structure at the boundaries of invaded and non-invaded sandy grasslands in Central Hungary. Using high-resolution transect sampling and quantitative boundary detection methods (Moving split window analysis with Squared Euclidean distance and Differential Renkonen index), compositional discontinuities were assessed across six transects representing spatial replicates of invasion front zones within a shared invasion context. The results reveal that significant vegetation boundaries – termed "novel ecotones" – frequently precede or lag behind the visible shoot front of *A. syriaca*, indicating complex, non-linear invasion dynamics. These boundaries vary in sharpness, width, and spatial offset, suggesting that *A. syriaca* impacts community structure beyond its current spatial distribution. Contrary to expectations, species richness remained relatively stable, with shifts primarily affecting species dominance patterns rather than outright loss. The identification of ecotonal dissimilarity maxima demonstrates that spatial boundary metrics can help reveal invasion-related spatial patterns and can inform conservation and management strategies, particularly in identifying ecologically sensitive transitional zones. The approach appears more suitable for detailed ecological assessment and management planning than for rapid early detection. In particular, it may help identify transition zones where early intervention could be more effective. This study contributes to the integration of invasion ecology and boundary theory, emphasizing the spatial dimension of biotic restructuring by invasive species.

Key words: Differential Renkonen index (DREN), dissimilarity analysis, invasion ecology, moving split-window (MSW), spatial ecology, squared Euclidean distance (SED), vegetation boundary

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Introduction

Biological invasions are among the major drivers of global biodiversity loss, with well-documented ecological and socio-economic impacts (Seebens et al. 2017; IPBES 2023). While these impacts are often assessed at broader spatial scales, the fine-scale mechanisms through which invasive plants interact with and restructure native communities remain less understood (Powell et al. 2013). In particular, traditional approaches based on comparisons between invaded and non-invaded sites may overlook the spatial complexity of invasion front line and the gradual nature of compositional change (Beckage et al. 2011). These limitations point to the need for spatially explicit approaches that treat invasion as a gradient process unfolding across ecological boundaries (Fortin and Dale 2005).

Ecotones are transition zones between ecological communities, characterized by changes in species composition, structure, or function across space (Delcourt and Delcourt 1992). Invasive species can contribute to the formation of such boundaries through mechanisms including competitive interactions, allelopathy, and feedback processes that restructure community composition (Hierro and Callaway 2003; Eppinga et al. 2006; Hobbs et al. 2006). These invasion-driven transitions may form spatially complex and dynamic boundaries, yet their fine-scale empirical characterization remains limited, particularly at active invasion fronts. Integrating spatial boundary analysis into invasion ecology shifts the perspective from binary invaded–uninvaded comparisons toward gradient-based processes. In this context, invasion-driven ecotones can be interpreted as spatial expressions of community reorganization, providing insight into how invasive species alter vegetation structure across boundaries.

Asclepias syriaca L. (common milkweed) is a clonal, rhizomatous perennial native to North America, and currently one of the most rapidly spreading invasive species in Central Europe. Its success is linked to both vegetative propagation and seed production, enabling persistent expansion and resistance to management efforts (Bakacsy and Bagi 2020; Follak et al. 2021). In addition to vegetative dominance, it can exert allelopathic effects and alter soil moisture, thereby suppressing native species regeneration (Bakacsy et al. 2024; Tölgyesi et al. 2024). In sandy grasslands of Hungary, it forms dense stands that restructure native plant communities and promote biotic homogenization (Follak et al. 2021). These processes can give rise to spatially structured, invader-induced boundaries – so-called novel ecotones – that are unlikely to be explained solely by broad-scale abiotic gradients, although fine-scale environmental heterogeneity was not explicitly quantified (Delcourt and Delcourt 1992; Fortin and Dale 2005).

This paper uses high-resolution spatial sampling and quantitative boundary detection methods to assess how *A. syriaca* alters native community structure along its invasion front. The central research questions are: (i) Can a transition zone – a novel ecotone – be detected between *A. syriaca*-dominated and native vegetation? (ii) What is the structural nature of this boundary: sharp, gradual, or zonal? (iii) How can boundary characteristics (contrast, sharpness, width, and potential asymmetry) be quantified? (iv) Is there a spatial offset between the visible invasion front and the point of maximal compositional change? (v) How does *A. syriaca* affect species associations in the boundary zone? It is hypothesized that *A. syriaca* not only replaces native species locally but also induces spatially structured transitions in vegetation. These effects are expected to vary based on habitat heterogeneity and species interactions, with compositional changes potentially preceding visible colonization. By identifying and characterizing these invasion boundaries, this study aims to deepen the conceptual link between invasion ecology and spatial boundary theory, providing insights into invasion processes and potential management implications.

Materials and methods

Study site

The study was conducted in the strictly protected core area of the UNESCO Biosphere Reserve near Fülöpháza, located within the Kiskunság National Park, Central Hungary (46°52'N, 19°25'E; Fig. 1). The region lies within the Danube–

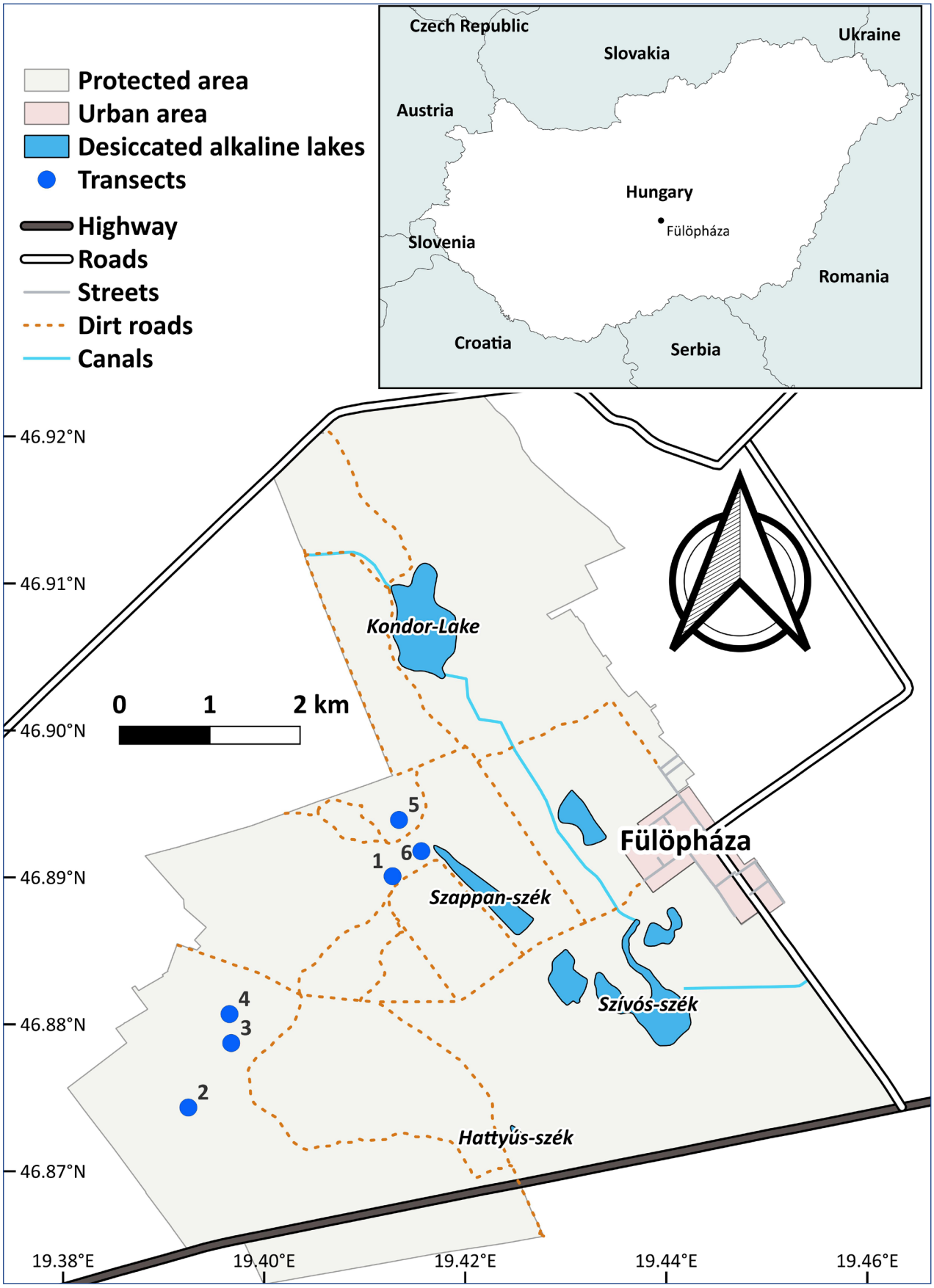


Figure 1. Location of the six selected transects in this study. The inserted image in the upper right corner shows the special protected Fülöpháza Sand Dunes, as a part of Kiskunság National Park in Central Hungary.

Tisza Interfluve, a unique landscape characterized by calcareous sand dunes, and is part of the Pannonic sand steppe habitat (Natura 2000 code: 6260), a priority ecosystem under the EU Habitats Directive (92/43/EEC) due to its high biodiversity and endemic flora (Molnár et al. 2011; Erdős et al. 2018). The climate is temperate continental with sub-Mediterranean influences, featuring increasing annual temperatures and erratic precipitation patterns over recent decades (Bartha et al. 2022). Based on long-term climatic records, the mean annual temperature ranges between 10–11.3 °C, and the mean annual precipitation is approximately 520–582 mm (Kovács-Láng et al. 2000; Szitár et al. 2014). The soil is a weakly developed, nutrient-poor calcareous sand with over 95% sand content, low humus (<1%), and very low water-holding capacity (Kovács-Láng et al. 2000). The groundwater table typically lies below 2 m depth (Tóth 1996). The native vegetation is dominated by open perennial sand steppe grasslands (*Festucetum vaginatae*), often forming a mosaic with forest-steppe patches (*Junipero-Populetum*), where *Populus alba* L. and *P.* × *canescens* (Aiton) Sm. form small groves (Molnár et al. 2011). The grasslands are typically dominated by two perennial bunchgrasses: *Festuca vaginata* Waldst. & Kit. ex Willd. (endemic to the region) and *Stipa borysthenica* Klokov & Prokudin in Wulf., which occur in various proportions depending on local microtopography, moisture availability, and disturbance regimes (Fekete 1992; Biró and Molnár 1998). The vegetation is typically sparse, with total vascular plant cover around 30–35%, and an additional cryptogamic layer of mosses and lichens covering bare ground between tussocks (Csecserits 2007; Fűrész et al. 2022).

A total of six invaded stands of *Asclepias syriaca* were selected for sampling in May–June 2023. Sites were chosen to represent a gradient in shoot density and spatial invasion patterns, covering a range of structural configurations across the sand steppe landscape. Site selection criteria included the exclusion of areas near roads, wheel tracks, or locations subject to intense trampling, in order to minimize anthropogenic disturbance as a confounding factor in vegetation structure. Furthermore, all selected stands and their respective transects were positioned to avoid significant topographical variation, which could otherwise influence vegetation patterns independently of the invasion process. The spatial locations of selected stands were mapped using QGIS version 3.40.7 (QGIS Development Team 2024) (Fig. 1).

Although detailed site-specific historical data are limited, *A. syriaca* has been present in the Kiskunság region since at least the early 20th century, with documented expansion in sandy grasslands driven by both clonal growth and seed dispersal (Follak et al. 2021). While precise invasion trajectories at the selected transects are unknown, the studied stands likely represent different stages of a long-term regional invasion process. According to available land-use classifications (MePAR system 2026), the studied sites are located within semi-natural grassland categories, including areas designated as Natura 2000 habitats, indicating a relatively low level of direct anthropogenic disturbance.

Sampling and sampling design

Field sampling was carried out during the peak vegetation season in May–June 2023, under stable weather conditions to ensure optimal detection of vascular plant and cryptogam presence. In each of the six selected stands, a single 12 m × 1 m linear belt transect was established, positioned perpendicular to the *Asclepias syriaca* invasion front (Fig. 2). The transects were placed using a gradsect approach

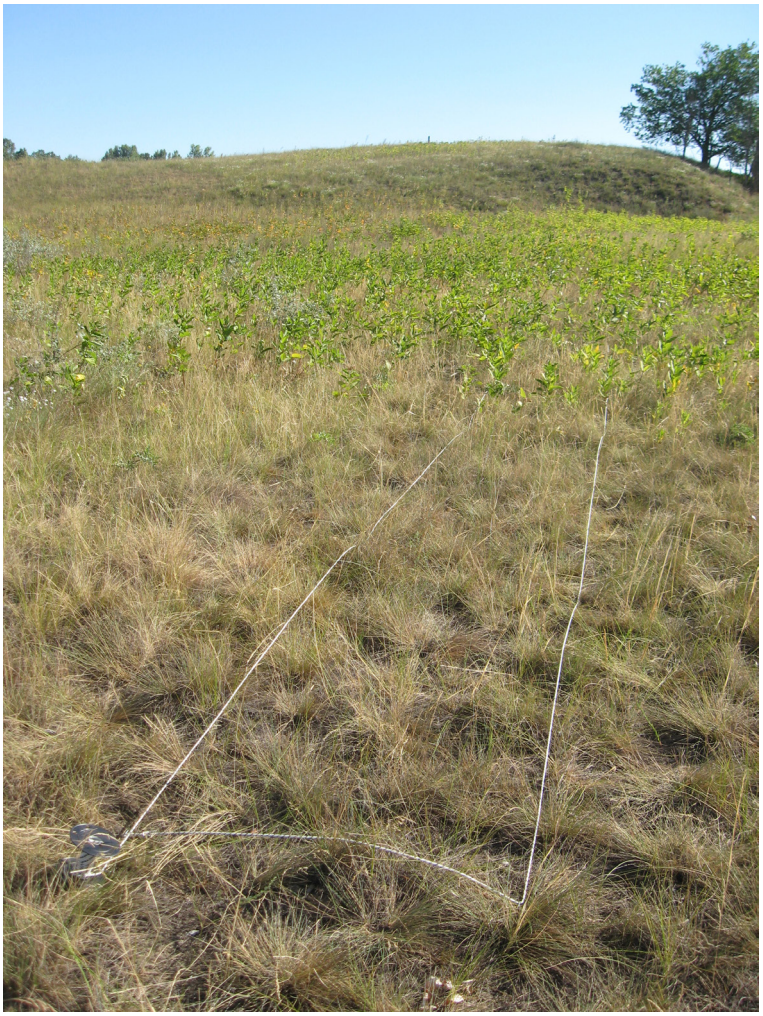


Figure 2. The location of the fourth transect (12 m × 1 m). Almost half of the transect is located in vegetation dominated by common milkweed (invaded vegetation), while the remaining part is in natural vegetation.

to maximize the detection of species turnover and spatial discontinuities across the invaded and adjacent non-invaded vegetation. Each transect was subdivided into 1200 contiguous 10 cm × 10 cm sampling units (quadrats). Transects were deliberately positioned (not randomly) so that the central section (6 m) contained the last detected shoots of *A. syriaca*, ensuring that the invasion front was captured within the transect. This design ensured consistent representation of invaded, non-invaded, and transitional vegetation within each transect. Thus, transect placement was constrained rather than random, ensuring that each transect intersected a clearly identifiable invasion front. Transects were selectively placed to capture clearly identifiable invasion fronts while minimizing major environmental heterogeneity. The selected transects were treated as spatially independent sampling units within a shared invasion context, as they were located in spatially separated stands without direct physical connection. However, they should be interpreted as spatial replicates within the same invasion context rather than fully independent invasion events.

Within each quadrat, species presence was recorded in each 10 cm × 10 cm quadrat for all vascular plants, mosses, and terricolous lichens, and the data were later aggregated into frequency values for analysis. Species identification followed Király (2009) for vascular plants, and Kecskés et al. (2003) for bryophytes and lichens.

Data processing and statistical analysis

To identify and characterize vegetation boundaries along the invasion front, the Moving Split Window (MSW) technique was applied, which is a commonly used method for detecting discontinuities in one-dimensional ecological data sets (Erdős et al. 2014). MSW profiles were generated using the bord-ER software developed by Körmöczi and Varró (2015), which allows for the computation of dissimilarity profiles and confidence limits based on randomization procedures. The method is based on computing dissimilarity between adjacent segments (half-windows) of a transect, and identifying significant peaks in the resulting dissimilarity profile that correspond to boundaries. Although vegetation data were recorded at a resolution of 10 cm × 10 cm quadrats, data were aggregated across the full width of the transect (1 m). For each 10 cm segment along the transect, species frequencies were calculated as the number of occupied quadrats (out of 10), resulting in a one-dimensional dataset capturing fine-scale variation in species composition. In practice, the MSW compares species composition between adjacent segments of the transect using sliding windows, allowing the detection of positions where compositional change is maximized. In the present study, these segments correspond to 10 cm × 1 m units derived from aggregating presence data across the transect width, ensuring that comparisons reflect fine-scale variation in species frequencies along the transect. The MSW analysis was applied to this frequency-based dataset, where dissimilarity was calculated between adjacent segments (half-windows) of increasing size to capture scale-dependent patterns. This transformation results in a one-dimensional sequence derived from the original two-dimensional sampling design, which is suitable for boundary detection analysis (Körmöczi and Varró 2015; Körmöczi et al. 2016; Erdős et al. 2018). Half-window widths ranged from 1 to 10 segments, corresponding to 10–100 cm along the transect (with each segment representing a 10 cm × 1 m unit). Thus, dissimilarity was calculated between adjacent segments of 10–100 cm on each side of the moving window, allowing the detection of boundaries at multiple spatial scales. At each position along the transect, dissimilarity was calculated between two adjacent segments of equal size (half-windows), and this comparison was repeated while moving along the transect, generating a dissimilarity profile. This approach effectively transforms the original two-dimensional sampling design into a one-dimensional sequence suitable for boundary detection.

The Squared Euclidean Distance (SED) was primarily used as the dissimilarity function, as it is sensitive to differences in species frequencies across adjacent segments, and is commonly applied in boundary detection studies. In addition, to further capture differences in species composition and detect asymmetrical species turnover across the invasion front, dissimilarity profiles were also calculated based on the Differential Renkonen Index (DREN). This index is particularly suitable for identifying sharp changes in species relative frequencies and has been shown to effectively highlight vegetation transitions in heterogeneous environments. The transect data were analyzed with increasing half-window widths to examine the scale-dependent nature of boundary structure. The full raw and standardized dissimilarity profiles for both SED and DREN across all transects are provided in the Supplementary material (Suppl. materials 6, 7).

To determine statistical significance of detected boundaries, the random shift permutation method was employed (a form of restricted randomization), with

1000 Monte Carlo iterations used to generate null models based on species-level shifts within the transect, preserving spatial autocorrelation patterns (Körmöczi et al. 2016). This approach minimizes the scale-dependency of the expected dissimilarity profile and provides more reliable detection of significant discontinuities.

The resulting dissimilarity values were standardized using Z-score transformation, where the observed dissimilarity values were compared to the distribution of values obtained from the randomized data sets. A threshold of Z = 1.65 as critical value (corresponding to a one-tailed test at $p = 0.05$) was used to identify statistically significant peaks, i.e., vegetation boundaries (Zalatnai et al. 2007, 2008). Only peaks exceeding this threshold were considered true compositional discontinuities.

Profiles were interpreted by examining peak height (indicating boundary sharpness or contrast), peak width (representing the spatial extent of the transition) and boundary position (i.e. the spatial location of the transition along the transect). These parameters were used to distinguish among sharp edges, gradual gradients, and extended transition zones (novel ecotones) across the invasion front. Due to the linear layout of transects, boundary curvature could not be estimated.

Results

To provide context for the boundary analyses, basic patterns of species richness and dominance were first examined across transects. A total of 21 to 38 vascular plant species were recorded per transect (Table 1, Suppl. material 1). The invasive *Asclepias syriaca* occurred with consistently high abundance across all transects (42–64 individuals), indicating its dominance across the sampled transects. The highest shoot count was observed in Transect 1 (64), and the lowest in Transect 2 (42), although these differences were moderate. Several other species showed notable dominance or codominance patterns, including *Secale sylvestre* Host (e.g. 788 shoots in Transect 1), *Stipa borysthenica* (51–457 shoots across transects), and *Tortula muralis* Hedw., which occurred in very high numbers in all transects (1044–1199 individuals). Certain taxa were highly localized yet abundant, such as *Bothriochloa ischaemum* (L.) Keng in Transect 6 (744) and *Carex liparicarpos* Gaudin (545) also in Transect 6, suggesting microhabitat variation (Table 1). Species richness was highest in Transect 6 (38 species), which also showed high total abundance and co-occurrence of multiple dominant species. Interestingly, no clear inverse relationship was observed within the sampled transects between *A. syriaca* abundance and total species richness, indicating that the species was integrated into relatively diverse communities rather than entirely displacing other taxa (Table 1, Suppl. material 1). These patterns provide context for interpreting the spatial vegetation discontinuities analyzed below, where shifts in species dominance and frequency patterns were assessed using dissimilarity indices.

The bottom row shows the number of species recorded per transect (Species number), and the location of the invasion front line (in meters), defined as the position of the last observed *A. syriaca* shoot along each transect. A dash (–) indicates absence of the species in the respective transect.

To characterize structural transitions between invaded and non-invaded vegetation, two key spatial markers were compared along each transect: the invasion front line (IFL) – defined as the position of the last observed shoot of *Asclepias syriaca*, representing the visible edge of the species' distribution – and the ecotonal dissimilarity maximum (EDM) – defined as the location(s) of statistically signif-

Table 1. Species abundances recorded along six vegetation transects located at the boundary between *Asclepias syriaca*-invaded and non-invaded patches. Values represent the total number of individuals observed per species in each transect.

Species	Transects					
	1	**2**	**3**	**4**	**5**	**6**
Achillea ochroleuca	-	-	-	12	-	-
Alkanna tinctoria	-	-	7	-	-	1
Alyssum desertorum (*turkestanicum*)	7	-	9	52	34	36
Anthemis ruthenica	-	-	-	1	-	65
Apera spica-venti	-	-	-	1	-	-
Artemisia campestris	14	-	17	-	10	-
Asclepias syriaca	64	42	63	51	58	57
Asparagus officinalis	-	-	-	2	-	-
Bassia laniflora	27	101	27	197	6	47
Bothriochloa ischaemum	-	76	32	235	-	744
Bromus tectorum	63	81	252	202	-	430
Buglossoides arvensis	-	-	-	-	-	7
Carex liparicarpos	-	-	-	-	-	545
Centaurea arenaria	3	-	1	8	-	6
Cerastium semidecandrum	-	5	6	21	2	57
Chenopodium album	-	-	1	-	-	-
Chondrilla juncea	-	1	-	-	3	2
Conyza canadensis	-	-	1	1	2	98
Crepis rhoaedifolia	6	-	1	9	4	485
Equisetum ramosissimum	-	141	-	575	51	177
Eryngium campestre	-	-	-	26	4	34
Euphorbia segueriana	28	24	14	14	-	6
Festuca vaginata	-	25	212	419	474	19
Galium verum	-	-	-	2	-	-
Koeleria glauca	38	-	-	-	2	1
Linaria genistifolia	-	-	-	-	26	2
Medicago minima	58	3	19	5	7	59
Minuartia glomerata	3	8	14	49	-	8
Minuartia viscosa	7	-	-	-	-	-
Muscari comosum (*Leopoldia comosa*)	-	-	-	-	-	31
Plantago indica/arenaria	-	1	-	-	-	54
Poa angustifolia	-	-	-	-	-	16
Polygonum arenarium	23	62	17	105	-	218
Scabiosa ochroleuca	-	-	1	9	-	2
Secale sylvestre	788	569	429	575	9	468
Silene alba/latifolia	-	1	6	-	-	-
Silene conica	12	40	9	35	1	30
Silene otites	-	-	1	-	1	-
Stipa borysthenica	457	230	51	166	397	184
Stipa capillata	41	11	-	10	11	-
Syrenia cana	-	42	65	42	-	23
Thymus glabrescens subsp. *degenianus*	-	-	-	-	23	-
Tortula muralis	1199	1174	1044	1199	1184	1188
Tragopogon floccosus	-	-	2	5	1	3

Species	Transects					
	1	2	3	4	5	6
Verbascum phlomoides	-	-	-	-	1	7
Veronica praecox	-	-	28	-	-	-
Vicia cracca	-	-	1	-	3	4
Viola arvensis	6	-	2	-	6	100
Cladonia convoluta	73	187	64	-	1	1
Cladonia furcata	6	21	27	-	-	-
Cladonia magyarica	-	-	-	-	248	1
Species number	21	22	31	29	27	38
Invasion front line (m)	6.5	6.2	7.4	6.5	6.6	6.3

icant peaks in vegetation dissimilarity, as calculated by the SED and DREN. The spatial offset between these two markers provides insight into the structure and dynamics of the invasion boundary.

SED is a widely applied measure for detecting shifts in community composition, calculated as the sum of squared differences in species abundances between adjacent plots. It is sensitive to differences in species frequencies and changes in dominance. Transect 1 displayed two moderate EDM at 5.4 m (Z = 1.833) and 5.6 m (Z = 1.670), while the invasion front line was observed at 6.5 m. This indicates a 0.9 m forward shift of the invader beyond the compositional discontinuity zone (Fig. 3, Suppl. materials 2, 4). In Transect 2, a single significant EDM occurred at 6.9 m (Z = 2.300), positioned 0.7 m beyond the invasion front line at 6.2 m. Transect 3 exhibited a more complex structure, with multiple EDM clustered between 3.9–4.2 m (Z = 1.849, 2.551, 2.271, 1.778). The invasion front line was detected considerably further along, at 7.4 m, resulting in a 3.2 m gap (Fig. 3, Suppl. materials 2, 4). In Transect 4, the EDM at 6.1 m, 6.3 m, 6.5 m, and 6.6 m (Z = 1.819–2.226) closely matched the invasion front line, observed at 6.5 m – indicating a near-coincident spatial alignment (Fig. 3, Suppl. materials 2, 4). Transect 5 presented an ecotonal dissimilarity zone between 3.6–3.8 m (Z = 3.146, 2.471, 1.782), while the invasion front line was located at 6.6 m. This represents a 2.8 m offset, where *A. syriaca* had expanded well beyond the primary compositional shift (Fig. 3, Suppl. materials 2, 4). In Transect 6, a pronounced EDM was recorded at 5.2 m (Z = 2.774), whereas the invasion front line occurred at 6.3 m – a 1.1 m forward extension of the species beyond the dissimilarity boundary (Fig. 3, Suppl. materials 2, 4). The corresponding full dissimilarity profiles underlying these patterns are provided in Suppl. material 6.

To complement the SED analysis, vegetation discontinuities were also examined using the DREN, which captures relative dissimilarities in species dominance between adjacent plots. As before, positions of statistically significant dissimilarity peaks (ecotonal dissimilarity maxima) were compared with the invasion front line along each transect (Fig. 4, Suppl. materials 3, 5). Transect 1 did not exhibit any ecotonal dissimilarity maxima based on DREN values. The absence of detectable change may indicate a more homogeneous dominance structure or a more gradual transition not captured by this index. In Transect 2, multiple ecotonal dissimilarity maxima were detected: three peaks in the early section at 1.4 m, 2.1 m, and 2.4 m (Z = 1.640, 1.694, 1.885), and two peaks later at 6.7 m and 6.8 m (Z = 1.841, 1.744). The invasion front line, located at 6.2 m, fell within the range of the latter peaks, indicating spatial overlap between community change and the species

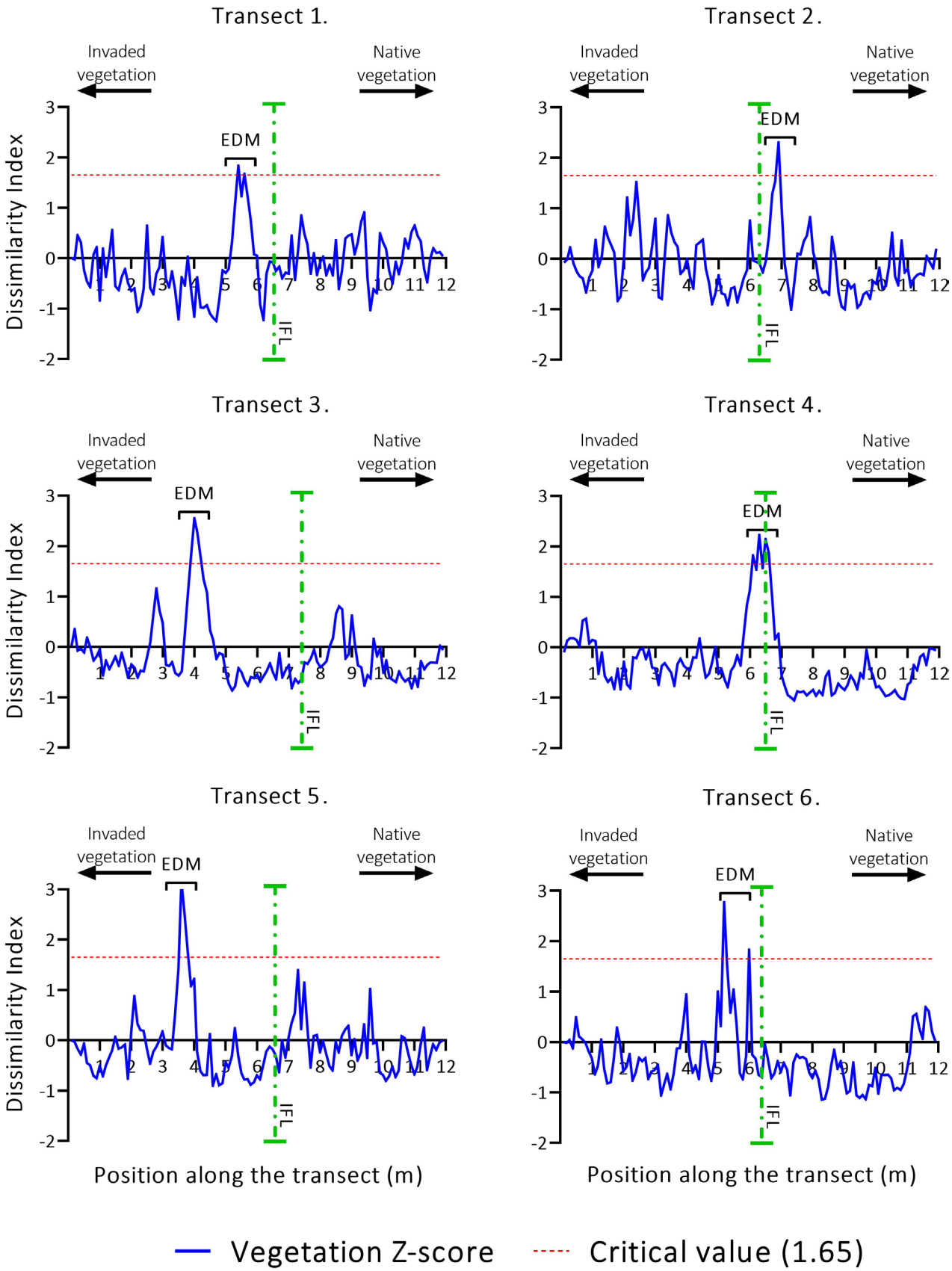


Figure 3. Dissimilarity profile of the six invaded-native boundaries transects. Calculated using Squared Euclidean Distance (SED) average Z-scores. IFL – invasion front line, EDM – ecotonal dissimilarity maximum.

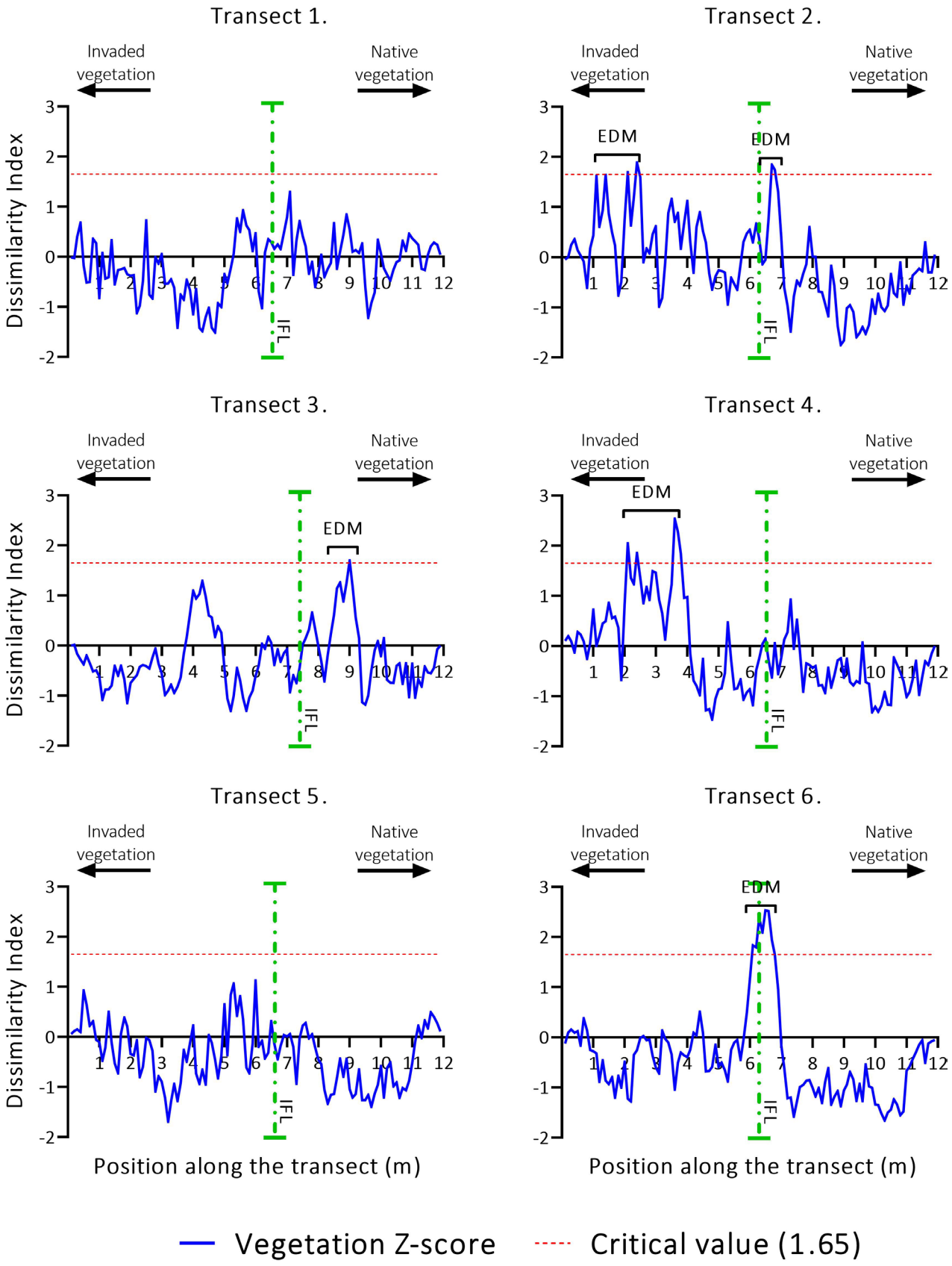


Figure 4. Dissimilarity profile of the six invaded-native boundaries transects. Calculated using Differential Renkonen Index (DREN) average Z-scores. IFL – invasion front line, EDM – ecotonal dissimilarity maximum.

boundary (Fig. 4, Suppl. materials 3, 5). Transect 3 displayed a single ecotonal dissimilarity maximum at 9.0 m (Z = 1.699), situated 1.6 m beyond the invasion front line at 7.4 m. This forward offset suggests a possible legacy zone or subtle shifts in dominance persisting after the visible shoot limit (Fig. 4, Suppl. materials 3, 5). In Transect 4, two distinct ecotonal dissimilarity zones were detected: one between 2.1–2.4 m (Z = 2.046, 1.852), and another between 3.6–3.8 m (Z = 2.535, 2.275, 1.842). Both zones precede the invasion front line at 6.5 m, suggesting pre-front structural changes in community composition. Transect 5 did not exhibit any statistically significant ecotonal dissimilarity maxima based on DREN. This may reflect a smoother species dominance gradient, or insufficient sensitivity of the metric under the given conditions (Fig. 4, Suppl. materials 3, 5). Transect 6 revealed a broad, continuous ecotonal dissimilarity zone extending from 6.1 m to 6.8 m (Z = 1.652–2.529). The invasion front line, located at 6.3 m, was situated within this zone, indicating overlap between dominance shifts and shoot presence (Fig. 4, Suppl. materials 3, 5). The complete DREN-based dissimilarity profiles are available in Suppl. material 7.

In most transects, the location of maximum compositional dissimilarity did not coincide precisely with the final shoot of common milkweed, frequently occurring either before or beyond the invasion front. The distance between the last shoot and the nearest dissimilarity peak ranged from near-perfect overlap (Transect 4) to over 3 meters (Transect 3), suggesting substantial variability in boundary sharpness and transition width. These spatial patterns may reflect underlying differences in the structure and progression of the invasion front and justify further analysis of boundary dynamics.

Discussion

Across all six transects, *Asclepias syriaca* occurred at consistently high shoot numbers (42–64), indicating its strong establishment at the studied patch edges. Importantly, this dominance was not associated with a marked decline in species richness. In fact, transects with higher *A. syriaca* counts (e.g. Transect 3 and Transect 6; Table 1) also showed high total richness and co-occurrence of several other dominant taxa such as *Secale sylvestre*, *Stipa borysthenica*, and *Tortula muralis*. This pattern indicates that, within the studied transects, *A. syriaca* was not associated with reduced species richness at the invasion front, but can instead alter dominance hierarchies, potentially shifting competitive balances rather than eliminating co-occurring species entirely (McKinney and Lockwood 1999; Powell et al. 2013). High shoot numbers of localized dominants (e.g. *Bothriochloa ischaemum*, *Carex liparicarpos*; Table 1) point toward small-scale habitat heterogeneity that could influence both invasion trajectory and boundary formation. These patterns probably reflect fine-scale microhabitat variation (e.g. soil moisture or microtopography), which may influence both invasion dynamics and boundary formation. In this context, boundary detection based solely on visible *A. syriaca* presence can underestimate ecological changes already in progress within the studied system.

An important result of this study is the systematic comparison between the invasion front line (IFL) – the last observed *A. syriaca* shoot – and the ecotonal dissimilarity maximum (EDM), i.e. the spatial position of statistically significant vegetation discontinuities, derived from SED and DREN metrics. In most transects, EDM and IFL did not spatially coincide. Rather, offsets ranging from 0.7

to 3.2 m were observed, with no consistent directionality: in some cases, EDM preceded the IFL (e.g. Transect 1, Transect 3, Transect 5; Fig. 3), while in others it lagged behind (e.g. Transect 2 for SED; Fig. 3, and Transect 3 for DREN; Fig. 4). This variability suggests that vegetation responses to invasion are not spatially uniform within the studied system, and that changes in community composition may either precede or follow the visible spread of the invader. In particular, Transect 3 exhibited the largest spatial gap (3.2 m) between IFL and SED-based EDM (Fig. 3), suggesting that structural changes in the vegetation may already be detectable before the arrival of visible shoots – which likely reflect processes operating ahead of the visible front, such as microclimatic effects, competition, or below-ground interactions (Powell et al. 2013; Zalatnai et al. 2007, 2008), although these were not directly tested in this study. Empirical observations by Bakacsy and Bagi (2020) similarly indicate that *A. syriaca* exerts ecological influence beyond its current shoot margin, particularly in disturbed or formerly treated areas, where vegetation reorganization can precede recolonization. In contrast, Transect 4 displayed near-complete spatial alignment between IFL and EDM, indicating a sharper transition boundary. Such patterns resemble the "limes convergens" concept by van der Maarel (1976), where ecological filters produce abrupt transitions in response to both biotic and abiotic constraints. These microsites may represent threshold-type boundaries, where *A. syriaca* expansion is constrained by edaphic or community resistance factors (Bakacsy 2019). DREN-based profiles often revealed additional or shifted EDMs relative to SED, suggesting the potential value of combining multiple indices. Since DREN captures relative changes in species dominance, it may detect diffuse or legacy-driven transitions that are less apparent in presence–absence-based approaches. This aligns with Zalatnai et al. (2008) and Delcourt and Delcourt (1992), who emphasized that different dissimilarity metrics reveal distinct facets of community boundaries.

The spatial patterns observed across transects are consistent with the concept of "novel ecotones" – transition zones not primarily explained by measured abiotic gradients, although unmeasured fine-scale environmental variation (e.g. moisture or microtopography) may also contribute, and these transitions are also associated with biotic restructuring linked to invasive species. In practical terms, these zones may represent areas where community reorganization is likely already underway, even if the visible invasion front has not yet reached them. While the notion of novel ecosystems is well-established (Hobbs et al. 2006; Morse et al. 2014), its extension to ecotonal contexts remains underdeveloped. In the case of *A. syriaca*, these ecotones were characterized by non-linear boundaries, variable offsets, and heterogeneous sharpness, ranging from abrupt to gradual shifts, as well as asymmetry, where compositional change is more pronounced on one side of the front. Such structurally diverse transitions may reflect a combination of processes, including propagule pressure and competitive displacement of resident species (Dainese et al. 2017). They are also likely shaped by disturbance-driven feedbacks, in which changes in vegetation promote conditions favorable to the invader, reinforcing its spread and ecological impact. Similar processes have been documented in grassland–forest mosaics, where boundary zones with directional shifts were described as ecologically meaningful and historically dynamic (Erdős et al. 2014). In the present study case, however, the transitions may not be fully explained by major abiotic gradients alone. This suggests that part of the observed boundary structure may be influenced by fine-scale environmental heterogeneity, although

this was not explicitly quantified in this study. The concept of novel ecotones can be useful for describing such invader-generated boundaries, which may be associated with ongoing invasion dynamics and highlight zones of potential management relevance. This idea also expands on earlier work by Fortin and Dale (2005), who emphasized that the structure of transition zones – their curvature, sharpness, and variability – offers critical ecological information. Considering invasive species as drivers of spatial patterning, rather than only responding to disturbance, boundary analysis can be better integrated into both invasion theory and conservation practice.

The direction and magnitude of the EDM–IFL offset provides insight into the spatial dynamics of invasion fronts. In transects where EDM precedes IFL (e.g. Transect 1, Transect 5 and Transect 6 in SED; Fig. 3), invasion can correspond to an active spread phase, with community restructuring occurring before shoot arrival. Conversely, when EDM follows IFL (e.g. Transect 2, Transect 3 in DREN; Fig. 4), the site may reflect legacy effects of past dominance, suggesting a regression or post-dominance state. This aligns with the concept of invasion debt, where community composition lags behind historical disturbance or invasion events (Jackson and Sax 2010). Such temporal-spatial dynamics underscore the inadequacy of simple "invaded vs. uninvaded" classifications and support the implementation of gradient-based monitoring approaches. Mapping both IFL and EDM can help identify pre-invasion tension zones, ecological memory effects, and variable transition sharpness as a proxy for resilience or vulnerability (Fortin and Dale 2005; Peters et al. 2006). Importantly, the results also show that even high-abundance *A. syriaca* populations do not necessarily coincide with species-poor assemblages. This supports earlier observations that structural and dominance shifts can occur without marked species loss, especially near invasion fronts (Simberloff et al. 2013; Guo et al. 2015). Such dynamics complicate conservation assessments that rely solely on species richness as an indicator of ecological integrity.

From a conservation perspective, the identification of ecotonal dissimilarity maxima can contribute to a better understanding of early-stage invasion patterns, but its direct application in early detection frameworks can be limited due to the required sampling effort. If shoot presence lags behind community change, then visible colonization can underestimate the invader's ecological footprint. Including spatially explicit dissimilarity metrics (SED, DREN) in monitoring frameworks can potentially support management planning. For practical application, this approach can be implemented by establishing short transects across suspected invasion fronts and calculating dissimilarity profiles (e.g. SED or DREN) to identify zones where compositional changes precede visible invasion. These zones can then be prioritized for targeted field surveys or localized management interventions, such as early removal or disturbance reduction before dense stands establish. Furthermore, zones with wide IFL–EDM offsets or multiple dissimilarity peaks can represent potential priority sites for restoration, as they reflect either emerging corridors of spread or ecologically weakened frontiers. This is especially relevant in semi-natural grasslands, where subtle boundary shifts often go unnoticed (Suding et al. 2004; Pyšek et al. 2012). Lastly, the emergence of novel, invader-driven ecotones reframes invasion not only as a biological threat, but also as a spatial phenomenon capable of generating new community architectures. As such, *Asclepias syriaca* does not only expand spatially, but can also influence the spatial organization of vegetation, adding a future perspective to invasion ecology. However, due

to the labor-intensive nature of the method, its primary applicability may lie in detailed ecological assessment and management planning rather than rapid early detection.

As with any field-based ecological study, this approach has inherent limitations. In addition, the lack of historical data on the establishment and spread of *A. syriaca* at the studied sites limits the interpretation of current spatial patterns in a temporal context. The analysis was conducted along six transects within a single habitat type, which may constrain the generalizability of the results across broader spatial or environmental contexts. Additionally, the study represents a temporal snapshot, preventing direct inference on invasion rate or direction over time. In particular, the lack of detailed microhabitat data (e.g. soil moisture, microtopography, or disturbance history) limits the ability to disentangle biotic effects from fine-scale environmental variation. Given the fine spatial scale of the study, such factors could play a substantial role in shaping boundary structure, and their inclusion would likely improve the interpretation of observed patterns. While the use of two dissimilarity metrics (SED and DREN) provided complementary perspectives on boundary structure, incorporating functional or below-ground data could further enrich interpretation in future studies. Despite these limitations, the spatial patterns revealed here offer insights into the structural complexity of invasion fronts and highlight the diagnostic potential of ecotonal metrics in invasion ecology. Although regional historical data confirm the long-term presence and expansion of *A. syriaca* in Hungarian sandy grasslands, the lack of site-specific invasion histories limits the ability to relate observed spatial patterns to invasion stages or rates of spread. Future integration of historical mapping or long-term monitoring data could help disentangle whether observed boundary structures reflect advancing, stable, or retreating invasion fronts.

Taken together, the results support the presence of spatially structured transition zones, demonstrate variability in boundary structure, confirm the occurrence of spatial offsets between invasion fronts and compositional change, and highlight shifts in species dominance patterns rather than species loss.

The results collectively address the main research questions as follows: (i) a distinct transition zone (novel ecotone) was detectable in most transects; (ii) boundary structure varied from sharp to gradual; (iii) boundary characteristics could be quantified using SED and DREN; (iv) spatial offsets between invasion front and compositional change were common; and (v) *A. syriaca* primarily altered species dominance patterns rather than reducing species richness.

Conclusion

This study shows that *Asclepias syriaca* induces spatially structured vegetation transitions – novel ecotones – at the invasion front, which often extend beyond the visible limits of the invader's shoot presence. By comparing the spatial positions of compositional discontinuities and the physical invasion line, the results show that ecological reorganization can precede or persist after colonization. These structural shifts are often subtle, do not necessarily correlate with species loss, and instead manifest as changes in species dominance or community configuration. The use of complementary dissimilarity indices (SED and DREN) enabled us to detect both sharp and diffuse boundaries, underscoring the value of multiple analytical perspectives in fine-scale invasion research.

The observed variability in boundary sharpness and offset suggests that invasion dynamics are highly context-dependent, influenced by local habitat heterogeneity, historical disturbance, and community resistance. These findings suggest that novel ecotones can be considered ecologically meaningful structures that both result from and mediate invasion processes. Importantly, these transitions may serve as potential indicators of ecological change, and can help identify spatial targets for conservation intervention. Incorporating spatially explicit boundary analysis into invasion research and monitoring frameworks can improve the understanding of spatial invasion dynamics and support management planning in sensitive habitats. While the approach provides detailed insights into invasion-driven spatial structure, its practical application is likely more suitable for targeted ecological assessments and management planning than for rapid early detection frameworks. This highlights the importance of considering spatial structure when assessing invasion impacts at fine scales. In practice, the approach may be most useful in targeted ecological assessment and management planning at selected invasion margins rather than in large-scale rapid detection schemes.

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Supplementary material 1

Species occurrences across transects based on 10 × 10 cm quadrats

Author: László Bakacsy

Data type: xlsx

Explanation note: Species occurrence data along six vegetation transects (T1–T6) established across *Asclepias syriaca* invasion boundaries. Values indicate the number of occupied 10 cm × 10 cm quadrats (maximum = 120 per transect) in which each species was recorded. Data reflect presence counts per species across the entire transect length.

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Link: https://doi.org/10.3897/neobiota.107.185747.suppl1

Supplementary material 2

Mean SED-based Z-scores along six vegetation transects

Author: László Bakacsy

Data type: xlsx

Explanation note: Mean standardized dissimilarity scores (Z-scores) based on Squared Euclidean Distance (SED) calculated along each 10 cm segment of six vegetation transects (T1–T6). Values represent average discontinuity strength per position along the transects, derived from pairwise comparisons of adjacent plots. Higher Z-scores indicate greater shifts in community composition. These values were used to identify ecotonal dissimilarity maxima (EDM) in relation to the invasion front line of *Asclepias syriaca*.

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Supplementary material 3

Mean DREN-based Z-scores along six vegetation transects

Author: László Bakacsy

Data type: xlsx

Explanation note: Mean standardized dissimilarity scores (Z-scores) based on the Differential Renkonen Index (DREN) calculated along each 10 cm segment of six vegetation transects (T1–T6). The index quantifies relative changes in species dominance between adjacent plots. Higher Z-scores reflect greater discontinuity in species composition and dominance structure. These data were used to detect ecotonal dissimilarity maxima (EDM) along each transect and assess their spatial offset from the invasion front line of *Asclepias syriaca*.

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Supplementary material 4

Positions of statistically significant dissimilarity peaks detected using the Moving Split Window (MSW) method based on Squared Euclidean Distance (SED)

Author: László Bakacsy

Data type: xlsx

Explanation note: For each transect, peak positions (in meters), corresponding Z-scores, and distances to the invasion front line (IFL) are presented. Only peaks exceeding the significance threshold (Z > critical value) are included. Negative values indicate peaks located before the invasion front, while positive values indicate peaks located after it.

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Link: https://doi.org/10.3897/neobiota.107.185747.suppl4

Supplementary material 5

Positions of statistically significant dissimilarity peaks detected using the Moving Split Window (MSW) method based on the Differential Renkonen Index (DREN)

Author: László Bakacsy

Data type: xlsx

Explanation note: For each transect, peak positions (in meters), corresponding Z-scores, and distances to the invasion front line (IFL) are presented. Negative values indicate peaks located before the invasion front, while positive values indicate peaks located after it.

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Link: https://doi.org/10.3897/neobiota.107.185747.suppl5

Supplementary material 6

Raw and standardized Moving Split Window (MSW) dissimilarity profiles based on Squared Euclidean Distance (SED) for all transects

Author: László Bakacsy

Data type: xlsx

Explanation note: For each transect, raw dissimilarity values are provided across sampling positions and half-window sizes (w1–w10), together with the corresponding standardized values (Z-scores). These data represent the full dissimilarity profiles used for detecting spatial transitions and identifying statistically significant peaks.

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Link: https://doi.org/10.3897/neobiota.107.185747.suppl6

Supplementary material 7

Raw and standardized Moving Split Window (MSW) dissimilarity profiles based on the Differential Renkonen Index (DREN) for all transects

Author: László Bakacsy

Data type: xlsx

Explanation note: For each transect, raw dissimilarity values are provided across sampling positions and half-window sizes (w1–w10), together with the corresponding standardized values (Z-scores). These data complement the peak-based summaries (Suppl. materials 4, 5) by providing the complete dissimilarity profiles underlying the analyses.

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Additional information

Conflict of interest

The author has declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Author contributions

Conceptualization; Formal analysis; Methodology; Visualization; Writing – original draft; Writing – review and editing; Data curation; Investigation; Supervision: LB.

Author ORCIDs

L. Bakacsy https://orcid.org/0000-0003-2593-1795

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.