



Invasion impact is conditioned by initial vegetation states

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Abstract: Biological invasion is a crucial problem in the world because of its negative consequences for protected areas. The degradation stage of vegetation might affect the success of invasion. One of the most abundant and threatening invasive species is the common milkweed (*Asclepias syriaca* L.) which has invaded already 23 countries of Europe and in several habitat types its further spreading is promoted by climate change. Pannonian sand grassland is one of the most threatened habitat by common milkweed invasion. Therefore, invasion in sand grassland vegetation is an important issue. However, the effects of the invasive plant in the open sand grassland are rather controversial. In order to clarify the existing contradictory results, the study was carried out in a strictly protected area, near Fülöpháza (Hungary) in a reserve core area in a UNESCO biosphere reserve. Microcoenological study was applied to determinate the fine-scale community characteristics of non-invaded and invaded stands in natural and seminatural vegetation and data were processed by Juhász-Nagy's information theory models. Shannon diversity of species combinations (compositional diversity) which describes the ways of the coexistence of species, and the number of realized species combinations were used for measuring beta diversity. Differences between stands were analyzed by two-way ANOVA. The maximum compositional diversity of species and main life-forms (annuals, perennials and cryptogams) did not differ significantly between the non-invaded and invaded stands. In contrast, significantly larger characteristic areas of compositional diversity were detected in the invaded stands. Based on these results, it could be concluded that diversity of species combinations did not change but those values have shifted to coarser scales in case of invaded stands. The direction of this change suggests a kind of impoverishment in the presence of *Asclepias*. Thus, it is worth mentioning from the invasion management point of view that protection of the habitats against disturbance is a more cost-effective and successful way than protection against the establishment or extirpation of invasive species, since disturbance facilitates the invasions throughout the impoverishment of the community.

Abbreviations: CD – Compositional (species combination) Diversity, CA – Characteristic Area, JNP-functions – Juhász-Nagy's functions, NRC – Number of Realized species Combinations .

Nomenclature: The study used the nomenclature for names of plant species and the life form categories by Raunkiaer as applied by Király (2009).

Introduction

Invasion in protected areas means serious problems for the biodiversity and functioning of ecosystems (Elton 1958, Sala et al. 2000, Weidenhamer and Callaway 2010, European Commission 2014). Disturbed vegetation units usually are not capable to resist against invasion (Alpert et al. 2000).

Common milkweed (*Asclepias syriaca* L.) is a tall perennial plant species, originated from North America. This species has characteristics that make it a noxious invasive species (e.g., fast growing, clonal spreading, and drought tolerance) (Bagi 2008, Tokarska-Guzik and Pisarczyk 2015, Kelemen et al. 2016). Despite the facts that common milkweed has invaded already 23 countries of Europe and further spread is promoted by climate change (Tokarska-Guzik and Pisarczyk 2015), very few studies have examined the effects of its invasion (Bagi and Szilágyi 1995, Kelemen et al. 2016, Szitár et al. 2014, 2016, 2018). The species has recently been added to the List of Invasive Alien Species of Union Concern in 2017 (European Commissions 2017). In Hungary, common

milkweed is one of the most abundant invasive species which has the largest cover in sandy old-fields (Török et al. 2003, Bagi 2008, Csecserits et al. 2011, Kelemen et al. 2016) due to some damaging processes, e.g., wildfire (Mojzes and Kalapos 2015, Sztatári et al. 2016) or previous uncontrolled land use (Csontos et al. 2009, Albert et al. 2014). Several studies have shown that disturbed vegetation colonized by *A. syriaca* could promote the spreading of this plant efficiently into surrounding seminatural communities (Csontos et al. 2009, Csecserits et al. 2011, Albert et al. 2014, Sztatári et al. 2014). Few studies have been reported controversial results about its effects on different vegetation types. First, milkweed did not influence the establishment of the dominant grasses following wildfire in alien pine plantations (Sztatári et al. 2014, 2016). Moreover, a recent study has shown that *Asclepias* could have nurse effects on the native grass establishment during early recovery in old-fields (Sztatári et al. 2018). Due to the deep roots, *Asclepias* is able to reach the unused water regimes of native species (Bagi 2008), so there is no competition for water storage or competition can be limited between these spe-

cies (Sztár et al. 2016). Second, in the presence of *Asclepias* the development of target vegetation has been reported to be slowed down (Albert et al. 2014). The presence of common milkweed has a negative impact on the cover of native species in the late successional sandy grasslands (Kelemen et al. 2016) which can be explained by its shading and allelopathic effects (Kazinczi et al. 2004). Negative impacts on the native fauna (arthropods) were also reported by Gallé et al. (2015) and Somogyi et al. (2017). Therefore, the organization and dynamics of vegetation invaded by milkweed deserves special attention from the point of view of nature conservation. Our knowledge is limited about the background of *Asclepias* invasion due to the relatively low number of published studies related to the initial vegetation states. A microecological study was carried out to inform about the characteristics of non-invaded and invaded stands of natural and seminatural vegetation at fine-scale.

Pannonian sand steppes or open sand steppes (Natura 2000 code: 6260) are of special importance for the European Union Habitat Directive (92/43/CEE). These dry, nutrient-poor, calcareous sand habitats are home to a large number of rare, endangered or endemic species (Tóth 1996, Lőkös and Verseggy 2001, Molnár 2003, Molnár and Kun 2011, Fekete et al. 2014, Veres and Csintalan 2017) and they are very vulnerable to biological invasion (Botta-Dukát 2008). A possible reason of high invasibility of open sand grasslands is the former land use (and the related disturbances) in the past (Botta-Dukát 2008). There are several negative impacts of disturbance such as decrease of diversity altered by composition of species with increasing portion of annual plants and ecosystem functions (Kovács-Láng et al. 2000). The link between disturbance and plant invasion is also widely recognized (Hobbs 1989, Alpert et al. 2000, Hierro et al. 2006, Csecerits et al. 2011, Pyšek et al. 2012, Lembrechts et al. 2016, Pyšek et al. 2017).

For a better understanding of invasion processes, detailed studies on vegetation structure and transitions with specific attention to the initial conditions are necessary. Thus, besides the use of conventional methods, the changes of the number of species and the relationship between fine-scale spatial structure and vegetation dynamics have to be measured. These require a complex approach, such as microecological methods which are used in several previous studies (Juhász-Nagy 1980, Juhász-Nagy and Podani 1983, Juhász-Nagy 1993, Horváth and Makrai 2000, Kovács-Láng et al. 2000, Bartha 2008, Bartha et al. 2008, Bartha et al. 2011). Two commonly used functions of the model family of Juhász-Nagy: compositional diversity (CD) and the number of realized species combinations (NRC) are sensitive indicators of community composition and structure. In spite of that, they have been used only in few studies in which the interaction of the invasive species and the invaded community were examined (Szigetvári 2002, Szentes et al. 2012, Kun et al. 2014).

The basic hypothesis of the study is that invasion is associated with decreasing beta diversity, i.e., invasion is facilitated by the decreasing diversity. The application of the two information theory functions; namely, the diversity of

species combinations and the number of realized species combinations inform us about beta diversity. According to the hypothesis, the values of the two functions are drastically reduced, while the characteristic areas of the two functions are shifted at coarser scales due to the decreasing beta diversity. Therefore, the maximum values and characteristic areas of non-invaded and invaded stands of natural and seminatural vegetation are compared. Furthermore, this study evaluated whether these differences are manifested in three main life-form categories (annuals, perennials and cryptogams).

Materials and methods

The study was carried out in the strictly protected UNESCO biosphere reserve core area near Fülöpháza in the Kiskunság National Park (GPS coordinates: N46°52.92' E0 19°23.94'), Central Hungary (Fig. 1 and Table S1 in the Appendix).

The native habitat type of the study site is open sand grassland (which belongs to the *Festucetum vaginatae* association), but there are some closed sand grasslands, poplar-juniper shrublands and disturbed and transformed habitats as well. The latter ones (plantations, abandoned fields) play an important role in the invasion of the sites by *Asclepias*. The groundwater level is at a high depth (Zsákovics et al. 2007, 2009) and the mean annual precipitation varies between 565 mm and 535 mm (Tóth 1996, Kovács-Láng et al. 2000, Kun 2001, Bartha et al. 2011). The mean annual temperature is between 10.07 °C and 10.33 °C (Kovács-Láng et al. 2000, Bartha et al. 2011). The nutrient deficient, weak soil profile developed on calcareous sand (Várallyay 1993, Kovács-Láng et al. 2000). Nonetheless, the area has many floristic values, characterized by a rich lichen flora (e.g., *Cladonia convoluta*, *Cladonia furcata*, *Cladonia magyarica*, *Cladonia rangiformis*) (Lőkös and Verseggy 2001, Molnár and Kun 2011, Veres and Csintalan 2017) and some typical endemic plants, e.g., *Festuca vaginata*, *Colchicum arenarium*, *Dianthus diutinus*, *Dianthus serotinus*, *Iris arenaria* (Tóth 1996, Molnár 2003, Magyarai et al. 2010, Molnár and Kun 2011, Rédei et al. 2014). The study area has been protected and abandoned since 1974, but it was used for grazing and military exercises before protection. It is important to note that there were also some agricultural activities (agricultural fields and farmsteads) in and around the sand dunes between the 1950's and 80's.

Five non-invaded (NI) (as control) and five invaded stand (I) pairs were examined by comparative microecological approaches. Vegetation sampling was performed from May to June, in 2015. Four (1-4) of the stands were located in old-fields as seminatural (SN) sites. (These stands were arable fields previously and have been abandoned since the 1960-70's. They have been spontaneously recovering since then.) The fifth stand was located in the undisturbed sand dune area. It was probably never ploughed and was considered as a natural (reference) site (N) (Fig. 1). The non-invaded stands were designated only a few meters away from their invaded stand pairs to have as similar abiotic conditions and vegetation history as possible. Each individual stand was analyzed and interpreted

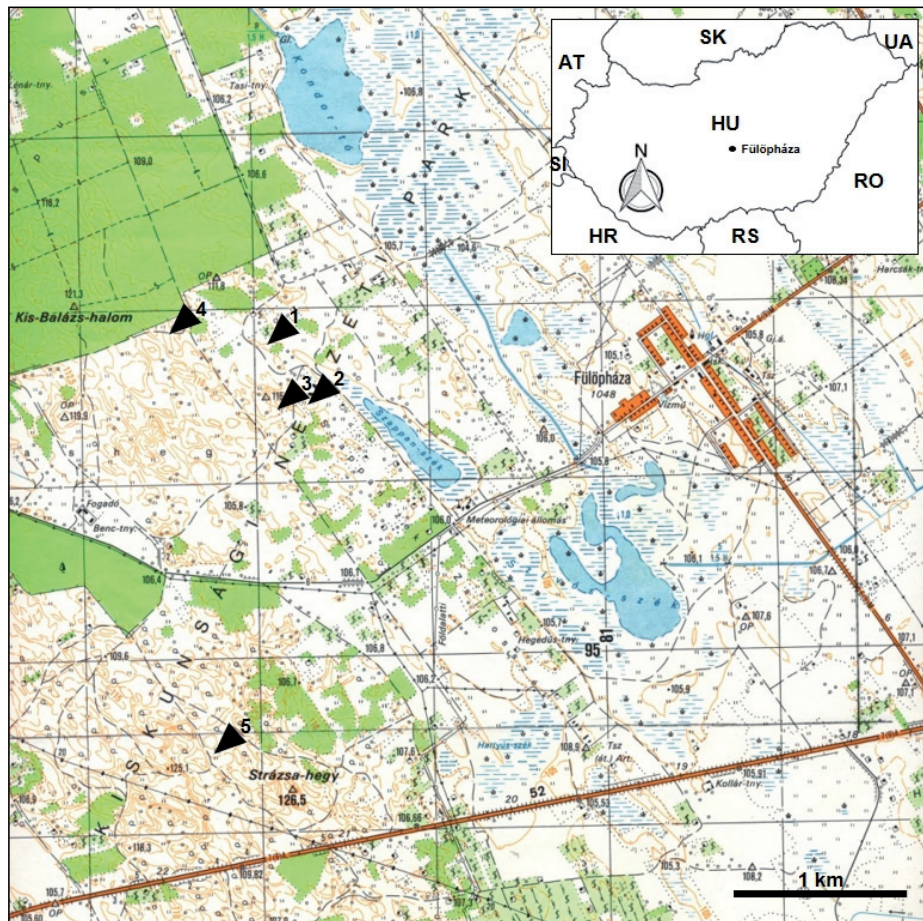


Figure 1. Map of the vegetation states examined in this study. The location of the study site in Hungary (Fülöpháza) is labeled by black arrows and their approximate positions of the stand-pairs are labeled by number 1-5. The four (1-4) of the stand-pairs are located on previous arable fields (seminatural vegetation), the fifth is located in the sand dune area (natural vegetation) (for finer classification of the stands cf. Table S4.).

in the contrast of its pair. Based on this design, we assume that differences in vegetation composition and patterns can be attributed to the effect of invasive species. The frequency of *Asclepias* and the other species in the five stands differed, as was determined from their presence. The selection criteria of individual stands were that they occur in homogeneous vegetation patches without larger visible disturbances large enough to place a 52 m long circular transect on them.

In sand grasslands, the following standard sampling procedure was used for microcoenological studies (Bartha and Kertész 1998, Szigetvári 2002, Bartha et al. 2008, Bartha et al. 2011, Szentes et al. 2012): The presence of plant species along 52 m long circular transects was recorded in each stand, every transect consisted of 1040 units of 5 cm × 5 cm contiguous microquadrats.

From each transect, the relative total frequency and relative frequency of three main life-forms were determined. The first is based on the number of presences of species in microquadrats. The second is based on the number of presences of species with similar life-forms in microquadrats.

For data analysis, two Juhász-Nagy's information theory models were used (Juhász-Nagy 1980, Juhász-Nagy and Podani 1983), hereafter abbreviated as JNP-functions: compositional diversity (CD) and the number of realized species combinations (NRC). The first function is the Shannon diversity of species combinations weighted by the frequency

of species combinations (given in logarithmic units, bits), while the latter one (NRC) expresses only the number of realized combinations. In this study, the maximum values and the characteristic areas (CA) were used (CA is the maximum quadrat size where the particular function reaches its maximum (Campetella et al. 1999, Campetella and Canullo 2001)). Transformations of the characteristic areas of CD and NRC inform us about changing beta diversity and they very sensitively detect fine changes in the patterns of species coexistence during succession or degradation (cf. Juhász-Nagy and Podani 1983, Bartha et al. 2011, Szentes et al. 2012).

INFOTHEM 3.01 program was used for performing spatial series analyses, and calculating JNP-functions (Horváth 1998). Species with frequency under 2% were excluded from the data processing as the rare species can lead to misleading results (Tóthmérész and Erdei 1992, Addicott et al. 2018) (Table S3).

Asclepias was excluded from the model in all analyses of invaded stands, because we use this species as an independent ("driver") variable.

Based on previous studies (Virágh et al. 2008, Szentes et al. 2012), we assume that the rank of the stands ordered by decreasing maximum CD indicates the degree of disturbance (Virágh et al. 2008, Szentes et al. 2012) (where lower CD indicates larger disturbance, Table S4). After the first level (*a priori*) distinction between natural and seminatural stands,

Table 1. The frequency of three major Raunkiaer life-form categories and invasive plants, and the species number. SN – seminatural sites (1-4), N – natural site (5), NI – non-invaded stands, I – invaded stands. Species with a frequency below 2% are not included in the analysis.

Sites	Stands	Annual species	Perennial species (without <i>Asclepias</i>)	Cryptogams	<i>Asclepias syriaca</i>	Total	Species number
SN	NI1	17.67%	2.21%	45.48%	0%	65.36%	13
	I1	13.17%	3.60%	35.38%	8.65%	60.8%	15
SN	NI2	15.09%	10.96%	30.12%	0%	56.17%	9
	I2	10.36%	6.17%	76.00%	7.30%	99.83%	11
SN	NI3	4.55%	15.45%	34.55%	0%	54.55%	10
	I3	6.87%	10.55%	38.04%	5.86%	61.32%	14
SN	NI4	18.63%	2.78%	37.50%	0%	58.91%	10
	I4	13.00%	6.10%	52.35%	8.26%	79.71%	9
N	NI5	5.40%	8.49%	43.14%	0%	57.03%	11
	I5	7.01%	13.36%	34.51%	10.86%	65.74%	7
Average	N	12.26%	7.97%	38.15%	0%	58.40%	10.6
	A	10.08%	7.95%	47.33%	8.18%	73.62%	11.2

these rankings provide additional (*a posteriori*) assessment of degradation. This *a posteriori* ordering of stands (based on decreasing beta diversity) has an important role in this paper as we expected larger responses to invasion in more degraded stands (cf. main hypothesis).

JNP-functions of the three main Raunkiaer life-form categories (annuals, perennials and cryptogams) were also analyzed by the program in separate tests. The settings were the same as in the above mentioned basic analyses: randomization procedure, 2% species frequency threshold was used and the *Asclepias* was excluded from the model (in the case of perennials).

Two-way ANOVA was used for the comparisons (the maximum values and CA of the CD, NRC and the maximum CD values and CA of the life-form categories). The invasion was analyzed together with the effect of stands (as explanatory variables).

The tests and the diagrams were performed by SigmaPlot 12.0 (Systat software, INC., San Jose, CA, USA).

Results

The frequency of species was analyzed in the different vegetation states (seminatural and natural) to detect the invasion impact on vegetation cover. Species frequency was higher in the three invaded stands (I2, I3 and I4) and was lower in two cases (I1 and I5) (Table 1). The frequency of *Asclepias* indicated the degree of the invasion, which was high compared to the frequency of annuals and perennials (Table 1). Interestingly, the highest frequency value of *Asclepias* was found in the invaded natural stand (I5). The three main life-forms were analyzed in order to detect the possible effects of invasion. No significant differences were observed between the sites and invasion in the case of the frequency of the annuals and perennials. The frequency of cryptogams was lower in

two invaded stands (I1 and I5) and higher in two other cases (I2; I3) (Table 1).

The CD and NRC functions were applied to the examination of species coexistence at the level of sites and invasion (Fig. 2, Table 2, Table S3 and Table S4). The maximum CD values did not differ significantly either in sites or in invasion (Fig. 2, Table 2). No significant difference was observed between sites in the CA of CD (Table 2). However, the CA of CD was significantly lower in the case of the invasion (Fig. 2 and Table 2) therefore, the maximum spatial diversity of species combinations was reached at a smaller spatial scale (25 – 35 cm²) by non-invaded stands. Contrariwise, the characteristic areas of the invaded stands were reached at larger scale, namely at 40 – 45 cm².

The analysis of the maximum NRC values and CA of the stands did not demonstrate any significant difference either in sites or in invasion (Table 2).

In order to express the degree of disturbances, the stands were ranked by decreasing maximum CD values. The invaded stands are located at the two ends of the disturbance scale, while the non-invaded ones are at the middle of the disturbance scale (Table S4).

The effects of invasion were tested on the three main life-form categories (annuals, perennials and cryptogams) by compositional diversity. However, the maximum CD values and the CA of the three main life-forms did not show significant differences in the comparison of the sites and invasion (Table S2).

Discussion

This study examined by microcoenological methods whether invasion impact is associated with decreasing beta diversity. We wanted to answer how invasion was affected by the initial stage of vegetation succession in open sand grassland. Based on the results, the species frequencies did

Table 2. The maximum CD and NRC values and characteristic areas in cm² (CA) where the functions reach their maximum. SN – semi-natural sites (1-4), N – natural site (5), NI – non-invaded stands, I – invaded stands. Significance at $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: *** and non significant: ns. Species with an abundance below 2% are not included in the analysis.

JNP-function	Sites	NI (max. value)	I (max. value)	NI (CA)	I (CA)	Comparison (for two-way ANOVA)	two-way ANOVA (p)
CD	SN	6.417	7.550	35	45	Site (max. values)	0.557 ns
	SN	5.611	5.372	35	45	Invasion (max. values)	0.497 ns
	SN	6.834	7.355	25	45	Site (CA)	0.279 ns
	SN	6.526	5.489	35	65	Invasion (CA)	0.009 **
	N	7.115	3.947	35	60		
NRC	SN	113	139	20	25	Site (max. values)	0.300 ns
	SN	059	51	20	30	Invasion (max. values)	0.506 ns
	SN	108	141	20	30	Site (CA)	0.990 ns
	SN	82	42	20	30	Invasion (CA)	0.456 ns
	N	115	17	30	15		

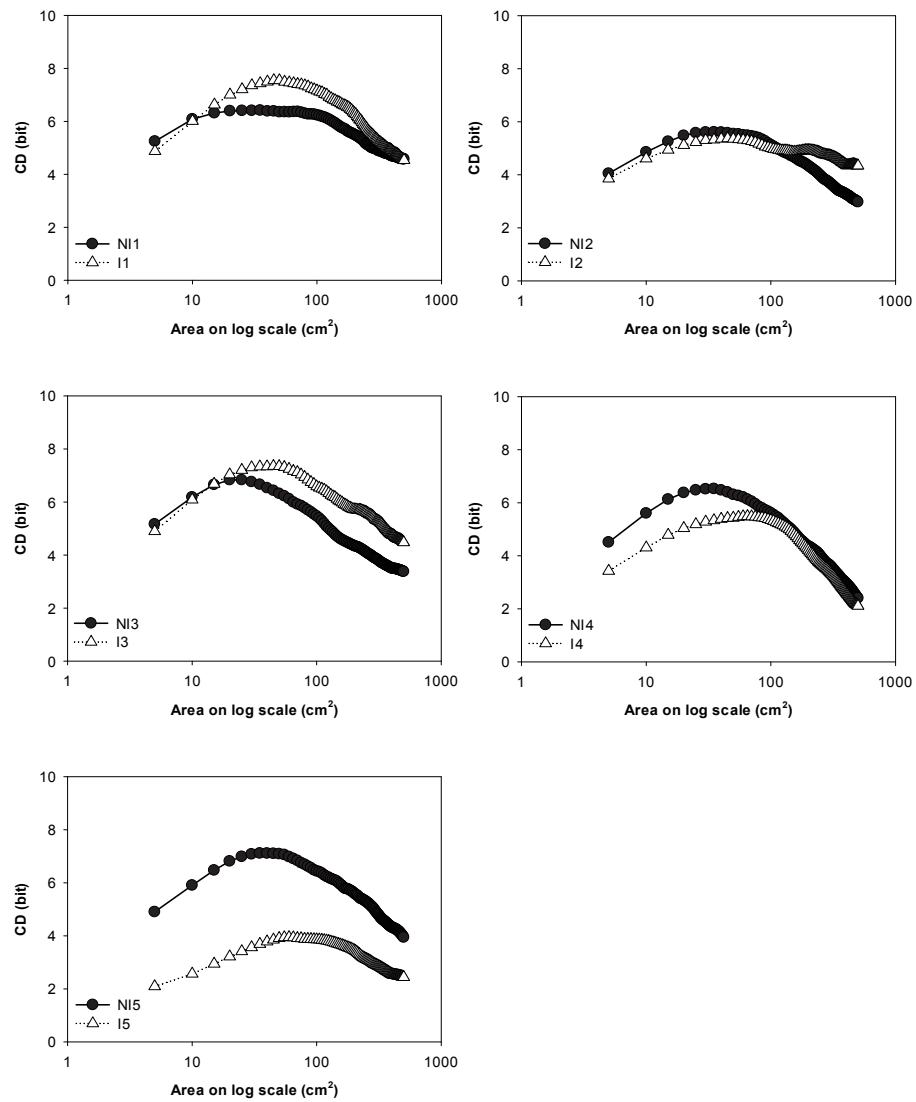


Figure 2. Compositional diversity of five stand-pairs as a function of increasing spatial scale. Species with abundance below 2% are not included in the analysis. Abbreviations: SN – seminatural sites (1-4), N – natural site (5), NI – non-invaded stands, I – invaded stands.

not show any consistent change in the presence of *Asclepias* in every stand. However, the frequency of milkweed showed that the invasion was rather widespread in the invaded stands, regardless of the sites.

Some invasion studies (Szentés et al. 2012, Kun et al. 2014) have found that the maximum CD and NRC values were lower and the CAs were typically higher during invasion, thus the invaded vegetation is less organized. Similar patterns can be detected in other degradation processes (Juhász-Nagy 1980, Juhász-Nagy and Podani 1983, Juhász-Nagy 1993, Horváth and Makrai 2000, Kovács-Láng et al. 2000, Bartha 2008, Bartha et al. 2008, Virágh et al. 2008, Bartha et al. 2011). The lower maximum values (CD or NRC) show a decrease of fine-scale structural complexity. While the higher characteristic areas of CD and NRC values can be interpreted that species are increasingly competing for space (Virágh et al. 2008). The CA shifts towards higher spatial-scales indicate a slight but consistent changes in community structure toward degradation (in line with Virágh et al. 2008 and Bartha et al. 2011). This study shows that only the CA of compositional diversity was significantly higher in the invaded stands, compared to non-invaded ones. Thus, invasion has influenced the pattern of beta diversity, which is a kind of impoverishment of the community. Beta diversity in the invaded stands reached similar values to non-invaded stands but only at coarser scale. Methodologically, this main result pointed out that the maximum of CA of the CD was more sensitive and robust than the maximum CA of the NRC. Also this shows clearly the relevance of using the JNP method, i.e., these results support the application of the methodology to detect fine-scale vegetation changes.

Similarly to the results based on particular life-form frequencies, the CD of life-forms did not differ significantly (Table S2). The reason for the lack of the significance of the CD of the life forms could be that these life-forms grow together and therefore affect each other. So in the analyses, the effects of *Asclepias* and the other life-forms probably were confounded and could not be separated in a snapshot analysis.

Our study partly supported the previous findings about the correlation between invasion success and the state of recipient vegetation (initial degree of degradation in the recipient community) (Kneitel and Perrault 2006, Virágh et al. 2008, Szentés et al. 2012) (cf. Bartha et al. 2011) (Table S4). The non-invaded stands are more unified and they are wedged among the invaded ones. The highest difference of CD values based on the analyzed JNP-functions was observed in the case of NI5-I5. It seems to be a contradiction because this stand-pair was located in the natural site. The highest difference may result from former disturbance (e.g., physical disturbance or drought effect), which created an appropriate situation for the invasion. The NI5-I5 stand-pair is a good example that *Asclepias* can penetrate from disturbed areas to natural places (Csontos et al. 2009, Cseceserits et al. 2011, Albert et al. 2014, Szitár et al. 2014) but it is less typical and the invasion process may slow down if surrounded by non-disturbed habitats. There are no major differences between the other stand-pairs, because all of them were in the semi-natural site (in disturbed condition). The most similar is the

NI2-I2 stand-pair, serious differences could not be detected between the invaded and non-invaded stands. Both of them had lower CD values, which is the feature of poorly organized, early stages of succession (Bartha 1990). The highest CD was found in the natural, undisturbed stand. If we assume that this non-invaded invaded pair had similarly high CD value at the time of first invasion impact, we can conclude that initially high CD did not increase the resistance to invasion in this vegetation type. However, this finding needs further tests because our study is limited by the low number of replicates and by the single survey. Moderate differences are detectable in three stand pairs (NI1-I1; NI3-I3 and NI4-I4). The most threatened non-invaded stand is NI1, which shows a rather disturbed condition. The other non-invaded stands (NI3 and NI4) were relatively safe. This is supported by Albert et al. (2014): milkweed cover increased significantly with decreased field age (time passed after the outset of disturbance) in the Kiskunság old-fields. It is reasonable to expect that CA values were shifted during invasion. Similarly, we can expect that after longer time and more invasion impact, the maximum CD values will decrease as well. This would be consistent with the fact that different plant communities resist differently to plant invasion (Vitousek et al. 1997, Alpert et al. 2000). The decreased spatial heterogeneity probably decreased the resilience (McNaughton 1988, Gunderson and Pritchard 2002, Bartha et al. 2011). These results can explain why Kelemen et al. (2016) found negative effect in the old-fields and why milkweed creates a novel ecosystem in open sand grasslands (in sandy old-fields). Szitár et al. (2016, 2018) found a „positive” effect of milkweed, when milkweed created favorable microclimatic conditions for native species by shading. Both phenomena could also be explained by the clonality of common milkweed: deeply penetrating plagiotropic roots can reach the ground-water and this can be translocated by clonal system and released into upper soil layers where they were later used as neighbor plants, as demonstrated by Ye et al. (2016) in the case of other clonal species. Clonal plants can maintain the spatial pattern and inhibit the regeneration of vegetation after disturbance or modify the successional process (Oborny and Bartha 1995, 1998). So it is not surprising that the most dangerous invasive species are often clonal plants (Pyšek 1997, Kolar and Lodge 2001, Liu et al. 2006, Speck et al. 2011).

The results of this comparative microcoenological study suggest that invasion by *Asclepias* occurs more often in previously disturbed habitats and less typical in the natural ones. *A. syriaca* could invade and reach a larger population where the community was already disturbed. This study is based on single time point observations, but it requires further (long-term) studies to clarify these questions. It is worth mentioning from the invasion management point of view, that protection of the habitats against disturbance is a more cost-effective and successful way than the protection against the establishment or extirpation of invasive species, since disturbance facilitates invasion throughout the impoverishment of the community.

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Supplementary material

Table S1. GPS coordinates of the five stand-pairs.

Table S2. Maximum CD values and characteristic areas (CA) of the three life-forms and those two-way ANOVA test.

Table S3. Results of the complete randomization (the average of the Monte-Carlo simulations and its significance tests).

Table S4. The quantification of degree of disturbances for each stands (where the decreasing max. CD values indicate the degree of disturbances).

The appendix may be downloaded from www.akademiai.com.

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