Supplementary material

Neutral effect of an invasive plant species with specialized flower structure on native pollinator communities

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Detailed information on the studied invasive plant species

Common milkweed (*Asclepias syriaca* L., Apocynaceae, subfamily Asclepiadoideae) is native to North America. It was introduced to Europe as an ornamental plant in the 17th century (Gaertner 1979), and by now it is an invasive and expanding species across Europe, especially in Hungary, Poland and Romania (EASIN Database; Botta-Dukát and Balogh 2008; Zimmermann et al. 2015; Rutkowski et al. 2016; Lapin 2017). In Hungary it did not spread remarkably during a long period after escaping from gardens in the 18th–19th century (Gönczy 1879; Borbás 1897; Bagi 2004) until around 1980 (Varga 1987; Bózsing and Cseresnyés 2006; Novák et al. 2011). In the last 40 years the increasing spread of common milkweed has seen to be unstoppable in Hungary, and its further invasion is also predicted (Varga 1987; Botta-Dukát and Balogh 2008; Novák et al. 2011). It became integrated into both agricultural and semi-natural ecosystems and is now a hazardous invasive weed species that causes severe problems in conservation (Varga 1987; Bózsing and Cseresnyés 2006; Botta-Dukát and Balogh 2008; Novák et al. 2011; Csiszár and Korda 2015), and it can be found in the narrow list of European Union invasive species list (EU list 2017).

Common milkweed is a robust, 80–150 cm high, perennial plant with large (15–25 x 5–9 cm) leaves, reproducing both asexually by rhizomatic roots and sexually through insect-pollinated flowers (Botta-Dukát and Balogh 2008; Csontos et al. 2009; Züst et al. 2015). All parts of the plant contain white, milky toxic sap (cardenolides) to defend against herbivores, and have an allelopathic, shading and space-occupying effect to compete with other plants (Malcolm 1991; Botta-Dukát and Balogh 2008; Züst et al. 2015).

Common milkweed is flowering normally from June to August (Botta-Dukát and Balogh 2008), however, in the year of our study, it was also blooming scarcely in May and September (while the peak was in June). The clustered inflorescences are 5–10 cm large umbellate cymes, located mostly terminally. The pentamerous, androgynous, about 1 cm diameter flowers constitute the ball-shaped large inflorescences (Liede and Weberling 1995). Flowers are white, pink or red, insect pollinated, and produce a vast amount of nectar hidden in the hood-like saccules of the corolla (Willson and Bertin 1979; Morse and Fritz 1983; Crane et al. 1984; Farkas and Zajácz 2007). The pollen is located in small packets called pollinia (five pairs per flowers), that can be

carried only by large insects. Pollinia can modify pollinators' behavior, and they can jam into the flower, lose a leg or sometimes even die in flowers (Morse 1981). The main flower visitors of common milkweed in North-America are bees, wasps, hoverflies, butterflies and moths (Willson and Bertin 1979; Morse 1981; Tooker et al. 2006; Howard and Barrows 2014). The fruit ripens between August and September, it is an ovale-shaped 10 cm long follicle, containing a lot of seeds with long, white, flossy hairs (Botta-Dukát and Balogh 2008).

The common milkweed has some ideal trait (e.g. perennial lifestyle; effective sexual and asexual reproduction; allelopathic effect; large leaf area) to be a highly aggressive and competitive invasive plant (Sárkány et al. 2008; Kelemen et al. 2016). It was widely used by intensive agricultural management (ca. 1870–1950) to produce fiber, flakes, rubber and oil, but it was finally not economically profitable (Gaertner 1979; Botta-Dukát and Balogh 2008). It has been also used for honey-production from 19th century (Kühne 1884) to nowadays (Fehér 2006; Farkas and Zajácz 2007; Botta-Dukát and Balogh 2008). At now, milkweed is establishing in semi-arid ecosystems, appearing mostly in sandy soil, in degraded, disturbed areas, such as wastelands, old fields, plough lands, urban habitats, along railways and roads, degraded forests, secondary and annual grasslands across Europe, where it inhibits the successional processes (Varga 1987; Botta-Dukát and Balogh 2008; Pauková et al. 2013; Albert et al. 2014; Csecserits et al. 2016; Rutkowski et al. 2016; Szitár et al. 2018) and influences the native fauna (Gallé et al. 2015; Züst et al. 2015).

SM-Table 1. Information about the location, milkweed coverage, habitat type, history and management of ten sampled (control-invaded) site pairs. Absolute cover of milkweed means milkweed cover percentages in three 3×3m quadrats, while relative cover means that milkweed was compared to the total green cover (note it is smaller than 100% in sandy old fields, because of the significant part of bare surface).

Location	Coordinates (in WGS84 system)		Site type	Absolute cover of common milkweed [%]	Relative cover of common milkweed [%]	Habitat type (all sites are degraded more or less; and invaded sites similar to its control pair even though the invasion)	Site history	Management
Ballószög	19.562581	46.872548	control	2.0	2.2	Uncharacteristic dry and semi-dry grassland transition phase to open sand steppe	Old field: arable field abandoned about 10-20 years ago	mowed after 2nd, 3rd observation
Ballószög	19.552014	46.878287	invaded	30.0	41.9	Stand of invasive forbs	Old field: alfalfa field abandoned about 10-20 years ago	mowed after 2nd, 3rd observation
Fót	19.192262	47.598379	control	0.1	0.3	Uncharacteristic dry and semi-dry grassland transition phase to open sand steppe	Old field: plowed peach orchard abandoned about 10-20 years ago	mowed after 1st observation
Fót	19.186036	47.597070	invaded	30.0	40.0	Stand of invasive forbs	Old field: plowed peach orchard abandoned about 10-20 years ago	half of the site mowed after 2nd observation, other half of the site mowed after 3rd observation
Fülöpszállás	19.394916	46.866633	control	1.1	1.9	Open sand steppe	Old field: mosaic farmstead with arable field abandoned about 10-20 years ago	no sign of management during sampling
Fülöpszállás	19.391038	46.870230	invaded	25.7	53.2	Invaded open sand steppe	Old field: mosaic farmstead with arable field abandoned about 10-20 years ago	no sign of management during sampling
Isaszeg	19.447657	47.544466	control	0.7	0.7	Uncharacteristic dry and semi-dry grassland	Old field (degraded meadow) within forest: cropfield for games abandoned about 5-15 years ago	mowed after 2nd observation
Isaszeg	19.450850	47.549147	invaded	43.3	47.6	Stand of invasive forbs	Old field (degraded meadow) within forest: cropfield for games abandoned about 5-15 years ago	mowed after 2nd observation
Lajosmizse	19.543183	47.073830	control	0.0	0.0	Uncharacteristic dry and semi-dry grassland transition phase to open sand steppe	Old field: arable field abandoned about 10-20 years ago	mowed after 1st, 3rd observation
Lajosmizse	19.538170	47.075429	invaded	48.3	58.0	Stand of invasive forbs	Old field: arable field abandoned about 5-15 years ago	mowed after 3rd observation
Nagykáta	19.749968	47.396860	control	0.7	0.8	Open sand steppe	Old field: arable field abandoned about 10-20 years ago	no sign of management during sampling
Nagykáta	19.741542	47.398633	invaded	35.0	40.4	Stand of invasive forbs	Old field: arable field abandoned about 10-20 years ago	no sign of management during sampling
Pirtó	19.423389	46.529198	control	1.0	1.4	Open sand steppe	Old field: arable field abandoned about 5-10 years ago	mowed after 2nd observation
Pirtó	19.420537	46.532395	invaded	30.0	50.0	Stand of invasive forbs	Old field: arable field abandoned about 5-10 years ago	mowed after 2nd observation
Tápióság	19.661120	47.408296	control	0.0	0.0	Open sand steppe	Old field (sheep pasture): arable field abandoned about 10-20 years ago than used as a pasture	grazed by sheep after 1st, 2nd, 3rd observation
Tápióság	19.670534	47.402843	invaded	33.3	44.4	Stand of invasive forbs	Old field: arable field abandoned about 5-10 years ago	occasionally grazed by sheep after 2nd, 3rd observation
Tura	19.653976	47.572002	control	2.0	2.5	Uncharacteristic dry and semi-dry grassland transition phase to open sand steppe	Old field: arable field abandoned about 10-20 years ago	no sign of management during sampling
Tura	19.653741	47.574940	invaded	27.3	32.8	Stand of invasive forbs	Old field: arable field abandoned about 10-20 years ago	no sign of management during sampling
Vecsés	19.305750	47.415807	control	1.9	2.1	Uncharacteristic dry and semi-dry grassland transition phase to open sand steppe	Old field: arable field abandoned about 10-20 years ago	mowed after 2nd observation
Vecsés	19.309172	47.413574	invaded	53.3	60.6	Stand of invasive forbs	Old field: sheep pasture plowed a few times 10-20 years ago and abandoned	no sign of management during sampling

Analyses of landscape composition

We calculated the proportion of different land-cover types in 200 m and 1000 m radius circles around the middle points of our study sites to test, whether landscape composition has any differences between invaded and (uninvaded) control sites. Based on the CORINE land cover (CLC 2012) data base (EEA 2016), we computed the percentage cover of arable fields, shrub-forest habitats and semi-natural grasslands including pastures and natural grasslands (*see* the merged CLC categories in SM-Table 2). The total coverage of the three applied categories exceeded always 75%, urban habitats and water courses were ignored. We compared the percentage cover of arable fields, shrub-forest habitats and semi-natural grasslands between control and invaded sites with paired non-parametric Brunner–Munzel tests (Munzel and Brunner 2002), because of the non-normal distribution and small sample size. We did not find significant differences in any landscape type (p-values of Brunner–Munzel test: at 200m: arable fields: 0.541, shrub-forest habitats: 0.822, semi-natural grasslands: 0.294; at 1000m: arable fields: 0.877, shrub-forest habitats: 0.259, semi-natural grasslands: 0.123), hence we did not apply the landscape composition as explanatory variable in our main analyses.

SM-Table 2. Merged CORINE land cover categories used for our analysis.

CORINE categories	**Used (merged) categories**
2.1.1 Non-irrigated arable land	arable fields
2.1.2 Permanently irrigated land	arable fields
2.1.3 Rice fields	arable fields
2.2.1 Vineyards	arable fields
2.2.2 Fruit trees and berry plantations	arable fields
2.2.3 Olive groves	arable fields
2.4.1 Annual crops associated with permanent crops	arable fields
2.4.2 Complex cultivation patterns	arable fields
2.4.4 Agro-forestry areas	shrub-forest habitats
3.1.1 Broad-leaved forest	shrub-forest habitats
3.1.2 Coniferous forest	shrub-forest habitats
3.1.3 Mixed forest	shrub-forest habitats
3.2.4 Transitional woodland-shrub	shrub-forest habitats
2.3.1 Pastures	semi-natural grasslands
2.4.3 Land principally occupied by agriculture, with significant areas of natural vegetation	semi-natural grasslands
3.2.1 Natural grasslands	semi-natural grasslands

Floral resources

We were interested in the differences between the invaded and control sites in flowering plants as foraging resources for pollinators. Therefore we compared flower abundance, species richness, diversity and community composition of the flowering plant species between the control and invaded sites.

Statistical analyses

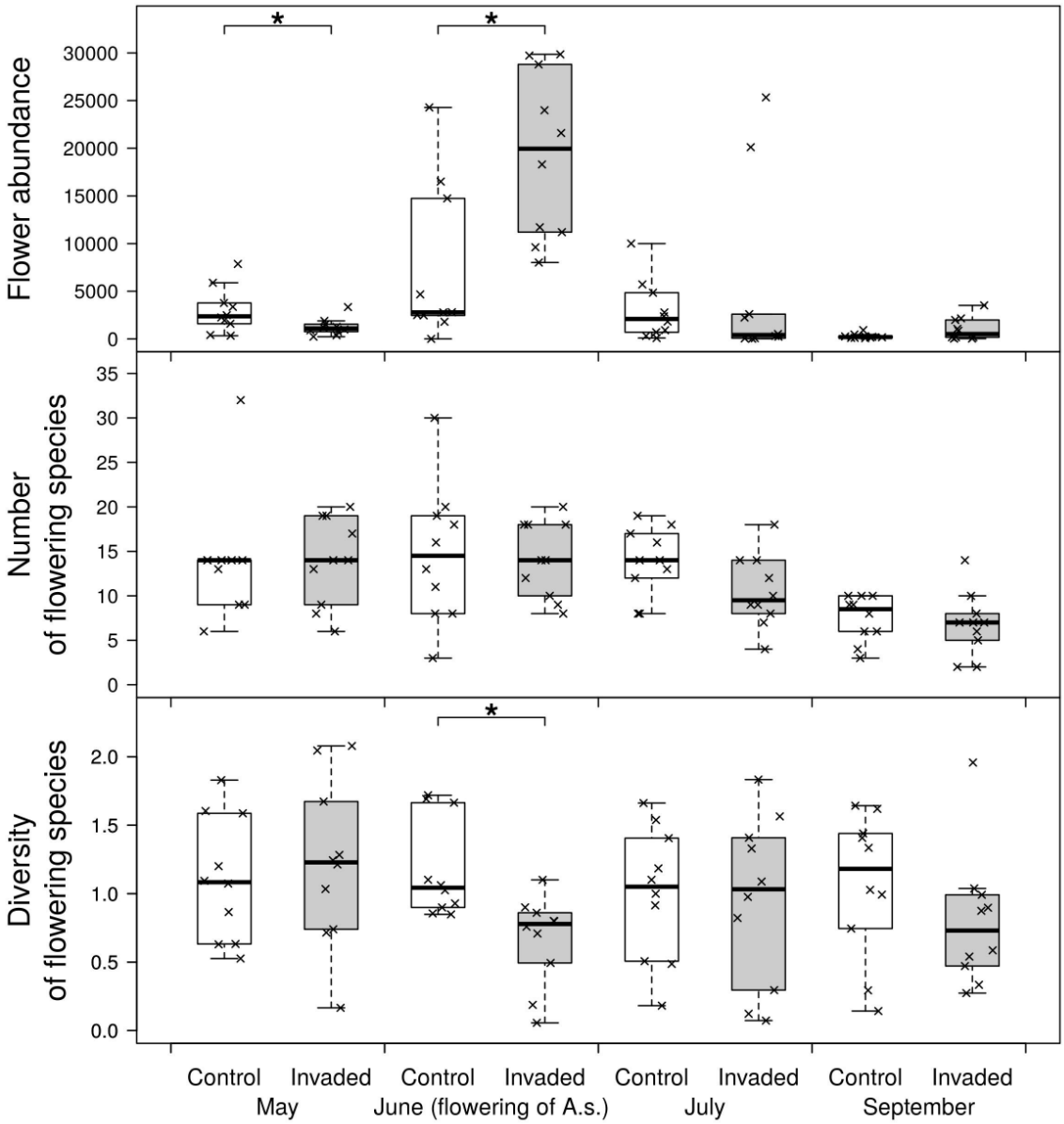
We analyzed the difference in abundance, species richness and Shannon diversity of flowers between the invaded and control sites during the four observation date separately. We used p-value adjusted paired non-parametric Brunner–Munzel tests (Munzel and Brunner 2002; Konietschke et al. 2015), due to the non-normal distribution of data, the relative small sample size and the paired design. We adjusted the p-values using the method of Benjamini and Hochberg (1995) for observation date, handling the investigated groups and measured values separately. We also repeated these analyses using dataset excluding milkweed flowers, only for the second occasion when the milkweed was flowering.

We analyzed the community composition of floral resources across the sites and observation dates, using Bray-Curtis dissimilarities (Borcard et al. 2018). We applied Permutational Multivariate Analysis of Variance (PERMANOVA) (Borcard et al. 2018) to analyze the effect of different explanatory variables on the community composition. We applied p-value based selection. The explanatory variables in our full model were: the invasion effect of common milkweed (invaded vs. control), coverage of the invasive plant and observation date. We visualized the species composition along the strongly affecting explanatory variables (PERMANOVA: $R^2>0.1$). We used the first two dimensions of non-metric multidimensional scaling (NMDS (Borcard et al. 2018), with zero-adjusted Bray-Curtis dissimilarities (Clarke et al. 2006)). We also repeated PERMANOVA using dataset excluding milkweed flowers.

Results

We found higher abundance of flowers in the control sites before the flowering of milkweed ($p=0.040$), and in the invaded sites when the milkweed was flowering ($p=0.020$; SM-Fig. 1, SM-Table 4). In contrast, the diversity of flowering plants was lower in the invaded sites during the second observation date ($p<0.001$; SM-Fig. 1, SM-Table 4). Separate analyzes of the dataset without milkweed during milkweed flowering showed no differences in the flower abundances ($p=1.000$), species richness ($p=0.684$) and diversity ($p=0.124$) of the native plant species between the invaded and control sites.

The floral species communities were explained by observation date (R^2=0.105, p=0.001; *see* SM-Fig. 2/a) and by invaded vs. control sites (R^2=0.021, p=0.015). Without milkweed the floral species communities did not show differences between the invaded and control sites (R^2=0.011, p=0.534), but the effect of observation date remained significant (R^2=0.109, p=0.001).



SM-Fig. 1 Abundance, species richness and diversity of flowering plant species in sites invaded by common milkweed and in uninvaded control sites, during four observation dates. Box plots show medians, lower and upper quartiles. Black × symbols represent sampling sites. Significant differences between the invaded and control sites according to the Brunner-Munzel test are indicated by stars (*) above the boxes (note: lack of * means non-significant differences).

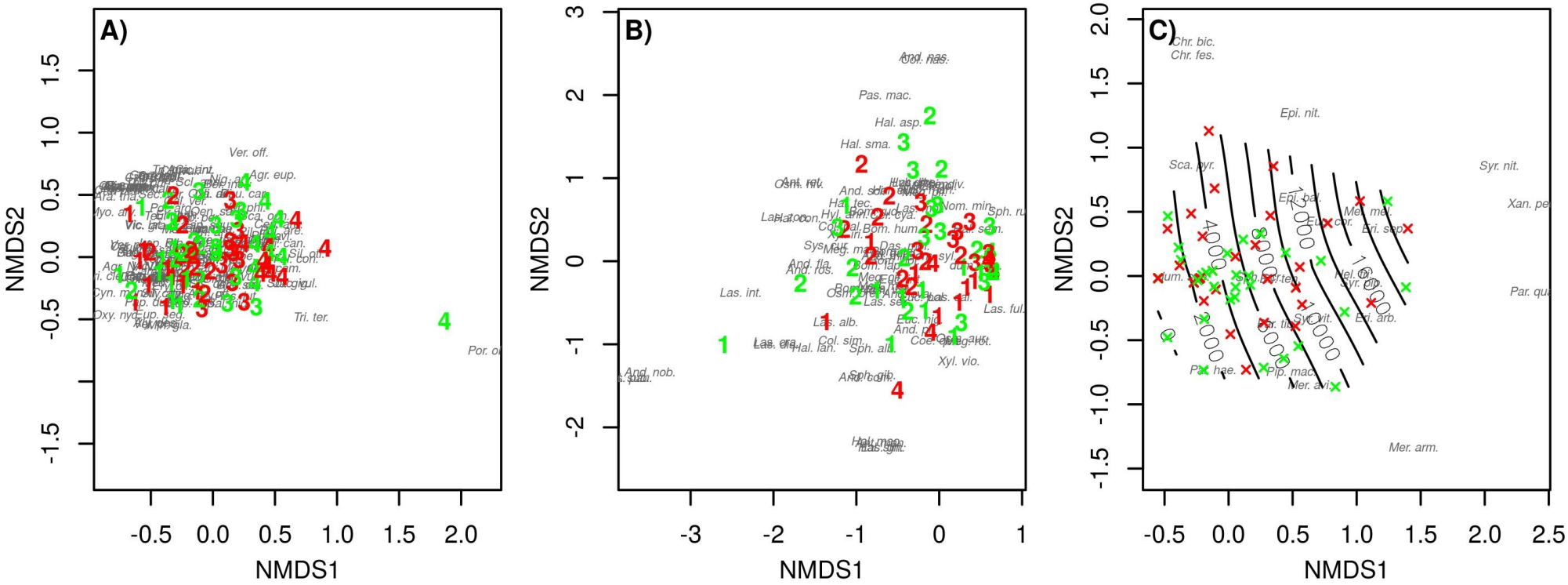
SM-Table 3. The list of bee and hoverfly species that were captured in invaded and control sites during four observation dates. Total number of recorded specimens and the number of individuals that were visiting flowers of common milkweed are shown separately.

species of Apiformes	# total recorded specimens		# recorded specimens on common milkweed	
	invaded	control	invaded	control
Andrena combaella		2		
Andrena flavipes	5	11	1	
Andrena minutula		1		
Andrena nasuta		1		
Andrena nobilis		1		
Andrena ovatula	11	15	2	
Andrena pilipes		1		
Andrena rosae		1		
Andrena scita	5	1		
Anthidium manicatum	1			
Anthophora bimaculata	2	3		
Anthophora retusa		1		
Apis mellifera	577	215	476	27
Bombus hortorum	15	2	14	
Bombus humilis	28	25	9	
Bombus lapidarius	30	18	22	1
Bombus pascuorum	22	11	4	
Bombus ruderarius	2	5	1	
Bombus sylvarum	10	2	3	
Bombus terrestris	32	21	30	4
Ceratina cyanea	2			
Coelioxys quadridentata	1			
Colletes nasutus		1		
Colletes pallescens	6	5		
Colletes similis		3		
Dasypoda morawitzi	2			
Eucera interrupta	2	4		
Eucera nigrescens	10	3		
Eucera pollinosa	15	19		
Halictus asperulus	1	5		
Halictus confusus	1			
Halictus eurygnathus	3	3		
Halictus langobardicus		3		
Halictus maculatus	1			
Halictus pollinosus		1		
Halictus quadricinctus	1	3		
Halictus semitectus	8	14		
Halictus simplex	2			
Halictus smaragdulus	1	1		
Halictus subauratus		1		
Halictus tectus		2		
Hoplitis manicata		1		
Hylaeus annularis	2			
Hylaeus gibbus	1			
Lasioglossum albipes	1	2		
Lasioglossum brevicorne aciculat	1	3		
Lasioglossum calceatum	4	1		
Lasioglossum crassepunctatum	1			
Lasioglossum discum	1			
Lasioglossum fulvicorne	1			
Lasioglossum griseolum	1			
Lasioglossum interruptum		1		
Lasioglossum morio	1		1	
Lasioglossum pauxillum		1		
Lasioglossum sexstrigatum	3	5		
Lasioglossum zonulum		1		
Megachile circumcincta		4		
Megachile maritima	5	2	1	
Megachile melanopyga	1			
Megachile pilidens	5	4		
Megachile rotundata		1		
Nomioides minutissimus	20	21	1	
Nomioides variegatus	2	1		
Osmia aurulenta	1	1		
Osmia brevicornis	1	4		
Osmia niveata		1		
Pasites maculatus		3		
Pseudapis diversipes	13	24		
Sphecodes albilabris		2		
Sphecodes gibbus		1		
Sphecodes rufiventris		1		
Systropha curvicornis	1	6		
Xylocopa iris	1			
Xylocopa violacea		5		

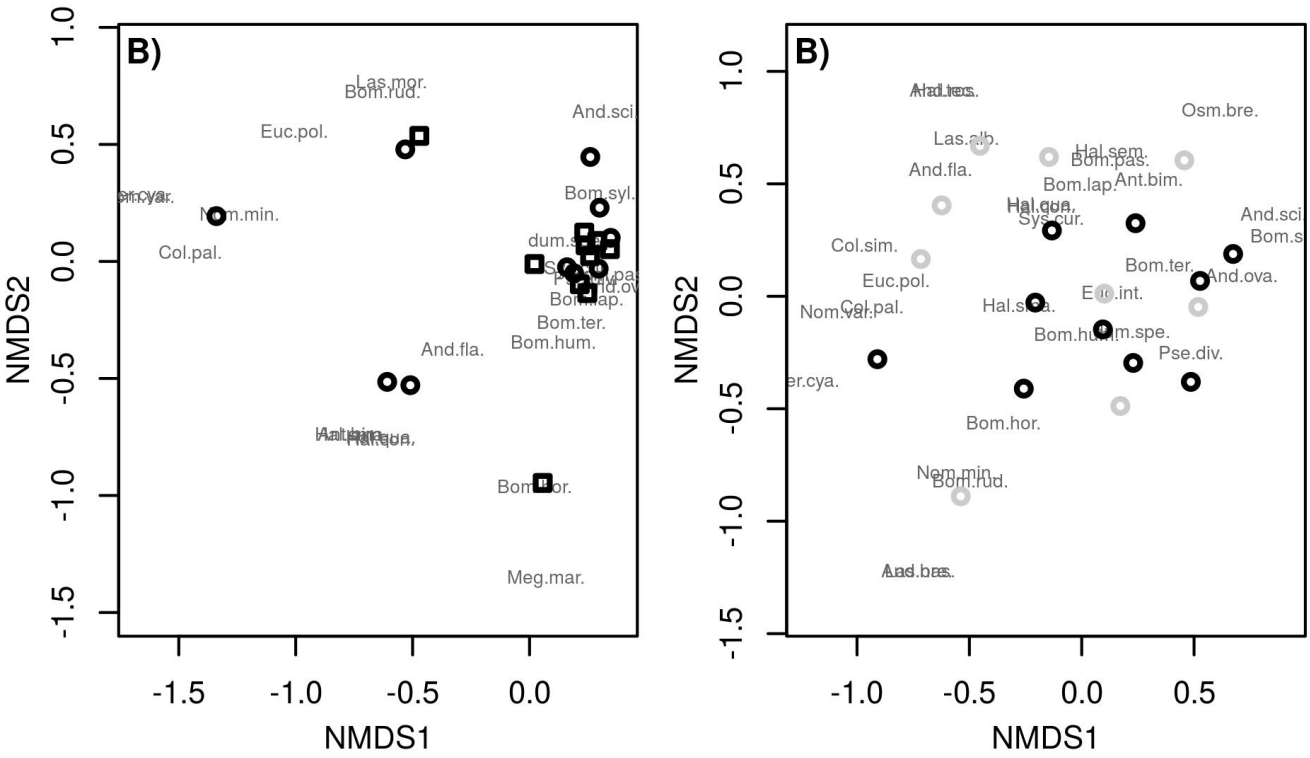
species of Syrphidae	# total recorded specimens		# recorded specimens on common milkweed	
	invaded	control	invaded	control
Chrysotoxum bicinctus	1			
Chrysotoxum festivum	1			
Epistrophe nitidicollis	1			
Episyrphus balteatus	21	18	1	
Eristalinius sepulcralis	3		1	
Eristalis arbustorum	7	15	1	
Eristalis tenax	15	34	2	
Eupeodes corollae	9	4		
Helophilus trivittatus	2	6		
Melanostoma mellinum	3	5		
Merodon armipes		2		
Merodon avidus	2	5		
Paragus haemorrhus	1	9		
Paragus quadrifasciatus		1		
Paragus tibialis	6	12		
Pipizella maculipennis	2	1		
Scaeva pyrastri	4	2		
Sphaerophoria scripta	256	271	3	
Syritta pipiens	16	17		
Syrphus nitidifrons		1		
Syrphus vitripennis	2			
Xantogramma pedisequm	1			

SM-Table 4. Differences between invaded and control sites in flower, wild bee, hoverfly abundances, species richness and diversity, and honey bee abundances for all the four observation dates separately. We show the adjusted p-values from Brunner-Munzel tests.

		adjusted p-value			
observation date	response variable	flower	wild bee	honey bee	hoverfly
1	abundance	**0.0400**	0.7290	0.3560	0.9040
2	abundance	**0.0200**	0.1707	**0.0000**	0.9040
3	abundance	0.2690	0.1180	0.2720	0.4920
4	abundance	0.2690	0.1180	0.8740	0.9040
1	number of species	0.8053	0.1550		0.2267
2	number of species	1.0000	0.1550		0.2267
3	number of species	0.1560	0.0540		0.2267
4	number of species	0.7960	**0.0440**		0.7810
1	diversity	0.3360	0.1347		0.7400
2	diversity	**0.0000**	0.2940		0.6160
3	diversity	0.8390	0.1347		0.4880
4	diversity	0.3360	0.1347		0.7400



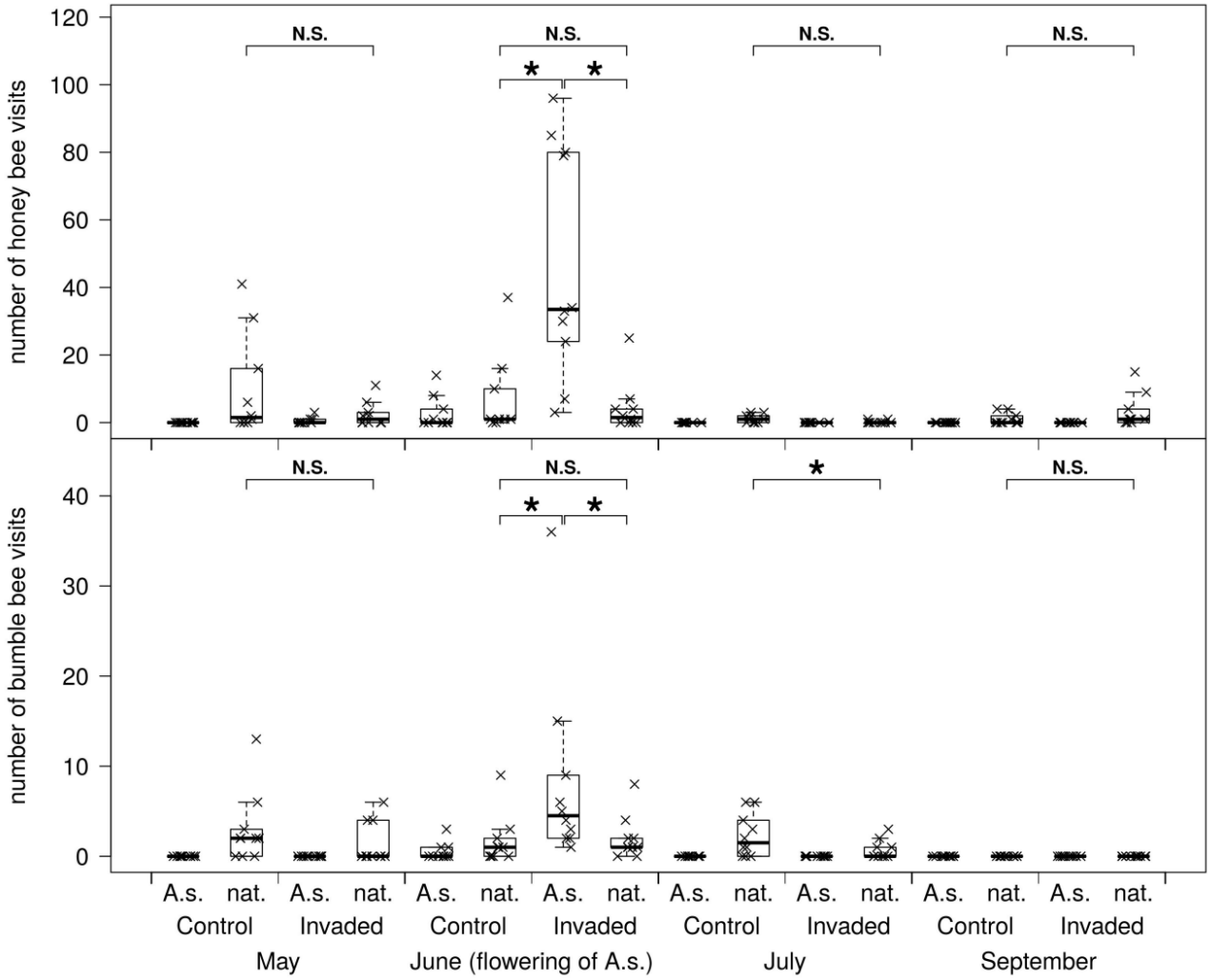
SM-Fig. 2 Non-metric multidimensional scaling (NMDS) for the A) floral plant B) wild bee C) hoverfly community compositions, presenting the explanatory variables with $0.1>R^2$ in PERMANOVAs. The numbers represent the sites grouped by observation date in A) and B), and × symbols represent sites, while smoothed gradient represent the flower abundances (using thin-plate fitted generalized additive models) in C). Data points from the invaded sites are marked by red, from the control sites by green. Gray text represents species' abbreviation (first three letters refer to the genus and second three letters to the species name).



SM-Fig. 3 Non-metric multidimensional scaling (NMDS) for the wild bee communities A) visited on common milkweed (square) or on native plant species (circle) in invaded sites and B) visited on native plants at control (gray circle) or invaded sites (black circle), during the second observation date. Gray text represents species' abbreviation (first three letters refer to the genus and second three letters to the species name).

SM-Table 5. Differences between invaded and control sites in flower visitation number on native plants for bumble bees and honey bees, for all the four observation dates separately, and differences between visitation on common milkweed and native floral species separately on invaded sites, and separately comparing invaded sites common milkweed visitation to native species visitation at control sites. We show the adjusted p-values from Brunner-Munzel tests.

			adjusted p-value	
observation date	**response variable**	**explanatory variable**	**bumble bee**	**honey bee**
1	visitation abundance	differences in visitation on native floral species between invaded and control sites	0.3480	0.5052
2	visitation abundance		0.4704	0.6310
3	visitation abundance		0.0480	0.0940
4	visitation abundance		1.0000	0.2355
2	visitation abundance	differences between visitaion on *Asclepias syriaca* and on native floral species in control sites	0.0060	<0.0001
2	visitation abundance	differences between visitaion on *Asclepias syriaca* and on native floral species in invaded sites	0.0090	<0.0001



SM-Fig. 4. Abundance of honey bees and bumble bees that visited common milkweed (A.s.) or native floral species (nat.) in the invaded and control sites, during the four observation dates. Boxplots show medians, lower, and upper quartiles. Black × symbols represent data per sampling sites. * above the boxes show significant differences according to the Brunner-Munzel test (note: N.S. represent non-significant differences). We compared both 1. the number of flower visitations on the native plants between the invaded and control sites for all observation dates together (*see* upper brackets) and 2. the number of flower visitations between the native plant species and common milkweed within the invaded sites and between the invaded and control sites only during the second observation date (*see* lower brackets).

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