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Influence of *Asclepias syriaca* on soil nematode communities

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Abstract

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The main goal of this study was to evaluate the impact of the invasive common milkweed (*Asclepias syriaca* L.) on soil nematode communities. The research was carried out in 2018 and 2019 in an ecosystem of permanent grassland in the basin of the Laborec River in land registries of Drahňov, a Vojany village in southeastern Slovakia. The ecosystem contained a total of 64 species of free-living and parasitic nematodes. The most prevalent trophic groups were bacterial feeders (*Acrobeloides nanus*), followed by plant parasites (*Helicotylenchus digonicus* and *Pratylenchus pratensis*), fungal feeders (*Aphelenchus avenae*), and omnivores (*Eudorylaimus carteri*). The number of nematode species, the composition of trophic groups and the structure of communities in areas with invasive plants were similar to those in areas with native vegetation during the two years of observation.

Keywords

common milkweed, diversity, ecology, soil nematodes

Introduction

Common milkweed (*Asclepias syriaca* L.) is an invasive species native to North America. *A. syriaca* is a broadleaf perennial herb, with simple stems sometimes as tall as 2 m. The leaves are short, smooth, and oppositely arranged on the stem. The flowers are pinkish but can vary from white to dark red and are usually arranged on both sides of the cymes. All parts of common milkweed contain a milky latex that contains toxic cardenolides (Bhowmik, 1994).

Invasive plant species are considered a major threat to the diversity of the flora and fauna of ecosystems (Jose et al., 2013), but their impact on soil nematofauna has rarely been studied worldwide (Belnap and Phillips, 2001; Liang et al., 2007). Soil nematodes are small filamentous organisms, whose adults have body lengths of 0.2–10.0 mm.

Nematode occurrence and activity (movement) are conditioned by the presence of water and by food sources, consisting of a wide range of organisms such as bacteria, fungi, plants, and other nematodes (Yeates et al., 1993). They are an important component of the soil biomass of all ecosystems. Nematodes are slow-moving ubiquitous organisms that represent about 80% of all multicellular organisms in soil (10^5–10^6 m^{-2}). They have a thin permeable cuticle that allows direct contact with the external environment. Some may survive or die in unfavourable soil conditions, in anabiotic or cyst stages, so they are useful bioindicators (Freckman, 1988; Bongers and Ferris, 1999; Hugot et al., 2001). Recent preliminary studies, however, have found that the impact of invasive plant species on soil nematodes depends on the plant species and the ecosystem.

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The main goal of this study was to use nematode communities as bioindicators to evaluate the impact of *A. syriaca* invasion on an ecosystem using functional and ecological indices (identification, occurrence, abundance, diversity, and community structure of nematode species) (Bongers, 1990; Ferris et al., 2001).

Materials and methods

The impact of the non-indigenous *A. syriaca* on soil nematodes was investigated in a permanent grassland in the southern part of eastern Slovakia in the Laborec River basin. Soil samples were collected from five 20-m^2 plots dominated by *A. syriaca* in June 2018 (AS1) and June 2019 (AS2) and from five adjacent control plots in (CO1) and (CO2) dominated by the grasses *Brachypodium pinnatum* and *Bromus tectorum* and containing no invasive plants.

Motile nematodes were isolated using sieves and the Baermann method with a set of two cotton propylene filters (Van Bezooijen, 2006). Nematodes were killed in a warm water bath (70 °C) and fixed with Ditlevsen's solution (Van Bezooijen, 2006). Permanent glycerine slides were prepared for 100 individuals of randomly selected nematodes two weeks after fixation. Nematodes on the slides were identified to species using an Eclipse 90i light microscope (Nikon Instruments Europe BV, Netherlands). Taxonomic and systematic monographs by Andrássy (2005; 2007; 2009), Meyl (1960), Hunt (1993), Brzeski (1998), Loof (1999), and Geraert (2008; 2010; 2011; 2013) were used for identification.

Evaluation of the nematode communities was based on the total number of nematodes per 100 g of soil, occurrence and number of species, a species diversity index (H'spp) (Shannon and Weaver, 1949), and the number of individuals in various trophic groups (Yeates et al., 1993; Wasilewska, 1997). The degree of dominance (D) of the species was determined using the scale proposed by Losos et al. (1984): eudominant (D > 10%), dominant (D = 5–10%), subdominant (D = 2–5%), and recendent (D < 2%). Species were divided into six trophic groups: bacterial feeders, predators, fungal feeders, omnivores, plant parasites, and root-fungal feeders (Yeates et al., 1993; Wasilewska, 1997). They were also divided into functional guilds using the c-p (coloniser-persister) value, which varies from 1 to 5 depending on the duration of their development cycle, trophic and reproductive strategies, and sensitivity to environmental alteration (Bongers, 1990).

We used an automated calculation system NINJA (Sieriebriennikov et al., 2014) for nematode-based biological monitoring to calculate i) ecological indices (maturity index, MI; summary maturity index, ΣMI; maturity index for nematodes with c–p values of 2–5, MI 2–5; and a plant parasitic index, PPI), ii) functional indices (enrichment index, EI; structural index SI; and channel index CI, which provide information about the conditions of the soil environment), and iii) total nematode biomass (Bongers, 1990; Bongers and Korthals, 1993; Ferris et al., 2001). The nematode channel ratio NCR defined by Yeates (2003), and the Jaccard index of faunistic similarity Js defined by Jaccard (1908), were also calculated. Data were statistically analysed using PlotIT Ver. 3.2 (Scientific Programming Enterprises, Haslett, USA) and were compared using Student's *t*-tests.

Results

A total of 64 species of free-living and plant parasitic nematodes were found in the soil samples. The control plots contained more species than the invaded plots (44 vs 41) in 2018 but fewer in 2019 (45 vs 48). The total number of individuals in 2018 was 9,895 and was slightly higher in the control plots (5,017) than the invaded plots (4,878) (Table 1). The total number of individuals was higher in 2019 (12,378) than 2018 (9,895). The differences in abundance between the invaded and control plots, however, were not significant.

The eudominant (>10%) bacterial feeder *Acrobeloides nanus* (509 individuals, D = 10.4%, in 2018; 669 individuals, D = 11.0%, in 2019) and the fungal feeder *Aphelenchus avenae* (486 individuals, D = 10.0%, in 2018 only) were the most abundant nematodes in the invaded plots. The dominant (5–10%) omnivore *Eudorylaimus carteri*, the obligate plant parasites *Helicotylenchus digonicus* and *Pratylenchus pratensis*, some subdominant species (2–5%) such as *Oxydirus oxycephalus* (predator), *Aporcelaimellus obtusicaudatus* (omnivore), and the facultative plant parasites *Aglenchus agricola* and *Boleodorus volutus* were also relatively abundant in the invaded plots. The number and dominance of the nematodes were similar in the control plots. Some species were nevertheless present only in the invaded plots, regardless of year of observation, such as *Acrolobus emarginatus*, *Anaplectus granulosus*, *Ereptonema arcticum*, *Clarkus papillatus*, *Tylencholaimus stecki*, *Campydora demonstrans*, *Microdorylaimus parvus*, *Pratylenchoides crenicauda*, and *Trophurus sculptus*. In contrast, other nematode species such as *Prismatolaimus intermedius*, *Tylencholaimellus striatus*, *Mesocriconema curvatum*, *Heterodera* sp. (juveniles), *Longidorus* sp. (juveniles), and *Tylenchus elegans* were found only in the control plots (Table 1).

All soil samples contained all nematode trophic groups, regardless of the presence or absence of invasive plants. Bacterial feeders and plant parasites followed by fungal feeders were the most abundant trophic groups in both years. The proportions of all trophic groups did not differ significantly between the invaded and control plots (Fig. 1).

Maturity indices (MI, MI 2–5, and ΣMI) were slightly higher in the control than the invaded plots in both years. CI and SI were slightly higher and lower, respectively, in the invaded plots in both years. Total nematode biomass and NCR were lower in the invaded than the control plots, but not significantly. Js was 63.46 in 2018 and 63.16 in 2019 (Table 2).

When plotting the EI and SI, for analysis of food webs, the soil samples from invaded and control plots mostly (95% of samples) ended up in quadrats B and C

Table 1. Nematode total abundance (A) in 100 g of soil and dominance of nematode species (D %) in samples collected in June 2018 and 2019 (n = 5) from areas with presence of *Asclepias syriaca* (AS1, AS2) and with native vegetation (control area) (CO1, CO2). TG – trophic groups: B – bacterial feeders, P – predators, F – fungal feeders, O – omnivores, PP – plant parasites, RFF – root-fungal feeders; c-p value according Bongers (1990)

TG	Nematode species	c-p	2018				2019			
			AS1		CO1		AS2		CO2	
			A	D %	A	D %	A	D %	A	D %
B	*Acrobeloides nanus* (de Man, 1880) Anderson, 1968	2	509	10.4	275	5.5	669	11.0	655	10.4
B	*Acrolobus emarginatus* (de Man, 1880) Boström, 1986	2	–	–	–	–	37	0.6	–	–
B	*Alaimus primitivus* de Man, 1880	4	75	1.5	106	2.1	79	1.3	87	1.4
B	*Amphidelus elegans* (de Man, 1921) Thorne, 1939	4	41	0.8	46	0.9	–	–	22	0.4
B	*Anaplectus granulosus* (Bastian, 1865) De Coninck & Schuurmans Stekhoven, 1933	2	–	–	–	–	57	0.9	–	–
B	*Cephalobus persegnis*Bastian, 1865	2	159	3.3	26	0.5	190	3.1	80	1.3
B	*Cervidellus vexilliger* (de Man, 1880) Thorne, 1937	2	7	0.2	37	0.7	28	0.5	73	1.1
B	*Ereptonema arcticum* Loof, 1971	2	–	–	–	–	8	0.1	–	–
B	*Eucephalobus oxyuroides* (de Man, 1876) Steiner, 1936	2	22	0.4	40	0.8	76	1.2	86	1.4
B	*Eucephalobus striatus (Bastian, 1865) Thorne, 1937*	2	68	1.4	113	2.3	148	2.4	254	4.0
B	*Chiloplacus propinquus* (de Man, 1921) Thorne, 1937	2	118	2.4	26	0.5	232	3.8	94	1.5
B	*Mesorhabditis sp* .Osche, 1952	1	150	3.1	59	1.2	100	1.7	174	2.8
B	*Panagrolaimus rigidus* (Schneider, 1866) Thorne, 1937	1	138	2.8	85	1.7	14	0.2	109	1.7
B	*Plectus parietinus* Bastian, 1865	2	80	1.6	25	0.5	42	0.7	192	3.0
B	*Plectus parvus* Bastian, 1865	2	38	0.8	79	1.6	51	0.8	91	1.4
B	*Plectus silvaticus* Andrássy, 1985	2	–	–	59	1.2	72	1.2	86	1.4
B	*Prismatolaimus intermedius* (Bütschli, 1873) de Man, 1880	3	–	–	30	0.6	–	–	75	1.2
B	*Protorhabditis filiformis* (Bütschli, 1873) Sudhaus, 1976	1	56	1.1	75	1.5	24	0.4	67	1.1
B	*Teratocephalus terrestris* (Bütschli, 1873) de Man, 1876	3	–	–	–	–	27	0.5	64	1.0
B	*Wilsonema schuurmansstekhoveni* (De Coninck, 1931) Zell, 1985	2	–	–	33	0.7	63	1.0	–	–
B	*Eumonhystera vulgaris* (de Man, 1880) Andrássy, 1981	2	32	0.6	84	1.7	–	–	41	0.7
			1,493		1,198		1,917		2,250	
P	*Clarkus papillatus* (Bastian, 1865) Jairajpuri, 1970	4	23	0.5	–	–	–	–	–	–
P	*Mylonchulus sigmaturus* Cobb, 1917	4	15	0.3	–	–	40	0.7	58	0.9
P	*Tripyla filiformis* de Man, 1880	3	33	0.7	–	–	40	0.7	26	0.4
P	*Oxydirus oxycephalus* (de Man, 1885) Thorne, 1939	5	208	4.3	171	3.4	–	–	124	2.0

Table 1. Continued

F	*Aphelenchoides composticola* Franklin, 1957	2	28	0.6	99	2.0	63	1.0	73	1.2
F	*Aphelenchoides parietinus* (Bastian,1865) Steiner, 1932	2	136	2.8	17	0.3	181	3.0	220	3.5
F	*Aphelenchoides limberi* Steiner, 1936	2	43	0.9	10	0.2	54	0.9	101	1.6
F	*Aphelenchus avenae* Bastian, 1865	2	486	10.0	258	5.1	347	5.7	265	4.2
F	*Diphtherophora communis*de Man, 1880	3	76	1.6	67	1.3	136	2.2	–	–
F	*Ditylenchus intermedius* (de Man, 1880) Filipjev, 1936	2	73	1.5	112	2.2	83	1.4	40	0.6
F	*Ditylenchus medicaginis* Wasilewska, 1965	2	–	–	–	–	43	0.7	50	0.8
F	*Paraphelenchus pseudoparietinus* Micoletzky, 1922	2	8	0.2	–	–	17	0.3	64	1.0
F	*Tylencholaimus stecki* Steiner, 1914	4	–	–	–	–	76	1.2	–	–
F	*Tylencholaimus mirabilis* (Bütschli, 1873) de Man, 1876	4	–	–	–	–	101	1.7	26	0.4
F	*Tylencholaimellus striatus* Thorne, 1939	4	–	–	118	2.4	–	–	102	1.6
F	*Dorylaimoides micoletzkyi* (de Man, 1921) Thornne & Swanger, 1936	4	25	0.5	–	–	27	0.5	114	1.8
F	*Doryllium uniforme* Cobb, 1920	4	–	–	41	0.8	–	–	–	–
			875		722		1,128		1,055	
O	*Campydora demonstrans* Cobb, 1920	4	–	–	–	–	12	0.2	–	–
O	*Aporcelaimellus obtusicaudatus* (Bastian, 1865) Altherr, 1968	5	155	3.2	155	3.1	213	3.5	196	3.1
O	*Crassolabium ettersbergense* (de Man, 1885) Peña-Santiago & Ciobanu, 2008	4	46	0.9	104	2.1	80	1.3	156	2.5
O	*Ecumenicus monohystera* (de Man, 1880) Thorne, 1974	4	–	–	86	1.7	66	1.1	–	–
O	*Eudorylaimus carteri* (Bastian, 1865) Andrássy, 1959	4	243	5.0	221	4.4	14	0.2	81	1.3
O	*Mesodorylaimus bastiani* (Bütschli, 1873) Andrássy, 1959	4	32	0.6	50	1.0	–	–	105	1.7
O	*Microdorylaimus parvus* (de Man, 1880) Andrássy, 1986	4	50	1.0	–	–	–	–	–	–
O	*Prodorylaimus longicaudatus* Altherr, 1968	4	–	–	85	1.7	67	1.1	–	–
O	*Pungentus silvestris* (de Man, 1912) Coomans & Geraert, 1962	4	56	1.1	36	0.7	–	–	25	0.4
			582		737		452		563	
PP	*Criconemoides informis* (Micoletzky, 1922) Taylor, 1936	3	–	–	220	4.4	51	0.8	–	–
PP	*Merlinius brevidens* (Allen, 1955) Siddiqi, 1970	3	17	0.3	52	1.0	78	1.3	276	4.4
PP	*Helicotylenchus digonicus* Perry in Perry, Darling & Thorne, 1959	3	404	8.3	566	11.3	527	8.7	541	8.6
PP	*Heterodera sp. juvs.* Schmidt, 1871	3	–	–	–	–	–	–	26	0.4
PP	*Longidorus sp. juvs.* Micoletzky, 1922	5	–	–	–	–	–	–	26	0.4
PP	*Mesocriconema curvatum* (Raski, 1952) Loof & De Grisse, 1989	3	–	–	205	4.1	–	–	–	–
PP	*Paratylenchus microdorus* Andrássy, 1959	2	165	3.4	282	5.6	239	3.9	296	4.7

PP	*Paratylenchus similis* Khan, Prasat & Mathur, 1967	2	–	–	–	–	273	4.5	91	1.4
PP	*Pratylenchoides crenicauda* Winslow, 1958	3	215	4.4	–	–	–	–	–	–
PP	*Pratylenchus pratensis* (de Man, 1880) Filipjev, 1936	3	310	6.3	317	6.3	435	7.2	267	4.2
PP	*Trophurus sculptus* Loof 1956	3	69	1.4	–	–	120	2.0	–	–
			1,180		1,642		1,723		1,523	
RFF	*Aglenchus agricola* (de Man, 1884) Andrássy, 1954	2	153	3.1	–	0.2	–	–	–	–
RFF	*Boleodorus volutus* Lima & Siddiqi, 1963	2	176	3.6	124	2.5	500	8.2	307	4.9
RFF	*Coslenchus costatus* (de Man, 1921) Siddiqi, 1978	2	–	–	–	–	71	1.2	68	1.1
RFF	*Filenchus vulgaris* (Brzeski, 1963) Lownsbery & Lownsbery, 1985	2	140	2.9	119	2.4	124	2.0	340	5.4
RFF	*Malenchus exiguus* (Massey, 1969) Andrássy, 1980	2	–	–	241	4.8	69	1.1	–	–
RFF	*Tylenchus elegans* de Man, 1876	2	–	–	54	1.1	–	–	–	–
	Total number of nematodes		4,878		5,017		6,064		6,314	
	Number of nematode species		41		44		48		45	

Table 2. Ecological and functional indices of nematodes from soil samples collected in June 2018 and 2019 from plots with presence of *Asclepias syriaca* (AS1, AS2) and control plots with native vegetation (CO1, CO2). Evaluated indices: diversity index for species H‘spp. and Jaccard index of faunistic similarity

Evaluated indices	2018				2019			
	AS1		CO1		AS2		CO2	
	Mean	S.D	Mean	S.D	Mean	S.D	Mean	S.D
Number of individuals	975.4 ns	180.3	1003.5	167.7	1213.0 ns	228.1	1267.7	169.6
H'spp.	2.8 ns	0.1	3.1	0.1	2.9 ns	0.2	3.0	0.220
Maturity index	2.6 ns	0.4	2.9	0.2	2.5 ns	0.1	2.6	0.2
Maturity index 2–5	2.8 ns	0.4	3.1	0.2	2.6 ns	0.1	2.6	0.2
Σ Maturity index	2.6 ns	0.3	2.8	0.1	2.5 ns	0.1	2.6	0.1
Plant parasitic index	2.7 ns	0.1	2.7	0.1	2.5 ns	0.2	2.6	0.2
Channel index	49.3 ns	29.3	48.5	21.5	68.3 ns	23.3	44.0	7.5
Enrichment index	51.9 ns	13.7	19.2	10.4	36.1 ns	8.6	47.1	5.5
Structure index	68.4 ns	13.9	80.1	4.5	60.8 ns	7.6	64.3	10.4
NCR (BF/BF + FF)	0.6 ns	0.6	0.7	0.6	0.6 ns	0.6	0.7	0.8
Total biomass (mg)	0.9 ns	0.7	1.2	0.5	1.1 ns	0.3	1.2	0.6
Jaccard index	63.5				63.2			

ns, non-significant.

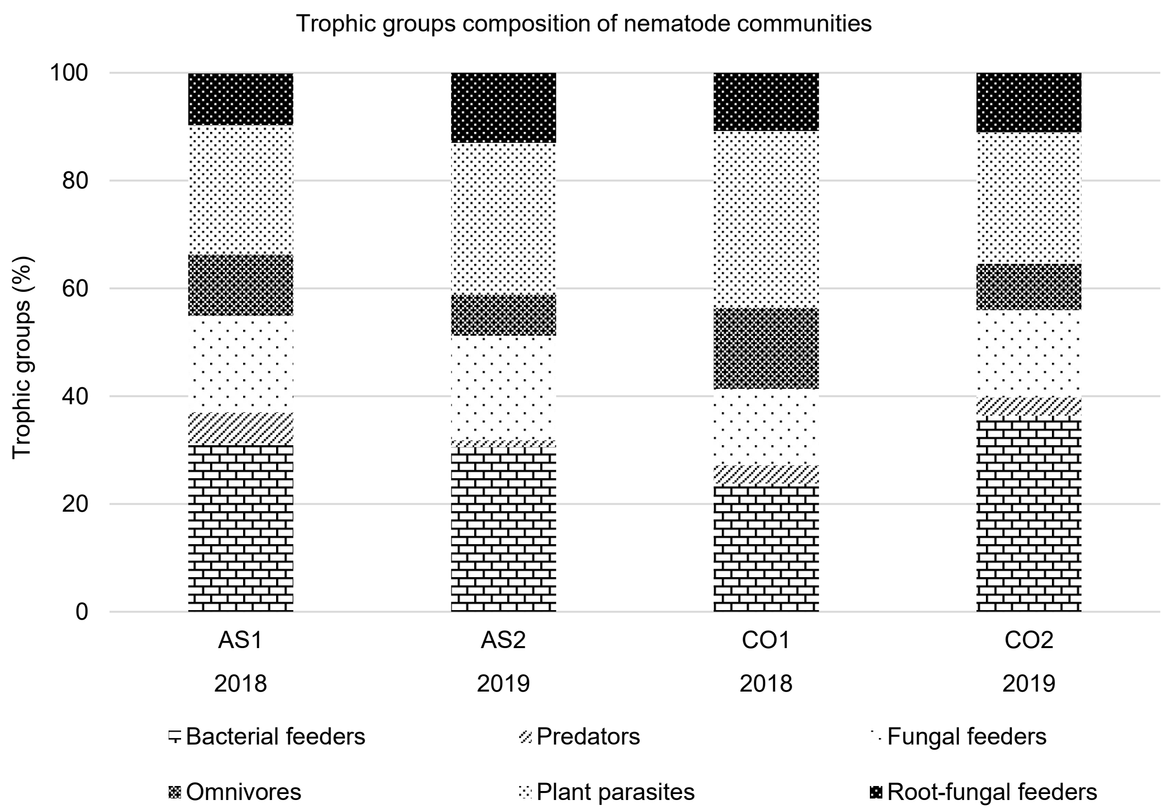

Fig. 1. Percentage proportion of nematodes in trophic groups in invaded plots by *Asclepias syriaca* (AS1, AS2) and control plots with native vegetation (CO1, CO2) in June 2018 and 2019 (n = 5).

(Fig. 2). These quadrants indicated that both types of soil environments had been little disturbed and had balanced nutrient supplies. Bacterial and fungal feeders were equally involved in the decomposition of organic matter, and the food web was mature.

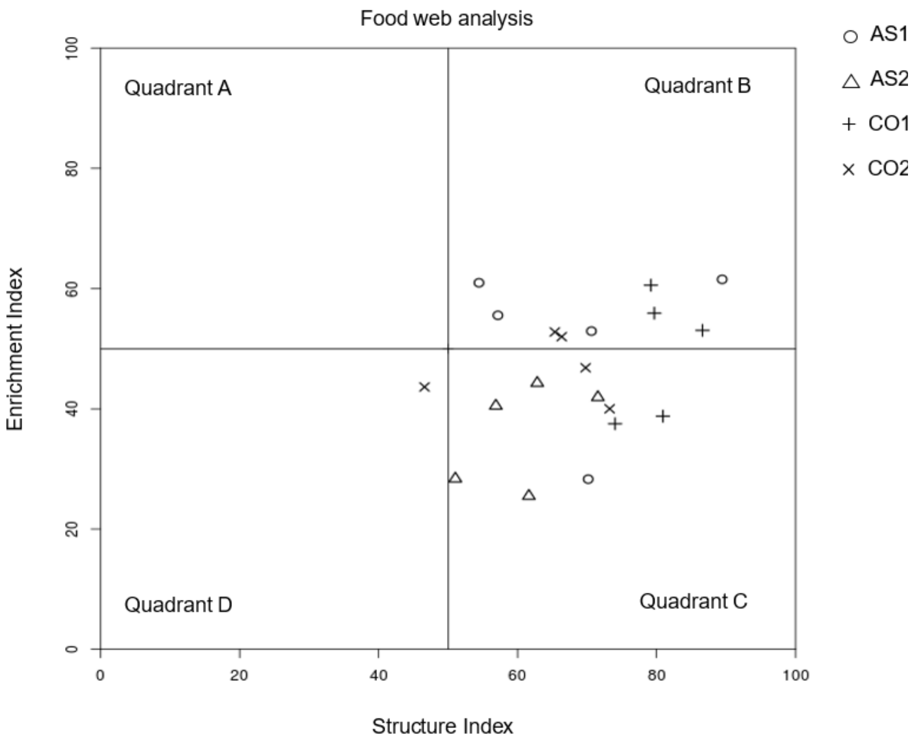

Fig. 2. Graphical representation of trophic webs and conditions in soil environment by values of Enrichment Index and Structure Index in invaded plots by *Asclepias syriaca* (AS1, AS2) and control plots with native vegetation (CO1, CO2) in June 2018 and 2019 (n = 5).

Discussion and conclusions

Recent studies have found that the impact of invasive plant species on ecosystem soil nematofauna could be positive, neutral, or negative. Nematode species diversity was affected positively in conjunction with invasion by *Impatiens parviflora* and *I. glandulifera* (Renčo et al., 2013) and negatively in conjunction with invasion by *Solidago gigantea* or *Fallopia japonica* (Čerevková et al., 2019a; 2019b).

Yeates (1999) reported that the species spectrum of plant root composition in soil directly influenced the occurrence and behaviour of plant parasitic nematodes, consistent with the findings by De Deyn et al. (2004). Changes in the diversity of plant species and roots and the quality and quantity of biomass primarily affect plant parasites and only indirectly (secondarily) affect other trophic groups, such as fungal feeders, predators, or bacterial feeders. In our study, the invasion by common milkweed had no effect on the numbers of bacterivorous nematodes. We found that the total abundance of obligate plant parasitic nematodes was similar in the invaded and control plots, what was consistent with the results obtained by Jurová et al. (2019) in a previous study of the effect of *A. syriaca* on soil nematodes. We therefore hypothesised that the common milkweed or its roots may host some plant parasitic nematodes responsible for the reduction in yield of economically important crops. Many weeds are important hosts for many plant parasitic nematodes (cyst-forming nematodes and root-knot nematodes), so the roots of *A. syriaca* may also be hosts.

Nematodes of trophic groups omnivores and predators are the most sensitive to changes in their environment, because they have a low reproductive capacity and long developmental cycles (Bongers, 1990; Ferris et al., 2001). Restoring the numbers to levels before environmental damage requires more time for omnivores and predators than for bacterial or fungal feeders (r-strategists). The abundances of omnivores and predators during the two years of observation were not affected by the invasion by common milkweed in this permanent grassland. Omnivores and predators in some cases can respond to invasion by non-native plant species as typical K-strategists, and sometimes vice versa (Renčo and Baležentiené 2015; Renčo et al. 2019). These groups are also characterised by their species diversity, food strategies, and species biology, which impede the interpretation of results (Cesarz et al., 2015). Fauna can also be differentially affected by various environmental conditions, such as invasion by non-native plants, and the properties of these plants (Jose et al., 2013).

Fungal feeders in our study ranged from 24 to 33% of the total nematofauna. Fungal feeders of the c-p2 group dominated, especially *A. avenae* and *Aphelenchoides parietinus*. The proportion and number of fungal feeders, however, did not differ among the soils, indicating that invasion by common milkweed did not affect the structure of the fungal communities. No data are available on the impact of *A. syriaca* on soil fungal communities. Vannette and Hunter (2011), though, found that mycorrhizal fungi lived on the roots of common milkweed and positively affected its growth, the production of its milky exudate, and leaf area.

We also calculated various ecological and functional indices of communities to comprehensively evaluate our results, although changes to the abundance, number of species, species diversity, and representation of trophic and c-p groups were not confirmed in the nematode communities. The indices did not differ significantly between the invaded and control plots during the two years of observation, as we assumed. The analysis of the structures of food webs using EI and SI indicated that the soil environments of both types of plots was little disturbed and had balanced supplies of nutrients. Bacterial and fungal feeders were equally involved in the decomposition of organic matter, and the food web was mature.

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