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How does an invasive *Heracleum sosnowskyi* affect soil nematode communities in natural conditions?

Marek RENČO [1,*], Franciszek Wojciech KORNOBIS [2], Krzysztof DOMARADZKI [3], Anna JAKUBSKA-BUSSE [4], Jana JUROVÁ [1] and Zuzana HOMOLOVÁ [5]

[1] *Institute of Parasitology, Slovak Academy of Sciences, Hlinkova 3, 040 01, Košice, Slovak Republic*
[2] *Department of Entomology, Animal Pests and Biotechnology, Institute of Plant Protection – National Research Institute, Władysława Węgorka 20, 60-318 Poznań, Poland*
[3] *Institute of Soil Sciences and Plant Cultivation – State Research Institute Department of Weed Sciences and Soil Tillage Systems, Orzechowa 61, 50-540 Wroclaw, Poland*
[4] *Department of Botany, Laboratory of Plant Taxonomy, Institute of Environmental Biology, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, 50-328 Wroclaw, Poland*
[5] *Research Station of the State Forest of the Tatra National Park, 059 60 Tatranska Lomnica, Slovakia*

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Summary – We analysed the effect of the invasive perennial plant *Heracleum sosnowskyi* on soil nematode communities and diversity, and plant species composition, by comparing invaded and non-invaded (control) areas in natural conditions. Invasion of *H. sosnowskyi* caused significant shifts in plant species composition, which subsequently modified nematode assemblages. Stress-sensitive omnivores, fungivores and root-biomass-dependent obligate plant parasites best reflected changes in soil nematode communities under the influence of *H. sosnowskyi* invasion. The negative effect of *H. sosnowskyi* was most evident on *Aphelenchus*, *Tylencholaimus*, *Geocenamus*, *Helicotylenchus*, *Pratylenchus*, *Tylenchorhynchus* and *Aporcelaimellus*. Our results indicate that significant changes in the herbaceous layer after *H. sosnowskyi* invasion in ecosystems where *H. sosnowskyi* eventually became dominant impacted soil nematode communities but did not affect nematode diversity. This was in contrast to the habitats where a solitary plant of *H. sosnowskyi* grew and no significant changes in nematode communities were observed.

Keywords – alien plant species, biodiversity, ecosystem, functional guilds, indicators, multivariate analysis, Nematoda.

The current rate of non-native species invasions in new geographic localities is the highest in history (MacDougal & Turkington, 2005). According to the most recent study by Seebens *et al*. (2017), 37% of all first records of invasive species were reported within the period of 1970-2014. Among these organisms an important role is played by invasive plants, which have wreaked havoc in ecosystems. They are considered to be one of the leading threats to the ecological integrity of native flora and fauna by establishment of monospecific stands (Jose *et al*., 2013; Meyerson *et al*., 2016). Some of these species become extremely abundant in their new range, especially in habitats that have ideal conditions allowing their establishment (Richards *et al*., 2006). This situation occurs rapidly due to global climate change causing alterations to environmental conditions (Burgiel & Muir, 2010).

Some of the most invasive plant species in Europe fall within the genus *Heracleum*. This genus consists of about 60 species, which are found primarily in the temperate northern hemisphere. However, recent human activity has led to a displacement of several species of the genus into new localities. For example, in Poland, until the middle of the 20th century only one species of the genus, non-invasive *H. sphondylium*, grew in the wild as a native plant. In the second half of the century new species such as *H. sosnowskyi* (Sosnowski's hogweed) and *H. mantegazzianum* (giant hogweed) were introduced from the Caucasus to Europe for decorative purposes or as fodder plants. Both species are now widespread, not only in Poland, and are now considered as the most problematic

* Corresponding author, e-mail: renco@saske.sk

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and dangerous invasive plant species (Jakubska-Busse *et al*., 2013).

Recent scientific studies have aimed at exploring the relationship between invasive plants and soil-dwelling arthropod fauna, as well as the changes related to the abundance and diversity in species structure (Gallé *et al*., 2015; Coyle *et al*., 2017). Litt *et al*. (2014) reviewed 87 articles published in the peer-reviewed literature to evaluate the responses of arthropod communities and functional groups to non-native invasive plants. In all studies the abundance of arthropods decreased by 62% and taxonomic richness decreased by 48%. The numbers of herbivorous arthropods decreased in response to the plant invasions by 48%, probably due to the direct effects of decreased plant diversity. Predaceous arthropods decreased in response to invasive plants in 44% of studies, which may reflect the indirect effects due to reductions in prey. However, the behaviour and response of large groups of small soil inhabitants, *e.g.*, nematodes, to the incidence of invasive plants have been less well studied (Belnap *et al*., 2005; Chen *et al*., 2007; Renčo & Baležentienė, 2015). Furthermore, in previous studies different invasive plant species growing in different ecosystems (habitats) and climatic areas were studied; therefore, results are not comparable or universal. Soil nematodes are useful indicators of environmental conditions (Bongers, 1990; Ferris *et al*., 2001) due to their known taxonomy and trophic roles (Gupta & Yeates, 1997). Nematodes exhibit many biological features (ubiquity, abundance, permeable cuticles, species richness, and easy sampling and assignment to trophic and ecological groups) that qualify them as good indicators of soil quality and soil disturbance at the family level (Bongers, 1990; Ferris *et al*., 2001). Different ecosystems have more or less species-specific nematode assemblages (Sohlenius, 1980; Ruess, 2003; Neher *et al*., 2005). Since different invasive plants have the phenotypic plasticity to tolerate a broad range of environmental conditions (Richards *et al*., 2006), their impact on nematode communities can be different. In the case of *H. sosnowskyi*, the species mostly enters the colonised human-created habitats (roadsides, disturbed habitats, agricultural fields, abandoned farmyards and gardens) and semi-natural habitats (shrublands, grasslands, parks, pastures, abandoned orchards, wastelands and rail networks) (EPPO Bulletin, 2009). *Heracleum sosnowskyi* has also invaded riverbanks or adjacent floodlands and, in many cases, forest edges (Baležentienė & Bartkevičius, 2013). Therefore, evaluating the status of related changes in the structures of soil nematode communities after the establishment of an invasive plant must include the assessment of different habitats invaded by particular invasive species.

To our knowledge, data on the relationship of some of the invasive *Heracleum* species and soil nematodes are scarce. Databases include only our previous work on *H. sosnowskyi* performed in central Lithuania (Renčo & Baležentienė, 2015), where a long-term *H. sosnowskyi* dominance was associated with low abundances and faunal similarity of soil nematode communities, despite the fact that several nematode trophic groups (bacterivores, root fungivores, omnivores) and nematode species were not sensitive to invasion. However, due to the wide habitat preference of *H. sosnowskyi*, generalisations about the *H. sosnowskyi* impact on soil nematodes is problematic because only three invaded habitats on one locality have been examined (Renčo & Baležentienė, 2015).

Therefore, the present paper seeks to determine the effect of *H. sosnowskyi* invasion on nematode communities in Poland in four localities representing four different natural habitats that differ in native vegetation and *H. sosnowskyi* coverage, altitude or historical management (natural, semi-natural, managed). The study aims to answer the following questions: Does the *H. sosnowskyi* invasion affect nematode abundance, functional guilds, feeding groups and feeding strategy of nematodes due to plant community changes? Will the changes in the nematode communities be similar among the four habitats/localities? Will the impact of *H. sosnowskyi* invasion on nematode assemblages of Poland habitats be generally similar to those in Lithuania? In addition, we evaluated the bioindicative competence of nematode-based indicators to alien plant invasion.

Materials and methods

Site characteristics and design of the survey

The study was carried out in 2015 during the flowering stage (June) of *H. sosnowskyi* at four localities representing four different habitats within Poland. Elevation of the study habitats ranged from 72 to 128 m a.s.l. We selected a 20 m × 20 m area invaded by *H. sosnowskyi* in each habitat. An area of the same size that was not yet colonised by the invasive plant was chosen in proximity to the corresponding invaded one (mean distance between invaded and non-invaded area was 10 m). Pairs of invaded and non-invaded areas did not differ in elevation, inclination or exposition. In each invaded area, we randomly

Table 1. Habitat type, location, area code and vegetation characteristic of study areas.

Habitat type	Location/soil type	Area	Vegetation/cover
Wet dump ground depression surrounded by self-set tress (Gd)	Czerwonak, 52.46398°N, 16.98697°E, altitude 72 m a.s.l./sandy-loamy Cambisol	Control (DEPc)	*Phragmites australis* (55%), *Ipomoea carnea* (15%), *Lolium perenne* (15%), *Galium verum* (2%), *Symphytum officinale* (2%), *Urtica dioica* (2%), *Solidago* sp. (2%), *Calystegia sepium*.
		Invaded (DEPh)	Similar composition of native vegetation as in control area with several solitary mature *Heracleum sosnowskyi* plants.
Non-cultivated line between two agricultural fields (Af)	Niegolewo, 52.37262°N, 16.42805°E, altitude 82 m a.s.l./sandy-loamy Cambisol	Control (AGRc)	*Elymus repens* (41%), *Equisetum arvense* (15%), *Bromus* sp. (25%), *Artemisia campestris* (5%), *Urtica dioica* (4%) and *Potentilla reptans* (2%).
		Invaded (AGRh)	*Heracleum sosnowskyi* (91%), sporadically present undergrowth species of *Elymus repens*, *Artemisia campestris* and *Urtica dioica. Heracleum sosnowskyi* formed a coherent vegetation cover at the time of soil sampling.
Route edge leading to barns within private agricultural farm (former state farm) (Re)	Mojecice, 51.30149°N, 16.58355°E, altitude 128 m a.s.l./Loess soil	Control (REDc)	*Elymus repens* (45%), *Lamium purpureum* (13%), *Arhenatherum elatius* (9%), *Taraxacum officinale* (9%) and sporadically *Urtica dioica* (6%), *Erigeron canadensis* (4%), *Dactylis glomerata* (5%) and *Sisymbrium officinale* (2%).
		Invaded (REDh)	*Heracleum sosnowskyi* (83%) sporadically present undergrowth species of *Elymus repens*, *Urtica dioica*, *Lamium purpureum* and *Taraxacum officinale. Heracleum sosnowskyi* formed a coherent vegetation cover at the time of soil sampling.
Occasionally inundated abandoned alluvial meadow between Olawa River and railway (Am)	Siechnice, 51.03857°N, 17.15859°E, altitude 120 m a.s.l./Alluvial soil	Control (MEAc)	*Artemisia vulgaris* (55%), *Setaria viridis* (15%), *Erigeron annuus* (8%), *Echinochloa crus-galli* (12%) and *Matricaria inodora*.
		Invaded (MEAh)	*Heracleum sosnowskyi* (75%), sporadically present undergrowth species of *Erigeron annuus*, *Artemisia vulgaris* and *Urtica dioica. Heracleum sosnowskyi* formed a coherent vegetation cover at the time of soil sampling.

marked four 1 m × 1 m squares (plots) that had a similar cover of *H. sosnowskyi*. Similarly, four squares with an equal spatial distribution were marked in the non-invaded areas. This resulted in a total of 32 plots (four plots × two invasion states × four habitats). The non-invaded areas are included to represent the plant communities prior to the invasion by *H. sosnowskyi*. For the analysis of the understory plant community, the fixed 'Phytosociological Relevé' method was used (Braun-Blanquet, 1968). Each of four quadrats represented one frequency square. The vegetation was identified *in situ*. Habitat type, location and vegetation characteristics are shown in Table 1.

Data collection

To assess the impact of *H. sosnowskyi* on the soil community structures of free-living and plant-parasitic nematodes, we collected soil samples in each invaded and non-invaded plot (square) by a quadrant soil sampling method. On each of the squares, five sub-samples were collected in the following order – one from each corner of the square and one from its centre to obtain four representative average soil samples (1 kg). Sampling was conducted with a garden trowel up to the depth of 0-20 cm. A total of 32 representative soil samples were thus collected, eight from each of the four habitats (four invaded + four non-invaded). The soil samples were sealed in plastic bags and transferred to the laboratory. Until further processing, plastic bags were kept in a refrigerator at 5°C. Prior to nematode extraction, each sample was homogenised by soft hand-mixing and stones were removed.

The nematodes were extracted by combination of the Cobb sieving and decanting method (Cobb, 1918)

as well as by modified Baermann funnel method (van Bezooijen, 2006). Amount (100 g) of soil from each representative sample was soaked in 1 litre of tap water for 60 min in order to dissolve soil aggregates and promote active nematode motion. The soaked sample was carefully passed through the 1 mm sieve (16 mesh) to remove plant parts and debris; 2 min later the suspension was passed through a 50 μm sieve (300 mesh) to remove very fine soil particles. Afterwards, nematodes were extracted from the soil water suspension through a set of two cotton propylene filters put in the Baermann funnel. One or two filter trays were used per sample to allow material to be no more than 0.5 cm thick. Sub-samples were collected after 24 h of extraction at room temperature. Water suspensions were examined under a stereomicroscope (Leica S8AP0, Singapore; magnification 40 and 60×), excessive water was removed and the nematodes were fixed with hot solution of 99:1, 4% formaldehyde:pure glycerol (Seinhorst, 1962). Nematode abundance was expressed as no. individuals (100 g dry soil)$^{-1}$.

Soil moisture was estimated gravimetrically by oven-drying fresh soil at 105°C overnight and soil pH (H_2O) suspension was measured potentiometrically by a digital pH meter separately for each average soil sample.

Nematode identification and data handling

Nematodes were determined up to the genus level using Eclipse 90i Nikon light microscope (magnification 100, 200, 400, 600 and 1000×) from temporary slides using keys, including those of Brzeski (1990), Andrássy (2005, 2007, 2009) and Geraert (2008, 2010). To assess the effect of *H. sosnowskyi* invasion on structure of soil nematode communities in the four different invaded habitats, two kinds of indicators, the descriptive (nematode abundance, feeding groups, functional guilds) and evaluative (indices) were used (Heink & Kowarik, 2010).

Nematodes in each sample were arranged into trophic groups based on their feeding habits, according to Yeates *et al*. (1993) and Wasilewska (1997). The five nematode trophic groups consisted of bacterivores (Ba), fungivores (Fu), carnivores (Ca), omnivores (O) and plant parasites (Pp) (Wasilewska, 1997). The Pp included both Wasilewska's OPP (obligate plant parasites attacking plants) and Wasilewska's FPP (facultative plant parasites that may attack plants or can reproduce on fungi). Nematode genera (percentage individuals per area) were characterised as eudominant at $D > 10\%$, dominant at $D =$ 5-10%, subdominant at $D =$ 2-5%, recedent <2% (Losos *et al*., 1984).

Subsequently, 1-5 colonisers-persisters (c-p) scale characterising nematode life strategy was used (Bongers, 1990). C-p1 represents r-strategists (colonisers) with short life cycles, small eggs, high fecundity, high colonisation abilities and their tolerance to disturbance, eutrophication and anoxybiosis. In general colonisers live in ephemeral habitats. On the other end of the scale are c-p 5 nematodes, which represent k-strategists (persisters) with long generation times, large body sizes, low fecundity and great sensitivity to disturbance. They never belong to the dominant group in a sample and, in general, persisters live in habitats with a long durational stability where they eventually reach higher abundance. C-p scaling enables calculation of the basal Maturity Index (MI) for non-parasitic nematodes and the Plant Parasitic Index (PPI) for plant-parasitic nematodes only (Bongers, 1990).

Thereafter, Bongers & Bongers (1998) integrated c-p scaling with the life strategy concept, resulting in the concept of nematode functional guilds, each sharing the same feeding type and c-p value. They argue, that the assessment of soil quality based on the presence of all trophic groups and of all c-p groups alone is not sufficient to predict whether a soil ecosystem functions or not. Grouping nematodes to functional guilds was central to the framework of Ferris *et al*. (2001) where food web conditions were described as a "weighted faunal analysis concept". They described "basal, structured and enriched" conditions of the soil food web. In this concept, enrichment index (EI) and structure index (SI) are used to assess food web location along enrichment and structure trajectories depicted graphically. The EI contains fast-growing, bacterial- and fungal-feeding nematodes with a coloniser-persister (c-p) value of 1 or 2. The SI measures the slow growing and reproducing predatory and omnivorous nematodes with c-p values of 3, 4 and 5. Additionally, in the weighted faunal analysis concept the channel index (CI) was calculated (Ferris *et al*., 2001). The CI is a comparison of the size between fungal- to bacterial-feeding communities. The CI assesses the primary decomposition pathway of soil, where a value of 100 is being completely fungal and a value of 0 is completely bacterial. Similar information provides the Nematode Channel Ratio (NCR) as defined by Yeates (2003), where the relative activity of the bacterial-based energy channel and the slower fungal-based channel in decomposition processes in soil is assessed. The values of this index varied between 1 (totally bacterial-mediated decomposition) and 0 (totally fungal-mediated decomposition). In addition, the nematode Diversity Index (H'gen) was calculated for genus (natural

logarithms) by Shannon & Weaver (1949) and Jaccard's index of similarity between *H. sosnowskyi*-invaded and non-invaded areas of all habitats (Jaccard, 1908).

Statistical analysis

The statistical analyses were performed separately for each habitat and data compared between invaded and related non-invaded control areas. To avoid pseudo replication, plot was nested in area, area was nested in study habitat, and both were included as random factors. Invasion status and habitat type were included as fixed factors. All nematological data, including ecological and functional indices, were calculated as means for the individual plots and sampling areas and means compared by Tukey's honestly significant difference (HSD) *post hoc* test ($P < 0.05$; $P < 0.01$) of the PlotIt program. The data were log-transformed before the analysis to improve normality.

Co-correspondence analysis (Co-CA) of nematode functional guilds and plant communities was performed as a single-step, to identify how nematode community composition was affected by invasion status and plant community changes (ter Braak & Schaffers, 2004). The single-step approach makes Co-CA superior to canonical correspondence analysis (CCA) in this situation because the number of (predictors) species exceeds the number of sites (plots) ($n = 14$ nematode functional guilds, $n = 9$ plant species, $n = 8$ co-located sites) by an order of magnitude (ter Braak & Schaffers, 2004). Soil pH and soil moisture were used as supplementary variables. Redunancy analyses (RDA) was performed to identify differences between nematode communities from plots invaded by *H. sosnowskyi* and non-invaded areas based on the nematode genera. Both Co-CA and RDA analysis were performed using Canoco version 5 software (version 5.04; ter Braak & Šmilauer, 2012). Our approach was modelled after application of Co-CA to investigate association of plant communities and soil nematode communities (Neher *et al*., 2017)

Results

Nematode abundance, functional guilds and community composition

The response of nematode communities to *H. sosnowskyi* invasion differed among habitats. At the uncultivated line between two agricultural fields (AGR) significant changes in the nematode community on *H. sosnowskyi*-invaded plots (AGRh) compared to non-invaded (AGRc) were found. The nematode abundance, genera numbers, abundance of fungivores (Fu_2 – *Aphelenchus*), omnivores (Om_4; Om_5) and plant parasites (Pp_2; Pp_3) were significantly lower in the AGRh than in the AGRc plots ($P < 0.05$, except $P < 0.01$ for abundance and Fu_2) (Table 2). By contrast, the Ba_1 nematodes were significantly more abundant in the AGRh plots reflecting the high population density of *Panagrolaimus* nematodes. Similarly, *Cephalobus* and *Eucephalobus* nematodes (Ba_2) were more abundant in the AGRh plots than in the non-invaded control plots but *Aphelenchus* (Fu_2) abundance was lower in the AGRh plots (Table 3). Low abundance of plant parasites in the AGRh plots mainly reflects decrease in population density of the obligatory parasite *Geocenamus* (cp-3) and the facultative parasite *Aglenchus* (cp-2), and also *Longidorus* (cp-5).

The plots invaded by *H. sosnowskyi* had significantly distinct nematode communities, also in the route edge habitat (RED). The mean abundance of nematodes and genera numbers were significantly lower in the REDh than in the REDc plots ($P < 0.01$; $P < 0.05$, respectively) (Table 2). Bacterivores prevailed in population density in the REDc plots and were significantly lower in plots invaded by *H. sosnowskyi*, mainly because of Ba_1 (*Mesorhabditis*, *Rhabditis*) and Ba_2 (*Acrobeloides*). Plant parasites were the second most abundant feeding group in the REDc plots and showed a similar trend to bacteriovores in the REDh, even though the abundance of facultative parasites *Filenchus* (Pp_2) increased. By contrast, obligatory parasites of *Geocenamus*, *Tylenchorhynchus* and *Pratylenchus* genera were less abundant in the plots invaded by *H. sosnowskyi*. Interestingly, Pp_4 (*Trichodorus*) and Pp_5 (*Xiphinema*) increased in population density in soil under *H. sosnowskyi* (Table 3). The feeding groups of carnivores, omnivores and fungivores were significantly lower in the REDh than in REDc plots, represented mainly by Ca_4 (*Clarkus*, *Anatonchus*), Om_5 (*Aporcelaimellus*) and Fu_2 (*Aphelenchoides*, *Aphelenchus*) nematode genera (Tables 2, 3). The carnivores (predators) reached relatively high population density in both non-invaded and *H. sosnowskyi*-invaded plots on RED.

The plots of semi-natural alluvial meadow habitat (MEA) invaded by *H. sosnowskyi* also had significantly different nematode communities than non-invaded one (Tables 2, 3). Mean nematode abundance was slightly higher in the MEAh plots, which was reflected by sig-

Table 2. Mean total nematode abundance, number of genera, nematode feeding groups and functional guilds abundance associated with *Heracleum sosnowskyi* (*Hs*) invaded and control areas in four different habitats (non-cultivated line between agricultural fields, alluvial meadow, route edge, wet dump ground depression) in Poland.

	Non-cultivated line between fields		Route edge		Alluvial meadow		Wet dump depression	
	Control	*Hs*	Control	*Hs*	Control	*Hs*	Control	*Hs*
Abundance	510 ± 85	267 ± 47.4**	899 ± 167	404 ± 64.6**	281.5 ± 20.3	327 ± 70.6	756 ± 175	695 ± 118
Genera	37.3 ± 3.2	28.3 ± 3.3*	41.3 ± 2.2	28.5 ± 2.4*	31.8 ± 4.5	38.5 ± 4.8	39.2 ± 3.7	40.3 ± 2.5
Bacterivores	195 ± 46.5	164 ± 24.5	586 ± 127.9	192 ± 44.2**	63.3 ± 18.1	193 ± 39.6**	248.3 ± 105	230.8 ± 73
Ba_1	18 ± 8.7	43.3 ± 10.5*	294 ± 64.4	75.8 ± 45.1**	5.5 ± 7.9	43.5 ± 13.3**	11.8 ± 5.6	6.5 ± 4.5
Ba_2	166 ± 36.4	115 ± 30.3	271 ± 53.9	113 ± 17.3**	50.6 ± 13.9	116 ± 12.5**	227.5 ± 98.9	207.3 ± 67
Ba_3	7 ± 4.4	3.5 ± 4.1	5.5 ± 3.8	1.3 ± 0.9	2.7 ± 1.7	20.5 ± 14.3*	6.3 ± 2.8	6 ± 3.7
Ba_4	3.7 ± 2.5	1.8 ± 1.7	15.5 ± 9.7	2.3 ± 1.7	4.5 ± 3.0	13 ± 7.4	2.8 ± 2.6	11 ± 4.6*
Fungivores	127 ± 49.3	36.8 ± 5.7*	39.5 ± 16.9	14 ± 3.1*	64.8 ± 20.6	15.3 ± 10.6*	125 ± 28.8	131 ± 47.3
Fu_2	120 ± 23.6	35 ± 6.2**	36 ± 10.1	13 ± 6.8*	39.8 ± 13.7	8 ± 5.9*	117.3 ± 26.1	122.7 ± 46.9
Fu_3	2.7 ± 2.5	1.8 ± 2.4	2.5 ± 2.1	1 ± 1.1	–	–	3 ± 2.9	1 ± 1.1
Fu_4	5 ± 4.6	–	7.8 ± 2.0	–	25 ± 6.4	7.3 ± 6.6*	4.8 ± 3.7	7.2 ± 2.1
Omnivores	54.3 ± 11.9	23.3 ± 3.1*	46.8 ± 10.5	15.8 ± 10.7*	34.8 ± 15.8	28.8 ± 10.8	71 ± 20.9	62.8 ± 32.1
Om_4	34.3 ± 9.5	16.3 ± 1.8*	19 ± 5.0	7.5 ± 2.9*	14.8 ± 11.2	12.3 ± 4.4	55.3 ± 18.9	44.5 ± 18.1
Om_5	20 ± 2.4	7 ± 5.6*	27.8 ± 7.1	8.3 ± 5.4*	20 ± 7.6	16.5 ± 10.7	15.8 ± 3.6	18.6 ± 5.3
Carnivores	9.67 ± 5.1	7 ± 2.1	56 ± 7.3	37.8 ± 11.6	10.5 ± 6.5	14.5 ± 5.8	17.3 ± 3.4	12 ± 7.6
Ca_3	0.7 ± 1.0	–	45 ± 4.9	33.5 ± 8.0	1.5 ± 1.2	1.3 ± 1.5	2.6 ± 3.2	3 ± 2.9
Ca_4	9 ± 4.6	7 ± 2.1	11 ± 3.3	4.3 ± 1.3*	9 ± 7.4	13.3 ± 6.9	14.5 ± 3.7	9 ± 5.6
Plant parasites	143 ± 58.6	36.5 ± 18.3**	216 ± 13.7	168 ± 9.7*	100.5 ± 22.6	50.5 ± 24**	294 ± 103.4	258.8 ± 56.5
Pp_2	82 ± 54.7	21 ± 13*	18.8 ± 10.1	47.3 ± 4.7*	41.5 ± 9.7	23 ± 4*	65.5 ± 44.4	72.3 ± 15.1
Pp_3	58.3 ± 21.1	15.5 ± 5.5*	180 ± 31.1	73.3 ± 12.5*	58.8 ± 13.9	26.3 ± 4.7*	231.3 ± 77.1	189.5 ± 47.4
Pp_4	–	–	7 ± 3.9	18.8 ± 11.5	–	0.3 ± 0.5	–	–
Pp_5	3.7 ± 4.2	–	10 ± 1.4	28.3 ± 6.8*	1.8 ± 1.3	0.3 ± 0.5	–	–

Each data point is a mean of the individual plots and sampling areas (mean ± standard deviation).
* $P < 0.05$; ** $P < 0.01$, significant differences between the same control and invaded area.

Table 3. Mean abundance (A) and dominance (D%) ($n = 4$) of nematode genera associated with *Heracleum sosnowskyi* invaded and control areas in four different habitats.

Genus	TG	cp	AGRc		AGRh		REDc		REDh		MEAc		MEAh		DEPc		DEPh	
			Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%
Acrobeloides	Ba	2	81.5	15.99	31	11.61	123.8	13.77	35.8	8.9	12.8	5.77	42.8	5.81	103.5	13.70	116.8	12.89
Alaimus	Ba	4	4.0	0.78	1.75	0.66	11.5	1.28	2.3	0.6	4.5	2.03	7.0	1.96	2.75	0.36	10.5	1.51
Amphidelus	Ba	4	–	–	–	–	4.0	0.44	–	–	–	–	4.5	1.26	–	–	0.5	<0.1
Anaplecus	Ba	2	4.0	0.78	1.25	0.47	2.3	0.25	–	–	–	–	0.8	0.21	–	–	–	–
Aulolaimus	Ba	3	2.0	0.39	–	–	–	–	–	–	–	–	1.0	0.28	–	–	–	–
Cephalobus	Ba	2	9.8	1.91	19.25	7.21	23.0	2.55	32.0	7.9	1.8	0.79	14.5	5.46	35	4.63	40.5	5.83
Ceratoplectus	Ba	2	0.8	0.15	1.75	0.66	–	–	–	–	–	–	–	–	–	–	–	–
Cervidellus	Ba	2	43.5	8.53	7.5	2.81	5.8	0.64	4.3	1.0	–	–	–	–	–	–	–	–
Diploscapter	Ba	1	–	–	–	–	7.3	0.80	0.8	0.2	–	–	–	–	–	–	–	–
Eucephalobus	Ba	2	10.8	2.11	41.25	15.45	67.3	7.46	7.3	1.8	0.5	0.23	8.3	2.31	48.25	6.39	55.5	7.98
Eudiplogaster	Ba	1	–	–	–	–	4.3	0.47	0.3	0.1	–	–	–	–	–	–	–	–
Eumonhystera	Ba	2	0.8	0.15	–	–	5.5	0.61	3.0	0.7	–	–	2.5	0.70	2	0.26	0.5	>0.1
Euteratocephalus	Ba	2	–	–	–	–	–	–	–	–	0.3	0.11	–	–	–	–	–	–
Heterocephalobus	Ba	2	–	–	–	–	0.8	0.08	–	–	1.3	0.56	0.3	0.07	2	0.26	1.0	0.14
Chiloplacus	Ba	2	1.0	0.20	0.5	0.19	0.3	0.03	–	–	21.0	9.48	45.5	12.75	27	3.57	27.3	3.92
Mesorhabditis	Ba	1	1.8	0.34	1.5	0.56	100.5	11.13	29.0	7.1	1.0	0.45	9.5	2.66	2.5	0.33	1.8	0.25
Panagrolaimus	Ba	1	14.0	2.75	41.25	15.45	6.0	0.66	1.5	0.4	–	–	4.8	1.33	7.75	1.03	4.7	0.50
Paramphidelus	Ba	4	–	–	–	–	–	–	–	–	–	–	1.5	0.42	–	–	–	–
Plectus	Ba	2	7.0	1.37	7.25	2.72	40.8	4.51	28.8	7.0	10.3	4.63	18.8	5.25	7.75	1.03	7.8	1.11
Prismatolaimus	Ba	3	5.3	1.03	1	0.37	4.5	0.50	0.3	0.1	1.8	0.79	7.8	2.17	5.75	0.76	5.0	0.72
Pseudoaulolaimus	Ba	3	–	–	–	–	–	–	–	–	–	–	0.5	0.14	–	–	–	–
Rhabditis	Ba	1	0.5	0.10	0.5	0.19	165.3	18.19	44.3	10.8	4.5	2.03	29.3	8.19	1.5	0.20	1.3	0.18
Seleborca	Ba	2	1.3	0.25	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Teratocephalus	Ba	3	–	–	2.5	0.94	1.0	0.11	1.0	0.2	0.5	0.23	0.3	0.07	0.5	>0.1	1.0	0.14
Wilsonema	Ba	2	9.3	1.81	5.25	1.97	1.5	0.17	1.8	0.4	0.8	0.34	–	–	2	0.26	6.0	0.86
Aphelenchoides	Fu	2	47.8	9.37	12.25	4.59	9.5	1.05	3.5	0.9	8.8	2.45	5	2.26	6.75	0.89	8.8	1.26
Aphelenchus	Fu	2	68.8	13.49	20.75	7.77	22.8	2.51	9.5	2.3	30.5	8.54	2.5	1.13	104	13.77	104.8	15.07
Diphtherophora	Fu	3	2.0	0.39	1.75	0.66	2.5	0.28	1.0	0.2	–	–	–	–	3	0.40	1.0	0.14
Ditylenchus	Fu	2	–	–	2	0.75	3.8	0.41	–	–	0.5	0.14	0.5	0.23	3.5	0.46	1.5	0.22
Paraphelenchus	Fu	2	–	–	–	–	–	–	–	–	–	–	–	–	3	0.40	7.8	1.11
Tylencholaimellus	Fu	4	–	–	–	–	–	–	–	–	1.8	0.49	1.5	0.68	–	–	–	–
Tylencholaimus	Fu	4	4.0	0.78	–	–	12.0	1.31	–	–	23.3	6.51	8.8	3.95	4.75	0.63	7.3	1.04
Aporcelaimellus	Om	5	6.3	1.23	2.75	1.03	18.0	1.98	7.8	1.9	4.8	1.33	15.5	7.0	4.5	0.60	5.5	0.79
Axonchium	Om	5	0.8	0.15	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Campydora	Om	4	1.3	0.25	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 3. (Continued.)

Genus	TG	cp	AGRc		AGRh		REDc		REDh		MEAc		MEAh		DEPc		DEPh	
			Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%
Discolaimus	Om	5	3.0	0.59	–	–	3.3	0.36	–	–	3.0	0.84	–	–	–	–	–	–
Dorylaimoides	Om	4	–	–	–	–	–	–	–	–	3.5	0.98	–	–	3.75	0.50	3.8	0.54
Dorylaimus	Om	4	11.0	2.16	9.5	3.56	4.0	0.44	5.8	1.4	4.0	1.12	5.8	2.6	12.75	1.69	10.8	1.55
Ecumenicus	Om	4	2.3	0.44	–	–	3.3	0.36	0.5	0.1	–	–	–	–	3	0.40	3.5	0.50
Enchodelus	Om	4	2.8	0.54	–	–	–	–	–	–	2.0	0.56	1.8	0.79	–	–	–	–
Epidorylaimus	Om	4	–	–	–	–	–	–	–	–	–	–	–	–	1.25	0.17	–	–
Eudorylaimus	Om	4	8.0	1.57	5.25	1.97	11.0	1.21	11.3	2.7	3.8	1.05	4.8	2.14	5.75	0.76	5.8	0.83
Mesodorylaimus	Om	5	2.3	0.44	1	0.37	2.0	0.22	–	–	1.5	0.42	–	–	3.75	0.50	4.8	0.68
Microdorylaimus	Om	4	–	–	–	–	–	–	–	–	–	–	–	–	5	0.66	6.3	0.90
Nygolaimus	Om	5	2.8	0.54	2.75	1.03	–	–	–	–	4.3	1.19	–	–	–	–	–	–
Oxydirus	Om	5	–	–	–	–	–	–	–	–	5.8	1.61	1.0	0.45	2	0.26	3.3	0.47
Paraxonchium	Om	5	1.5	0.29	0.5	0.19	4.5	0.49	0.5	0.1	–	–	–	–	5.5	0.73	4.8	0.68
Prodorylaimus	Om	5	3.0	0.59	–	–	–	–	–	–	0.8	0.21	–	–	–	–	–	–
Pungentus	Om	4	3.0	0.59	1.5	0.56	–	–	–	–	–	–	–	–	5.5	0.73	8.0	1.15
Thonus	Om	4	4.3	0.83	–	–	0.8	0.08	–	–	1.5	0.42	–	–	18.25	2.42	6.5	0.93
Anatonchus	Ca	4	–	–	–	–	1.3	0.14	–	–	–	–	–	–	–	–	–	–
Clarkus	Ca	4	1.3	0.25	0.5	0.19	5.0	0.55	1.3	0.3	4.8	2.14	5.8	1.61	7.5	0.99	3.3	0.47
Ironus	Ca	4	–	–	–	–	–	–	–	–	–	–	–	–	1	0.13	2.5	0.36
Mononchus	Ca	4	2.8	0.54	3.5	1.31	3.3	0.36	3.0	0.7	1.3	0.56	5.5	1.54	–	–	–	–
Mylonchulus	Ca	4	–	–	2.5	0.94	1.5	0.16	–	–	3.0	1.35	2.0	0.56	6	0.79	3.3	0.47
Prionchulus	Ca	4	3.0	0.59	0.5	0.19	–	–	–	–	–	–	–	–	–	–	–	–
Tripyla	Ca	3	0.5	0.10	–	–	45.0	4.93	33.5	8.0	1.5	0.68	1.3	0.35	2.75	0.36	3.0	0.43
Amplimerlinius	Pp	3	–	–	0.25	>0.1	–	–	–	–	0.3	0.11	–	–	–	–	–	–
Bitylenchus	Pp	3	4.8	0.93	1	0.37	4.5	0.49	3.0	0.7	–	–	–	–	–	–	–	–
Criconemoides	Pp	3	–	–	–	–	–	–	–	–	0.8	0.34	0.5	0.14	–	–	–	–
Geocenamus	Pp	3	33.5	6.57	9	3.37	52.3	5.72	24.8	5.9	2.8	1.24	2.5	0.70	81.25	10.75	73.8	10.61
Gracilacus	Pp	2	–	–	–	–	–	–	–	–	1.3	0.56	1.8	0.49	5.5	0.73	4.0	0.58
Helicotylenchus	Pp	3	5.5	1.08	2.5	0.94	18.3	2.00	2.3	0.5	5.0	2.26	6.5	1.82	96.5	12.77	70.5	10.14
Hemicycliophora	Pp	3	–	–	–	–	–	–	–	–	9.8	4.40	1.0	0.28	–	–	–	–
Heterodera	Pp	3	3.5	0.69	0.25	>0.1	–	–	–	–	–	–	–	–	–	–	–	–
Longidorus	Pp	5	6.8	0.94	0.25	>0.1	–	–	–	–	4.8	0.79	0.3	0.07	–	–	–	–
Meloidogyne	Pp	3	–	–	–	–	–	–	–	–	18.0	8.13	3.0	0.84	3	0.40	5.8	0.83
Mesocriconema	Pp	3	2.0	0.39	0.25	>0.1	–	–	–	–	1.5	0.68	–	–	1	0.13	1.5	0.22
Ogma	Pp	3	–	–	–	–	1.5	0.16	0.8	0.2	–	–	0.3	0.07	–	–	–	–
Paratylenchus	Pp	2	2.3	0.44	1.25	0.47	12.5	1.36	–	–	0.8	0.34	2.0	0.56	–	–	0.3	>0.1
Pratylenchoides	Pp	3	–	–	–	–	–	–	–	–	5.8	2.60	2.0	0.56	9.5	1.26	16.8	2.41
Pratylenchus	Pp	3	4.3	0.83	1	0.37	22.3	2.43	7.5	1.8	11.5	5.19	7.5	2.10	13	1.72	6.3	0.90

Table 3. (Continued.)

Genus	TG	cp	AGRc		AGRh		REDc		REDh		MEAc		MEAh		DEPc		DEPh	
			Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%	Mean	D%
Rotylenchus	Pp	3	–	–	–	–	–	–	–	–	–	–	–	–	13.25	1.75	4.5	0.65
Trichodorus	Pp	4	–	–	–	–	7.0	0.76	18.8	4.4	–	–	0.3	0.07	–	–	–	–
Tylenchorhynchus	Pp	3	–	–	–	–	23.8	2.59	1.5	0.4	–	–	–	–	5.5	0.73	3.3	0.47
Xiphinema	Pp	5	–	–	–	–	10.0	1.09	28.3	6.7	–	–	–	–	–	–	–	–
Aglenchus	Pp	2	30.8	6.03	1.75	0.66	2.5	0.27	11.8	2.8	15.8	7.11	7.3	2.03	–	–	–	–
Basiria	Pp	2	–	–	0.75	0.28	–	–	–	–	0.8	0.34	0.3	0.07	2.5	0.33	2.0	0.29
Boleodorus	Pp	2	–	–	–	–	–	–	–	–	0.5	0.23	–	–	8.25	1.09	12.0	1.73
Cephalenchus	Pp	2	–	–	–	–	–	–	–	–	–	–	0.8	0.21	–	–	–	–
Coslenchus	Pp	2	11.8	2.31	7	2.62	4.0	0.44	4.0	0.9	6.8	3.05	2.8	0.77	23	3.04	29.0	4.17
Filenchus	Pp	2	9.3	1.81	0.5	0.19	9.0	0.98	31.5	7.4	10.5	4.74	11.0	3.08	12.5	1.65	14.8	2.12
Malenchus	Pp	2	20.3	3.97	10.5	3.93	2.5	0.27	–	–	6.5	2.93	0.8	0.21	18.75	2.48	8.3	1.19
Psilenchus	Pp	2	–	–	–	–	0.8	0.08	–	–	–	–	–	–	–	–	–	–
Tylenchus	Pp	2	0.3	>0.1	0.5	0.19	–	–	–	–	0.8	0.34	0.3	0.07	0.5	>0.1	6.3	0.90

AGR: non-cultivated line between two agricultural fields; RED: route edge near barns within agricultural farm; MEA: wet alluvial meadow, DEP: wet dump ground depression; TG: trophic group; C: control; h: invaded; cp: colonisers-persisters value; Ba: bacterivores; Fu: fungivores; Om: omnivores; Ca: carnivores; Pp: plant parasites.

nificantly higher population densities of bacterivores of Ba_1, Ba_2 (both $P < 0.01$) and Ba_3 ($P < 0.05$) functional guilds, represented mainly by *Rhabditis*, *Acrobeloides*, *Cephalobus*, *Chiloplacus*, *Plectus* and *Diphtherophora* nematodes. By contrast, the abundance of plant parasites, which prevailed in the control, was significantly lower in the invaded plots ($P < 0.01$). Mostly the facultative plant parasites of *Aglenchus* and *Filenchus* (Pp_2) and obligatory plant parasites of *Meloidogyne* or *Hemicycliophora* (Pp_3) genera were recorded. A similar trend for the fungivorous nematodes of *Aphelenchus* (Fu_2) and *Tylencholaimus* (Fu_4) genera was found. Omnivores and carnivores did not differ significantly between MEAc and MEAh plots.

At wet dump ground depression (DEP), no significant differences in nematode community composition, mean nematode abundance and genera numbers, as well as feeding strategy between DEPc and DEPh plots were found (Table 2). Only bacterivores of cp-4 were significantly higher in the DEPh plots ($P < 0.05$). Plant parasites were the most abundant trophic group comprising all functional guilds including facultative plant parasites of cp-2. High abundance of Pp nematodes in the DEPc and DEPh plots reflects high population densities of eudominant *Helicotylenchus* and *Geocenamus* nematodes (Pp_3) (Table 3).

Relationship between plants and nematode functional guilds

Co-correspondence analysis (Co-CA) carried out for separate habitats confirmed a significant negative interactions between *H. sosnowskyi* establishment and other plant species as well as the majority of nematode functional guilds.

At the non-cultivated line between two fields on agricultural soil (Fig. 1) both plant and nematode communities correlated with *H. sosnowskyi* invasion status. *Heracleum sosnowskyi* negatively correlated with all native plant species but soil pH tended to increase under *H. sosnowskyi*. Almost all nematode functional guilds of bacterivores (except $Ba_{1,2}$), omnivores, fungivores (except Fu_3), plant parasites and carnivores (except Ca_4) were associated with native plant species, so were in negative correlation with *H. sosnowskyi* invasion. Association between *H. sosnowskyi* and Ca_4 nematode was observed, but their abundance tended to be low under *H. sosnowskyi* invasion (Table 2).

A similar, *H. sosnowskyi vs* native vegetation and nematode functional guilds correlations in the route edge habitat have been found (Fig. 1). Om_4 were associated

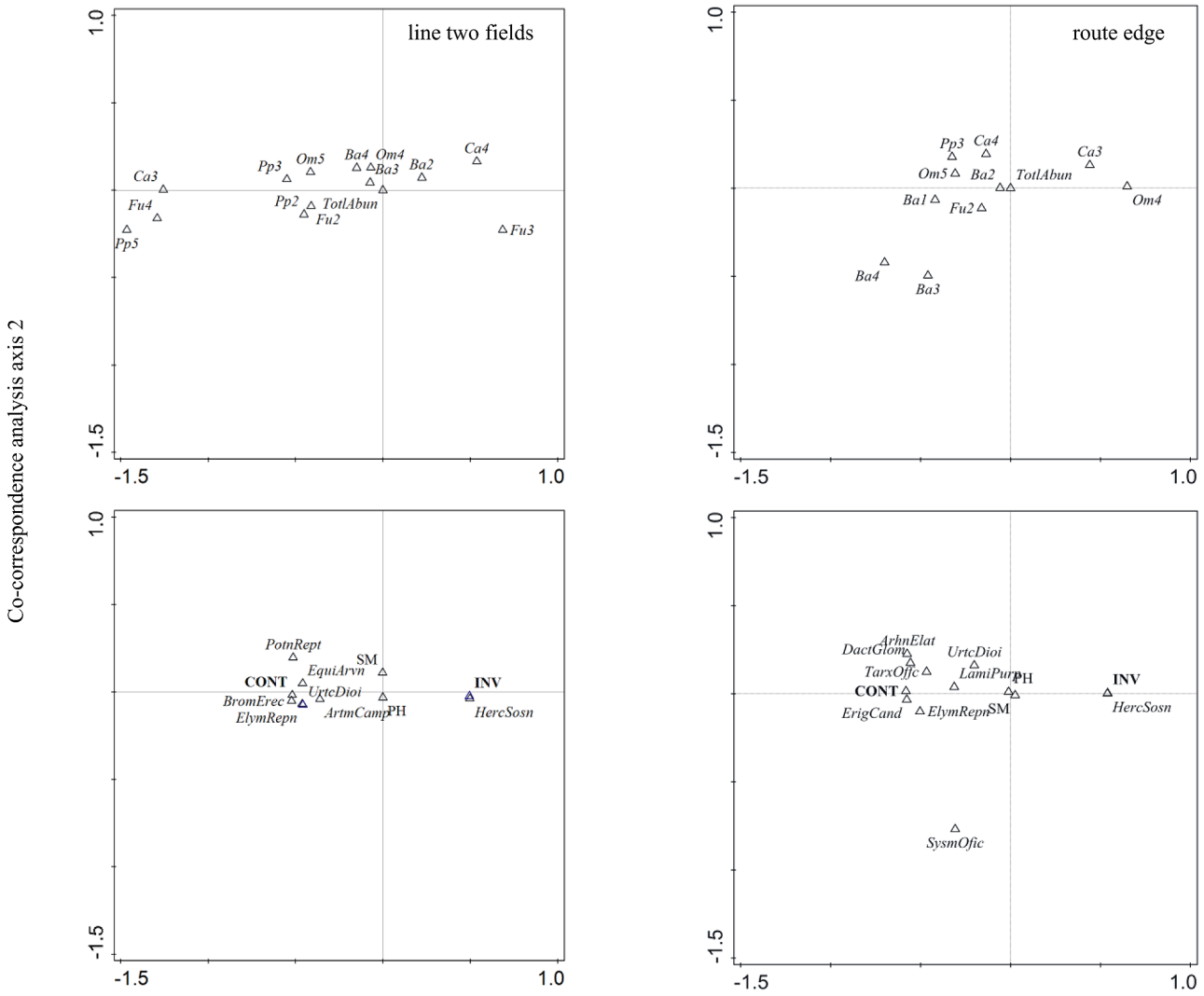

Fig. 1. Biplot based on symmetric co-correspondence analysis illustrating the nematode functional guilds (A) and main plant species (B) common on line between two fields and route edge habitats on *Heracleum sosnowskyi* invaded (INV) and non-invaded (CONT) areas, 26.44 and 32.05%, respectively, of the total variance of each data set. Correlation coefficients between nematode-derived and plant-derived site scores of the first three axes of symmetric correspondence canonical analysis (axis 1: 0.9124, $\lambda 1 = 0.264$, $P = 0.00400$, axis 2: 0.7888) and (axis 1: 0.9848, $\lambda 1 = 0.0318$, $P = 0.00220$, axis 2: 0.8154), respectively. Abbreviations used in panels B: *ArhnElat* = *Arhenatherum elatius*; *ArtmCamp* = *Artemisia campestris*; *BromErec* = *Bromus erectus*; *DactGlom* = *Dactylis glomerata*; *ElymRepn* = *Elymus repens*; *EquiArvn* = *Equisetum arvense*; *ErigCand* = *Erigeon canadensis*; *HercSosn* = *Heracleum sosnowskyi*; *LamiPurp* = *Lamium purpureum*; *PotnRept* = *Potentilla reptans*; *SysmOfic* – *Sysimbrium officinale*; *TarxOffc* – *Taraxacum officinale*; *UrticDioi* = *Urtica dioica*.

with *H. sosnowskyi*. By contrast, on the alluvial meadow habitat (Fig. 2), Co-CA indicated that *H. sosnowskyi* positively correlated with *Urtica dioica*, and associated with Ba_1, Ba_2, Ba_3, Ba_4, Fu_2 and Pp_4 nematode functional guilds as well as total nematode abundance. However, a negative *H. sosnowskyi* correlation with other native plants and higher functional guilds of nematodes (Om_4, Om_5, Pp_3, Pp_5 or Ca_3) was confirmed in this habitat.

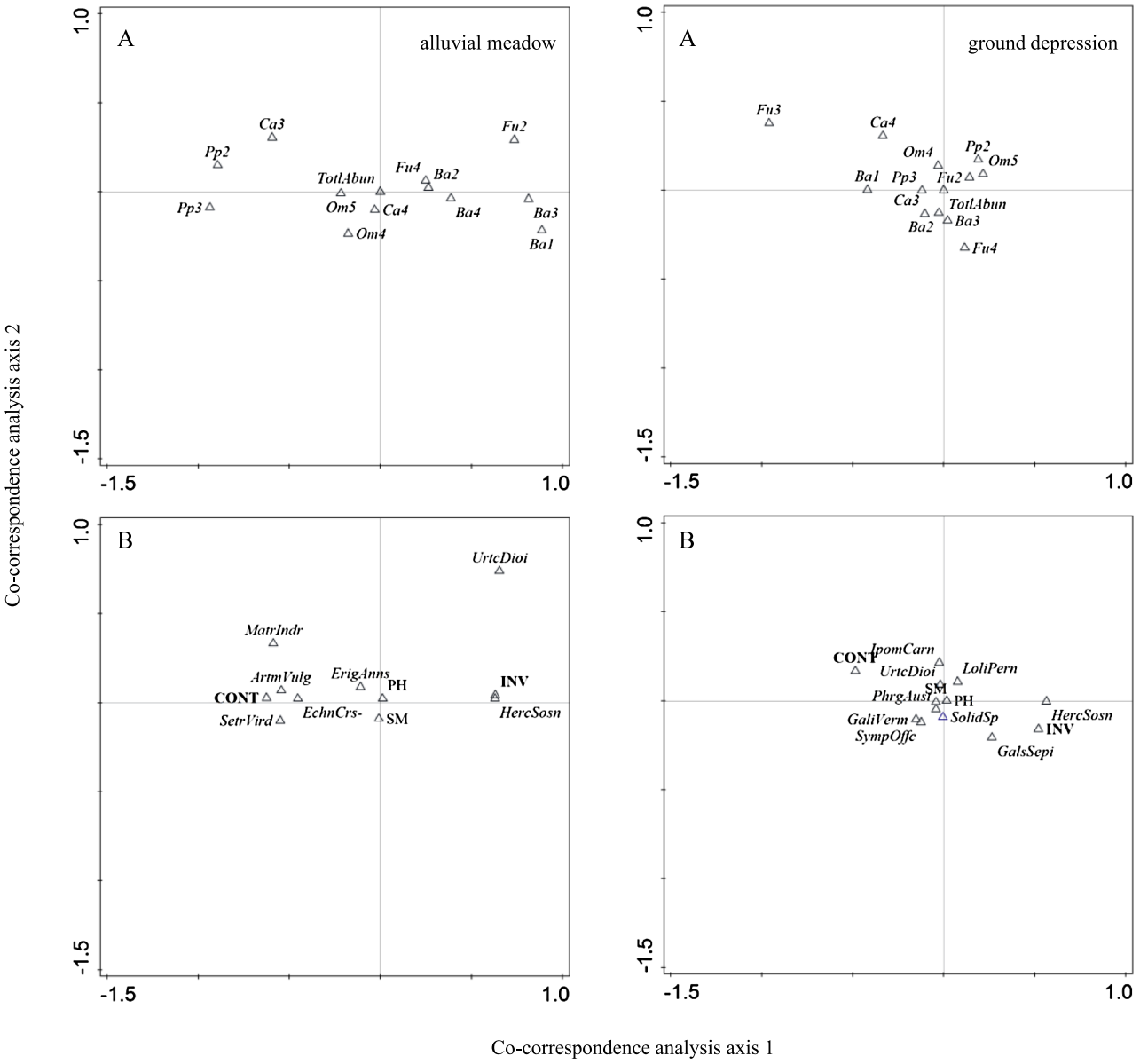

Fig. 2. Biplot based on symmetric co-correspondence analysis illustrating the nematode functional guilds (A) and main plant species (B) common on alluvial meadow and ground depression habitats on *Heracleum sosnowskyi* invaded (INV) and non-invaded (CONT) areas, 39.85 and 5.5%, respectively, of the total variance of each data set. Correlation coefficients between nematode-derived and plant-derived site scores of the first three axes of symmetric correspondence canonical analysis (axis 1: 0.9478, $\lambda 1 = 0.397$, $P = 0.03800$, axis 2: 0.9212) and (axis 1: 0.9136, $\lambda 1 = 0.0004$, $P = 0.89200$, axis 2: 0.8396), respectively. Abbreviations used in panels B: *ArtVulg* = *Artemisia vulgaris*; *EchnCrs* = *Echinachloa crus-galli*; *ErigAnns* =*Erigeon annus*; *HercSosno* = *Heracleum sosnowskyi*; *MatrIndr* = *Matricaria indora*; *SetrVird* = *Setaria viridis*; *UrtcDioi* – *Urtica dioica*; *GaliVerm* = *Galium verum*; *GalsSepi* = *Galystegia sepium*; *HercSosn* = *Heracleum sosnowskyi*; *IpomCarn* = *Ipomea carnea*; *LoliPern* = *Lolium perenne*; *PhrgAust* = *Phragmites australis*; *SoliSp* = *Solidago sp.*; *SysmOffc* = *Symphytum officinale*; *UrtcDioi* = *Urtica dioica*.

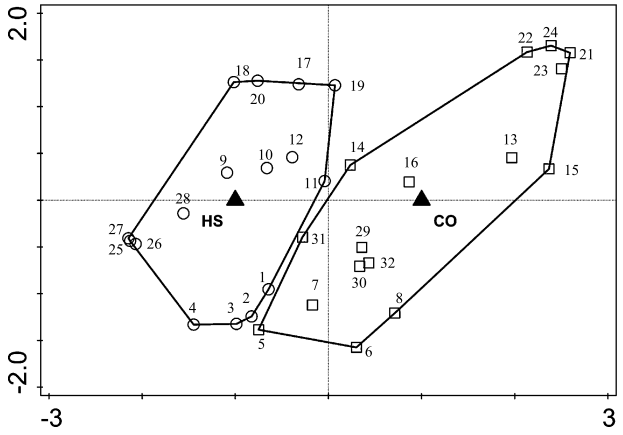

Fig. 3. Ordination of soil samples on the biplot resulting from the Redundancy analyses based on the nematode genera composition of the soil samples from plots invaded (circles) by *Heracleum sosnowskyi* (HS) and non-invaded (squares) plots (CO). (Wet dump ground depression 1-8; Line between agricultural fields 9-16; Route edge 17-24; Alluvial meadow 25-32.)

At wet dump ground depression (Fig. 2), *H. sosnowskyi* negatively correlated with *Phragmites australis*, *Galium verum*, *U. dioica* and *Symphytum officinale* plant species. Distributions of almost all nematode functional guilds in nematode communities within both invaded and non-invaded plots were similar. Composition of the nematode community different between *H. sosnowskyi*-invaded and non-invaded plots according to the RDA, showed smaller differences between DEPc and DEPh, while there were large differences between AGRc and AGRh, REDc and REDh, and MEAc and MEAh plots (Fig. 3). The first two RDA axis explained 29.1 and 26.6% of composition variation, respectively.

Nematode community indices

Mean values of the community indices in all four habitats, *H. sosnowskyi*-invaded and non-invaded plots, are presented in Table 4. At the non-cultivated line between agricultural field habitat the establishment of *H. sosnowskyi* was negatively associated with MI, PPI (both $P < 0.05$) and CI ($P < 0.01$) in the AGRIh plots. By contrast, the EI and NCR ratios were significantly higher in the invaded plots ($P < 0.05$). The Jaccard index of faunal similarity was 62.4%. A similar trend at the alluvial meadow habitat was found when values of MI, PPI and CI were significantly lower in the MEAh ($P < 0.05$). On the other hand, the EI was higher in the *H. sosnowskyi*-invaded areas when compared to control ($P < 0.05$). The Jaccard index of faunal similarity was 67.8%, while nematode diversity remained unchanged.

However, at the route edge habitat a significant decrease in population densities of bacterivores and an increase of cp-5 plant parasites (Table 1) in the REDh caused significantly higher PPI ($P < 0.01$). The CI was significantly higher under *H. sosnowskyi* impact, despite the fact that it reached the lowest values in all investigated habitats. The Jaccard index of faunal similarity was 52.5%. *Heracleum sosnowskyi* invasion may have influenced the nematode communities but had no apparent impact on nematode diversity (H′ gen) in the AGRI, MEA and RED habitats (Table 4). At the wet dump ground depression, where only several solitary individuals of *H. sosnowskyi* grew, none of the community indices differed significantly between the DEPc and DEPh plots. The Jaccard index of faunal similarity of the invaded and non-invaded areas was 94.3%.

Discussion

Relationships between *H. sosnowskyi* and native vegetation

Heracleum sosnowskyi is a biennial or perennial plant that has the ability to form pure monostands in invaded areas (Kabuce & Priede, 2010; Baležentienė & Bartkevičius, 2013; Dalke *et al*., 2015). *Heracleum sosnowskyi* grew in all the investigated habitats but in the 'wet-dump ground depression' it did not expand to become the dominant species (Table 1). An explanation is the presence of a stronger native plant competitor, *P. australis*, which grew quickly and formed denser vegetation, as well as relatively high soil moisture during the entire vegetation period in this habitat. By contrast, in the 'alluvial abandoned meadow', which was not as wet, *H. sosnowskyi* was able to form a monoculture and was positively correlated with soil moisture and *U. dioica* species. The prevalent plant species as subsidiary vegetation growing in the control area occurred only sporadically in the *H. sosnowskyi*-invaded area. A similar pattern was found for the Sosnowskyi hogweed in the non-cultivated line between fields and the ruderal route edge habitats. In both habitats *H. sosnowskyi* became the ascendant species. This suggests that *H. sosnowskyi* can modify the invaded environment through production of allelochemicals that inhibit growth of native plants (allelopathy) (Baležentienė, 2012; Baležentienė & Renčo, 2014;

Table 4. Nematode community structure and functional indices associated with *Heracleum sosnowskyi*-invaded and control areas in four different habitats.

Locality/habitat	Control	*Hs*	Significance (HSD test)
Non-cultivated line between fields			
H′ gen	2.87 (0.14)	2.69 (0.18)	–
MI	2.38 (0.09)	2.14 (0.15)	*
PPI	2.55 (0.14)	2.28 (0.04)	*
NCR	0.56 (0.1)	0.82 (0.02)	*
EI	37.5 (5.7)	62.5 (11.9)	*
SI	52.7 (6.9)	49.7 (8.9)	–
CI	62.1 (15.3)	20.8 (11.9)	**
BI	36.6 (4.4)	30.5 (9.2)	–
J_s	68.42		
Route edge within agricultural farm			
H′ gen	2.83 (0.09)	2.84 (0.08)	–
MI	1.91 (0.07)	2.13 (0.17)	–
PPI	3.01 (0.10)	3.54 (0.24)	**
NCR	0.94 (0.02)	0.93 (0.05)	–
EI	79.5 (0.9)	65.1 (13.6)	–
SI	59.9 (4.1)	58.6 (6.6)	–
CI	3.7 (1.1)	15.7 (4.3)	*
BI	15.7 (0.8)	22.9 (6.6)	–
J_s	72.54		
Wet alluvial meadow			
H′ gen	2.99 (0.15)	3.06 (0.12)	–
MI	2.92 (0.19)	2.52 (0.14)	*
PPI	2.64 (0.15)	2.29 (0.16)	*
NCR	0.78 (0.12)	0.76 (0.1)	–
EI	35.8 (13.7)	57.4 (6.7)	*
SI	78.9 (3.1)	70.1 (12.9)	–
CI	60.9 (19.7)	23.3 (11.9)	*
BI	18.7 (3.0)	21.1 (7.6)	–
J_s	67.78		
Wet dump ground depression			
H′ gen	2.83 (0.10)	2.97 (0.11)	–
MI	2.42 (0.05)	2.46 (0.21)	–
PPI	2.80 (0.11)	2.74 (0.03)	–
NCR	0.63 (0.13)	0.64 (0.10)	–
EI	33.4 (7.1)	32.5 (4.2)	–
SI	54.7 (3.3)	51.8 (13.1)	–
CI	74.2 (8.5)	83.1 (12.8)	–
BI	36.9 (10)	37.6 (3.9)	–
J_s	94.34		

H′ gen: Shannon-Weaver Index for genera; J_s: Jaccard's index of similarity (%); MI: Maturity index; PPI: Plant parasitic index; NCR: Nematode channel ratio; EI: Enrichment index; SI: Structure index; CI: Channel index; BI: Basal index.
$^{*}P < 0.05$; $^{**}P < 0.01$, significant differences between the same control and invaded areas.

Jandová *et al*., 2014) and altered nutrient cycling (EPPO, 2009). Our results, however, showed that soil pH had a tendency to be higher under *H. sosnowskyi* monoculture, confirming the finding of Jandová *et al*. (2014) with habitats invaded by the related species, *H. mantegazzianum*.

Bioindication of descriptive indicators to the *H. sosnowskyi* invasion in different habitats

Our study indicates that communities of soil nematodes mostly responded negatively to *H. sosnowskyi* invasion. Negative changes occurred only in the habitats where *H. sosnowskyi* formed a monoculture. By contrast, in the DEP habitat where only a few *H. sosnowskyi* plants grew, no significant changes in nematode communities were observed in comparison to the non-invaded control area. In the AGRh and REDh plots, the mean nematode abundance and genera numbers decreased, while the MEAh plots were not affected by *H. sosnowskyi* invasion. In agreement with our results, several previous studies have shown lower total nematode abundance under invasive plant species than under native plants, such as found by Renčo & Baležentienė (2015) in the *H. sosnowskyi* monocultures that formed in the forest edge, roadside slope and abandoned grassland; Belnap *et al*. (2005), after the exotic grass *Bromus tectorum* invasion of native *Hilaria jamesii*; or Zhang *et al*. (2018) after addition of roots and shoots litter of native *P. australis vs* invasive *Spartina alterniflora* to soil of non-vegetated area (bare mud flat) without any previous higher plants. This is in contrast with higher nematode numbers detected under the influence of the invasive weed, *Ambrosia trifida*, which proliferated on abandoned croplands (Liang *et al*., 2007).

Plant parasites depend on the establishment of higher plants with root systems serving as food sources (Bongers, 1990); therefore, the assessment of their abundance and species diversity reflects the variations in the nematode community due to changes in plant communities (Viketoft *et al*., 2005). This is in line with our findings when soil on plots with *H. sosnowskyi* predominance contained significantly fewer plant-parasitic nematodes than plots with diverse native plants, thus indicating the negative impact of *H. sosnowskyi* on plant-parasitic nematodes. This applies in particular to the Pp_3 functional guild nematodes (*Geocenamus*, *Helicotylenchus*, *Pratylenchus* and *Tylenchorhynchus*), which clearly confirms our earlier findings from the *H. sosnowskyi*-invaded habitats in Lithuania (Renčo & Baležentienė, 2015). This is probably caused partially by modification in undergrowth vegetation and root depletion in all habitats where *H. sosnowskyi* becomes prevalent, due to strong shading and allelopathic impact (Kabuce & Priede, 2010; Dalke *et al*., 2015). Additionally, *Heracleum* spp. belongs to the carrot family Apiaceae where mature perennial specimens have long pale roots with a tough cortex and only a few young roots that could be attacked by Pp nematodes. However, it is more likely that *H. sosnowskyi* plants contain toxic furanocoumarins that are produced by plants as a defence mechanism against the various types of predators, ranging from bacteria to insects and mammals (Abadollahi, 2013). Therefore, *H. sosnowskyi* plants are probably less vulnerable to nematodes of the Pp_3 functional guild. Additionally, it could be hypothesised that, in Caucas, where *H. sosnowskyi* grows naturally, some adversaries, such as fungi, cause either plant tissue necrosis or herbivores can reduce their populations. It could also be that some parasitic nematode species have evolved the ability to parasitise *H. sosnowskyi* and thus limit plant population growth. Only recently, a new species of plant-parasitic nematode, *Gracilacus wuae*, associated with a fairly common weed, *H. maximum*, has been described from Canada (Yu *et al*., 2016). However, these nematode species were not transferred with *H. sosnowskyi* plants to its new localities. Such a lack of some plant-parasitic nematodes could be regarded as one of the factors explaining the extensive adaptation success of *H. sosnowskyi* in novel areas; however, there are no comparative data from *H. sosnowskyi* native regions and soil nematofauna.

According to De Deyn *et al*. (2004), the changes in plant communities, root diversity and biomass production mainly affect primary (plant parasites) and secondary (bacterivores and fungivores) consumers but not the nematodes of higher trophic groups, such as predators and omnivores. Increases in root biomass can also indirectly support the abundance of organisms that are part of the decomposer subsystem of the soil food web. Bacterivorous and fungivorous nematodes serve as the basal resource for decomposition *via* increased amounts of litter or root exudates (Wardle *et al*., 2003). This partially corresponds with our current findings where significantly fewer fungivorous nematodes were found in the AGRh, REDh and MEAh plots compared to the related non-invaded plots, mainly Fu_2 *Aphelenchus* and Fu_4 *Tylencholaimus*. As suggested by Cesarz *et al*. (2015), these nematode functional guilds depend on different groups of fungi; Fu_2 feed on saprophytic and Fu_4 feed on arbuscular mycorrhizal fungi (AMF). We can speculate that reduced plant diversity together with *H. sosnowskyi* toxic

metabolites continuously released into the soil during decomposition could reduce the abundance and diversity of saprophytic and AMF fungi, leading to reduction in abundance of Fu_2 and Fu_4 nematode functional guilds. These claims can also be supported by our data obtained during a long-term study of the recovery of nematode communities after a catastrophic windstorm in the protected spruce forest of High Tatra National Park (Renčo *et al*., 2015) where aphelenchids and tylencholaimids were significantly more abundant in the destroyed research areas 9 years after the event. This was attributed to an improvement of microclimatic conditions, mainly due to secondary plant succession and changes in the herbaceous cover, which was more diverse than in the forest. Higher plant diversity, increase in plant parasites and fungivorous abundance was also considered by Kostenko *et al*. (2015) to be major factors. Similarly, Mummey & Rilling (2006) and Hawkes *et al*. (2006) found a reduction of AMF colonising roots of native plants after the establishment of invasive *Centaurea maculosa*, *Avena barbata*, *Bromus hordeaceus* and *B. tectorum*.

Interestingly, similarly to fungivores, bacterivores were also negatively influenced by *H. sosnowskyi* invasion, not only on the route edge in the present study, but also in the afforest edge (Renčo & Baležentienė, 2015), even though Bf are considered to be more tolerant than the other trophic groups to the changes in soil ecosystems (Bongers, 1990). Their tolerance to disturbance was evident in the alluvial meadow where all bacterial-feeding guilds were significantly higher in the *H. sosnowskyi*-invaded than non-invaded areas or in the non-cultivated line between two fields. A similar trend was found by Renčo & Baležentienė (2015) in the abandoned land and grassland on the roadside slope invaded by *H. sosnowskyi* and by Chen *at al*. (2007) under invasive *S. alterniflora*. These observations indicate that different habitat characteristics and environmental conditions *e.g.*, soil type (Lišková *et al*., 2008) can affect behaviour and response of bacterivorous nematodes to *H. sosnowskyi* invasion.

Omnivores and carnivores occupy a high trophic level position and are often used to indicate a more species-rich community and trophic link. Many have long life cycles, low reproduction ratio and, therefore, are thought to be more sensitive to ecosystem changes (Bongers, 1990; Yeates *et al*., 1993). Unlike De Deyn's statement (De Deyn *et al*., 2004), we found that besides Ba, Pp and Fu nematodes omnivore-feeding guilds were also significantly negatively affected by *H. sosnowskyi* invasion. Their abundance was lower under *H. sosnowskyi* predominance in the present study. By contrast, in the abandoned land and grassland on roadside slope habitats in the study by Renčo & Baležentienė (2015), omnivores were more abundant in *H. sosnowskyi*-invaded areas than in controls. The differences observed in our studies are also supported by the findings of Belnap *et al*. (2005) on the invasion of native habitats by *B. tectorum*, but were contrary to those of Liang *et al*. (2007) on the invasion of native *Chenopodium serotinum* by *A. trifida*. We can only speculate why omnivores in some habitats reacted to *H. sosnowskyi* invasion as typical K-strategist but not in others. It may be due to their diverse and often unknown feeding strategies that hamper data interpretation (Cesarz *et al*., 2015).

Only carnivorous nematodes remained unaffected after plant diversity changes caused by *H. sosnowskyi* invasion in all investigated habitats, thus confirming our previous findings (Renčo & Baležentienė, 2015). Similar conclusions were published by Kostenko *et al*. (2015), who found that the abundance of carnivorous nematodes was not directly related to plant diversity or the proportion of legumes, grasses and forbs in the plant community, consequently confirming De Deyn's statement. Overall, the carnivores have very low numbers or are absent in some soils or ecosystems, which often makes it difficult to use them as sensitive indicators of changes in the soil environment.

Bioindication of evaluative indicators to the *H. sosnowskyi* invasion in different habitats

The functioning of the soil food web depends on its component organisms and the environment in which they exist (Ferris & Bongers, 2006). The evaluative indicators point to functional changes in the soil food web based on functional analysis of nematode faunal composition. Similarly to descriptive indicators, none of the nematode evaluative indicators differed between the *H. sosnowskyi*-invaded and non-invaded areas in wet dump ground depression. This indicates that the presence of a few solitary specimens of *H. sosnowskyi* do not pose a threat to biodiversity loss in similar wet habitats such as wetlands or peatlands. The high value of J_s also confirmed that nematofauna in the *H. sosnowskyi*-invaded area (DEPh) was the same as that in the non-invaded control (DEPc), and thus was not affected by invasion. The CI values suggested a slowing fungal decomposition pathway of organic matter, whilst the NCR values indicated that bacterivores also play an important role in decomposition

in both the invaded and non-invaded areas (Ferris *et al*., 2001; Yeates, 2003).

In the habitats where *H. sosnowskyi* form dense vegetation, several shifts in values of indices occurred. Consistent with our previous findings from *H. sosnowskyi*-invaded abandoned land and grassland on a roadside slope (Renčo & Baležentienė, 2015), *H. sosnowskyi* invasion did not affect nematode diversity (H′ gen) in the present three investigated habitats. Biederman & Boutton (2009) also recorded that nematode diversity was unaffected by the invasion of the woody plant *Prosopis glandulosa* in areas that were once grassland. In addition, Keith *et al*. (2006) found that birch invasion of heather moorland increased nematode diversity. Long-term study of spruce forest recovery in the High Tatra National Park, Slovakia, after a catastrophic windstorm, showed no changes in nematode diversity due to secondary plant succession (Renčo *et al*., 2015). Nevertheless, a wildfire that subsequently affected a part of the windstorm-damaged area decreased soil nematode diversity for 9 years (Renčo & Čerevková, 2015).

Although the maturity index (MI) was developed to serve as a tool by which colonisation and subsequent succession could be monitored mainly in agroecosystems (Bongers, 1990), it has also been used successfully to distinguish heavily disturbed or stressed ecosystems (Wilson & Kakouli-Duarte, 2009). In our study, the effect of *H. sosnowskyi* invasion was revealed by the MI. The MI values were lower under *H. sosnowskyi* dominance on non-cultivated line between the agricultural field and the wet alluvial meadow, but did not differ significantly between *H. sosnowskyi*-invaded and non-invaded areas on route edge. Inconsistent shifts in the MI values under *H. sosnowskyi* invasion of different habitats were found by Renčo & Baležentienė (2015) and also by Neher *et al*. (2005) under disturbed and undisturbed wetlands, forests and agricultural soils.

Since the occurrence and abundance is largely determined by the community structure, host status and plant vigour growing in the soil, plant-parasitic nematodes were omitted from the MI calculation and were included in a separate Plant Parasitic Index (PPI). The persisters among the Pp nematodes also occur under stressed conditions and these are indications that a gradual increase in primary production correlates with an increase of Pp persiters (Bonger, 1990). The low values of PPI under *H. sosnowskyi* dominance at 'N' and 'S' sites in comparison to non-invaded controls confirmed our previous findings (Renčo & Baležentienė, 2015). We can conclude that *H. sosnowskyi* invasion decreased plant primary production. This was also confirmed by Co-CA analysis where negative correlations with other plant species were found. These changes led to a decrease in abundance of nematodes from the Pp_3 functional guild, which are considered as indicators of more stable habitats (persisters) corresponding to *Geocenamus*, *Helicotylenchus*, *Pratylenchus* or *Tylenchorhynchus* (Bongers, 1990). A similar reduction in population sizes of plant-parasitic nematodes was recorded by Biederman & Boutton (2009) after invasion of woody plants in grasslands and by Kostenko *et al*. (2014), where the abundance of Pp nematodes increased with proportion of grasses and decreased with proportion of forbs in the plant community.

In all *H. sosnowskyi*-dominant habitats (AGRh, REDh and MEAh), the values of CI and NCR indicated that the bacterial decomposition pathway was more important in the soil with *H. sosnowskyi* dominance than in its absence (Ferris *et al*., 2001; Yeates, 2003). This was confirmed by significantly fewer fungivorous nematodes under *H. sosnowskyi* ($P < 0.05$). The decline in numbers of fungal-feeding nematodes under invasive weeds was recorded also by Yeates & Williams (2001) where invasive *A. trifida* did not affect the abundance (Liang *et al*., 2007).

Conclusions

From an environmental viewpoint, the only baselines for assessing the quality of soils are biological attributes (Kroes, 1983). Therefore, we sought to understand how invasive *H. sosnowskyi* alters the nematode communities in the diverse habitats it invades. Here, the analysis of soil nematode communities in areas invaded by *H. sosnowskyi* compared with equivalent non-invaded control areas showed variable results. Nevertheless, some interesting results were found. The descriptive indicators such as nematode abundance and nematode taxa numbers showed a high variation in values with respect to the different habitats studied. Stress sensitive omnivores of high trophic level (Om_4, Om_5), fungi-dependent fungivores (Fu_2) and root-biomass-dependent obligate plant parasites (Pp_3) best reflected the changes in nematode communities under the influence of *H. sosnowskyi* invasion in the habitats where *H. sosnowskyi* become dominant. Evaluative indicators such as H′ gen and SI were not appropriate for the interpretation of changes in the soil nematode community structure in *H. sosnowskyi*-invaded areas. MI reflected changes in abundance of taxa that are higher on the cp scale (mainly omnivores) as well as lower on the cp scale (bacterivores). The PPI decreased as a result of

a reduced plant primary productivity under *H. sosnowskyi* and reflected the decline in obligate Pp_3 nematodes. CI, EI and NCR were useful for the clarification of prevailing decomposition pathway and function of soil food web in both the *H. sosnowskyi*-invaded and non-invaded control areas. Our results indicated that significant changes in the herbaceous layer after *H. sosnowskyi* invasion in ecosystems where *H. sosnowskyi* become dominant impacted soil nematode communities. However, functional guilds and nematode taxa differentiated between *H. sosnowskyi*-invaded and non-invaded areas, irrespective of the type of ecosystem, better than community indices, with the exception of the PPI.

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