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Influence of invasion by Sosnowsky's hogweed on nematode communities and microbial activity in forest and grassland ecosystems

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ABSTRACT

This study determined the effect of the invasive plant *Heracleum sosnowskyi* on selected soil microbial properties and the taxonomic and trophic composition of soil nematode communities in the Serpukhov district of Moscow region, Russia. We compared invaded by *H. sosnowskyi* (at least twenty years) and uninvaded plots in two ecosystems, forest and grassland. Soil was sampled and analysed in the autumn and spring. The forest and grassland ecosystems had substantially different soil microbial and nematode communities, but both were considerably altered by invasion. The soil microbial properties differed among the investigated plots and season, but the differences were observed to be non-significant between the invaded and the uninvaded plots. By contrast, invasion significantly negatively affected total nematode abundance and altered nematode numbers and the generic composition of two trophic groups, herbivores and omnivores, in both seasons, but significantly only in the spring. The numbers of bacterivorous, fungivorous, and predaceous nematodes were not affected by *H. sosnowskyi* invasion. The channel index indicated that bacteria strongly contributed to decomposition in all plots (grassland and forest), regardless of invasion status. Enrichment and structure indices suggested that resource availability and ecosystem disturbance were higher in the invaded than the uninvaded plots, but significantly only in the spring. Our results thus indicated that invasion by *H. sosnowskyi* influenced several nematode communities parameters while others remained unaffected, regardless of habitat were invasion take place.

1. Introduction

Invasive alien plants are an increasing cause for concern because no universal tool is currently available to stop their spread, reduce their impact, or prevent future invasions (Nielsen et al., 2005). Invasive plants transform multispecies communities into mono-dominant communities and thus reduce local plant biodiversity, cause considerable economic damage, and can sometimes be a hazard to human health (Thiele and Otte, 2007). It has estimated that about 13 000 plant species are

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growing outside their native ranges, creating their own populations (Van Kleunen et al., 2015). A total of 277 invasive plant species have been recorded in European Russia, with *Heracleum sosnowskyi* one of the most widespread invaders (21 of 45 regions) (Vinogradova et al., 2018). This species originates in the Caucasus, Transcaucasia, and Turkey (Jahodová et al., 2007a, 2007b), where it grows in mountainous areas along streams, in forests, or in alpine meadows. *H. sosnowskyi* develops large stands in natural habitats, is hardy, and can thrive in a cold climate. It was promoted as an agricultural crop for livestock fodder in Russia, where it was first introduced in 1947 but has since spread rapidly, infesting grasslands, forests, wetlands, riverbanks, urban areas, and abandoned agricultural land (Geltman, 2009). It was also cultivated in botanical and ornamental gardens (Grigorievskaya et al., 2004).

H. sosnowskyi is a serious threat to invaded environments due to its allelopathic potential (Mishyna et al., 2015), competitive ability (Thiele and Otte, 2006), and high rate of reproduction (15 000–20 000 seeds per plant) (Clements and DiTommaso, 2011; Bochkarev, 2011). Changes in plant cover have major impacts on ecosystem functions (Muller, 2004) and affect the richness, activity, abundance, and diversity of ecosystem biota (Sax and Gaines, 2003; Belnap et al., 2005). Soil microorganisms such as bacteria and fungi represent a primary energy sources for nematode communities, and the quantitative variation of these resources may affect the structural and trophic diversity of nematode communities (Biederman and Boutton, 2009). Bacterial, fungal, and nematode communities differ amongst soil types, ecosystems, and vegetation and are sensitive to various changes to the environments they inhabit (Bongers, 1990; Yeates et al., 2009; Scharfy et al., 2009; Čerevková et al., 2013). Gaggini et al. (2018), mentioned that invasive *Impatiens glandulifera* negatively altered the composition of the soil fungal community and the activity of the bacterial community in forest soil, and consistent with the results by Stefanowicz et al. (2016), where invasive *Fallopia japonica* significantly decreased microbial biomass, urease activity, and soil respiration. In contrast, Wang et al. (2018) reported that invasive *Erigeron annuus* and *Solidago canadensis* positively affected the abundance, the richness and diversity of soil fungal communities, indicating that not all invasive plants posed the same risks for microbial communities. Only a few studies, however, have investigated the impact of invasive *H. sosnowskyi* on soil microbial or nematode communities. *H. sosnowskyi* invasion has had a negative impact on populations of yeast, the ascomycetes *Candida vartiovaarae* and *Wickerhamomyces anomalus* (Glushakova et al., 2015) and on total nematode abundance and species diversity (Renčo and Baležentiené, 2015). Invasion by *H. sosnowskyi* increased populations of the yeast-like fungi *Trichosporon moniliforme* and *Trichosporon porosum* with high hydrolytic activity and populations of bacterivorous and fungivorous nematodes (Glushakova et al., 2015; Renčo and Baležentiené, 2015). Renčo et al. (2019), however, reported that nematode communities were affected by *H. sosnowskyi* invasion only in ecosystems where *H. sosnowskyi* was able to form mostly monocultures (75–95% cover) but not in habitats where *H. sosnowskyi* did not become the dominant species and where native plants (e.g. *Phragmites australis*) were stronger competitors.

We chose two ecosystems, a semi-natural grassland and a temperate mixed forest, invaded by *H. sosnowskyi* to assess and compare the responses of microbial and nematode communities to invasion as comprehensive study. We hypothesised that invasion by *H. sosnowskyi* in native habitats would 1) affect the content of soil microbial biomass carbon, basal soil respiration, and the microbial metabolic quotient, 2) decrease nematode abundance and diversity, and 3) affect selected ecological and functional indices due to changes in the trophic structure of the nematode communities.

2. Material and methods

2.1. Study area

This study was conducted in the Serpukhov district of Moscow region, Russia (54°47′N, 37°33′E). The region has a moderately continental climate characterised by warm summers and moderately cold winters with snow covers remaining until the beginning of April. Mean annual air temperature and precipitation in the last forty years were 5.1 °C and 673 mm (recorded at a monitoring station in Serpukhov). The soils are Phaeozems (WRB, 2014).

We identified areas invaded by *H. sosnowskyi* by actively searching suitable areas across the entire range of habitats and environmental conditions in which the species had been recorded for at least twenty years. Historical reports noted that the uncultivated (wild) form of *H. sosnowskyi* was first recorded in Serpukhov in 1948 (Ignatov et al., 1990) but has become widely distributed in the region since 1990 (Vinogradova et al., 2010). The invasion of *H. sosnowskyi* were found in a mixed forest (~70 y) and a semi-natural grassland (~10 y). In the forest the *H. sosnowskyi* community was distributed fragmentarily and it was possible to distinguish uninvaded and invaded areas. In the grassland there was a ploughed boundary line for the area isolation from occupied by *H. sosnowskyi*. Such management allowed avoiding the distribution of the plant to the private gardens, which located close to the studied site. The invaded and uninvaded plots (10 × 10 m) adjacent to each other (separated by a mean distance of approximately 50 m), were selected in each ecosystem. The studied plots were in highly similar habitats, and did not differ substantially in elevation, inclination, exposition, type, or management. The invaded plots had at least 60% coverage of *H. sosnowskyi*. The dominant plants and chemical properties of the soil are summarised in Table 1.

2.2. Sampling procedure

Samples of topsoil (0–10 cm) were collected in autumn (November 2017) and spring (May 2018) in four forest plots invaded by *H. sosnowskyi* (FHs), four adjacent uninvaded forest plots (F), four grassland plots invaded by *H. sosnowskyi* (GHs), and four adjacent uninvaded grassland plots (G). Composite samples were collected in each plot as five subsamples per plot

Table 1
Vegetation and soil chemical properties (pH; carbon, C; nitrogen, N) of the study plots (F, uninvaded forest; FHs, invaded forest; G, uninvaded grassland; GHs, invaded grassland). Value indicates the mean and standard error for each plot (November 2017).

Plots	Dominated plants	pH	C, %	N, %	C/N
F	*Betula pendula, Pinus sylvestris, Corylus avellana, Sorbus*	6.1 ± 0.2	4.2 ± 0.2	0.3 ± 0.0	15.4 ± 0.4
FHs	***H. sosnowskyi*** (60–70%) *Betula pendula, Pinus sylvestris, Corylus avellana, Sorbus,*	6.8 ± 0.2	2.3 ± 0.1	0.2 ± 0.0	11.8 ± 0.4
G	*Elytrigia, Sonchus, Poa, Trifolium, Festuca, Achillea millefolium*	6.8 ± 0.2	1.7 ± 0.1	0.2 ± 0.0	10.3 ± 0.1
GHs	***H. sosnowskyi*** (70%) *Tanacetum, Festuca, Poa, Trifolium, Salix caprea, Fragária, Carduus,*	6.2 ± 0.2	1.9 ± 0.1	0.2 ± 0.0	11.1 ± 0.1

(centre and corners) using an Edelman auger (Eijkelkamp, the Netherlands) with a diameter of 7 cm. The samples were transported to the lab and divided into three parts. The first part was used for nematode extraction. The second part was freshly sieved (2 mm mesh) and used for microbiological analysis (ISO 10381–6:1993). The third part was sieved and air-dried (22 °C) for chemical analysis.

2.3. Chemical and microbiological analyses

Microbiological and chemical analyses were performed for three analytical replicates of each sample, and the results are reported for oven-dried soil (105 °C, 8 h).

Soil pH in water (1:2.5) was determined using a pH meter (Ekoniks, Moscow, Russia). The total carbon (C) and nitrogen (N) contents were determined by spectrometry (CHN-932, LECO Corp., Saint Joseph, USA) after oxygen combustion (1100 °C). Soil microbial biomass C (MBC) was measured by substrate-induced respiration (SIR), which is based on recording maximum initial CO_2 production by microorganisms after glucose addition (Anderson and Domsch, 1978; Ananyeva et al., 2008). Briefly, 1 g of soil was placed into a 15-mL vial where a glucose solution was added one drop at the time for a total of 0.1 mL g^{-1} (10 mg glucose g^{-1}) (Ananyeva et al., 2008). The vial was hermetically sealed and incubated at 22 °C for 3.5–5.0 h, during which the glucose was oxidised and co-oxidised by soil microorganisms, excluding CO_2 consumed for growth. CO_2 concentration was measured by gas chromatography (KristaLLyuks 4000M, Ioshkar-Ola, Russia). The soil SIR rate (μL CO_2 g^{-1} soil h^{-1}) was calculated based on the CO_2 concentration, volume of the gas phase in the vial and incubation time. MBC content was calculated according to formula $= \text{SIR} \times 40.04 + 0.37$ (Anderson and Domsch, 1978). Basal respiration (BR) was measured in the samples (ISO 16072:2002) as described for SIR, but distilled water (0.1 ml g^{-1} soil) was added to the soil instead of the glucose solution, and the incubation period was 24 h at 22 °C. The microbial metabolic quotient, or specific respiration of microbial biomass (qCO_2), was calculated as the ratio of BR to MBC.

2.4. Nematode extraction and identification

Nematodes were isolated from 100 g of the mixed fresh soil samples using a modified Baermann technique (Van Bezooijen, 2006). Nematodes were extracted from aqueous soil suspensions using a set of two cotton-propylene filters. Subsamples were removed after extraction for 24 h at room temperature (20 °C). The aqueous suspensions containing nematodes were examined under a stereomicroscope, excess water was removed, and the nematodes were fixed with a hot 99:1 solution of 4% formaldehyde:pure glycerol and evaluated on permanent glycerine slides. All isolated nematodes were microscopically identified to genus from permanent glycerine slides using an Eclipse 90i light microscope (Nikon, Japan), using original species descriptions, and several taxonomic keys: Brzeski (1998), Loof (1999), Siddiqi (2000), Andrássy (2005, 2007; 2009), and Geraert (2008, 2010).

2.5. Nematode-community analysis and ecological and functional indices

Nematode genera were assigned to trophic groups (bacterivores, fungivores, herbivores, omnivores, and predators), as described by Yeates et al. (1993), Wasilewska (1997), and Sieriebriennikov et al. (2014). The total number of genera, mean nematode abundance, mean number of nematodes per trophic group, and the Shannon and Weaver genera diversity index (H'gen) (Shannon and Weaver, 1949) were determined. Basic ecological indices, i.e. $\sum$ maturity index ($\sum$MI) for all nematode taxa, maturity index (MI) for free-living taxa, and the plant parasite index (PPI) for plant-parasitic taxa (Bongers, 1990), were used to assess the status of the soil habitats using nematode communities. MI, $\sum$MI, and PPI were calculated using a coloniser-persister (c-p) value that represented the life-history characteristics of the nematode taxa associated with r- and K-selection. Species with c-p values of 1 or 2 are r-selected, i.e. colonisers. These species are very tolerant to disturbances due to their short generation times, large population fluctuations, and high fecundities. Species with a c-p value of 5 are K-selected, i.e. persisters, with long life cycles, low reproductive rates, low metabolic activities, and slow movement; they are thus very sensitive to disturbances. Low c-p values are indicative of more disturbed environments, and high values are characteristic of less disturbed environments (Bongers, 1990).

Functional indices such as the enrichment (EI), structure (SI), channel (CI) (Ferris et al., 2001), and basal (BI) (Berkelmans et al., 2003) indices associated with development of the maturity indices led to a functional guild classification of nematodes as a basis for studying and comparing ecosystem processes. Considering soil nematode taxa as representatives of functional guilds generates an indicator profile that is not constrained by population distribution patterns and microenvironment effects (Ferris and Bongers, 2006). Indices of soil food webs such as the EI, SI, CI and BI are used to infer food web complexity and the main pathways of organic matter decomposition (Ferris et al., 2004). EI is based on the abundance of enrichment opportunistic nematodes, and indicates rapid decomposition of low C:N organic matter mediated by bacteria. EI thus suggest whether the soil environment is nutrient enriched (high EI) or depleted (low EI). SI weights the prevalence of omnivore and predatory nematodes in the soil food web as an indicator of long and complex soil food webs with high connectome and numerous trophic links and indicates if the soil ecosystem is structured with more trophic links (high SI) or degraded with fewer trophic links (low SI). Channel index, on the contrary, is based on the abundance of fungal feeding opportunistic nematodes and indicates slower decomposition of high C:N organic matter mediated by fungi. A high CI (>50%) indicates a higher proportion of fungal decomposition while low CI (<50%) suggests bacterial decomposition channels (Ferris et al., 2001). The Basal Index (BI) is derived from the abundance of persistent microbial feeding nematodes; high BI values indicate short and depleted soil food webs. The EI, SI, CI and BI functional indices of soil food webs are used to infer the complexity of food webs and the main pathways of decomposition of organic matter (Ferris et al., 2004). The ecological and functional indices (MI, $\sum$MI, PPI, EI, SI, CI, and BI) were calculated using the online programme “*NINJA: An automated calculation system for nematode-based biological monitoring*” (Sieriebriennikov et al., 2014; https://sieriebriennikov.shinyapps.io/ninja/).

2.6. Statistical analysis

Microbial parameters, mean nematode abundance, H’gen, mean number of nematodes per trophic group, and the ecological and functional indices were analysed using Statistica (StatSoft, Inc., 2013).

The data were analysed with a repeated two-way ANOVA, with ‘ecosystem’ (F, G), ‘invasion status’ (invaded, uninvaded), ‘date’ (as a repeated measure), and their interactions as factors. Box-Cox transformation was applied to satisfy the assumptions of these parametric tests using maximum likelihood and the Golden Search iteration only on non-normally distributed variables. The factor ‘date’ strongly influenced the majority of the variables tested, so the data set was split to investigate the effects of ‘ecosystem’ and ‘invasion status’ separately with two-way ANOVAs for the samples from autumn 2017 and spring 2018. A main-factor ANOVA (factors ‘ecosystem’, ‘invasion status’, and no interaction) was used if ‘ecosystem’ and ‘invasion status’ did not interact. *t*-tests were applied separately for each ecosystem to determine the effect of ‘invasion status’ if ‘ecosystem’ and ‘invasion status’ interacted.

A redundancy analysis (RDA) was used on the nematode-community data separately for the two sampling dates, with explanatory variables soil pH, C/N ratio, ‘ecosystem’, and ‘invasion status’, to identify the relationships between the nematode taxa and soil properties. All data were log-transformed. A *t*-value biplot was used for some explanatory variables to determine diversity nematode genera, which answer positively or negatively to them. These ordination analyses were performed in Canoco 5 for Windows (Ter Braak and Šmilauer, 2012).

Non-metric multidimensional scaling (NMS) ordination was used to examine any changes in the structure of nematode genera community for the invaded and the uninvaded habitats in different ecosystems and two sampling dates. A two-dimensional solution was accepted as optimal after randomised runs. The NMS analysis was performed using the PC-ORD 6 package (McCune and Grace, 2002; McCune and Mefford, 2016) with the slow and thorough autopilot mode and Sörensen (Bray-Curtis) distances (recommended for community data).

3. Results

The impact of *H. sosnowskyi* invasion on soil microbial activity and the structure of soil nematode communities in the two habitats (forest and grassland) was assessed in the soil samples collected in invaded and uninvaded plots. MBC, BR, and nematode-community parameters (total abundance; abundance of bacterivores, fungivores, and herbivores; and selected ecological and functional indices) differed significantly between the forest and grassland plots, regardless of invasion status (Tables 2 and 3). We will thus focus on *H. sosnowskyi* invasion that significantly affected several parameters in both habitats for both sampling dates.

3.1. Soil microbial properties

The studied microbial properties (BR, MBC, and $q\text{CO}_2$) were more depended on ecosystem type, than invasion status (Tables 2 and 3). The assessment of impact the invasion status on the microbial properties within ecosystems showed the irregular patterns for each time period. For instance, in the autumn the invasion effect on BR of forest soil had a negative effect, but for grassland – positive (Table 4). In the spring the significant difference between invaded and uninvaded plots was found only for $q\text{CO}_2$ of the grassland soil.

Table 2
Two-way ANOVAs results (F (1,12) values with significance level) for factors ‘ecosystem’ (Forest, Grassland) and ‘invasion status’ (Invaded, Uninvaded) and its combination. Means (n = 8) ± standard deviation of basal respiration (BR), microbial biomass carbon (MBC), metabolic quotient (qCO_2), nematode abundance, genera diversity index, abundance nematodes in trophic groups, ecological and functional indices. Soil sampling in autumn 2017.

Evaluated indices	Ecosystem	Invasion	Ecosystem × Invasion	Forest	Grassland	Uninvaded	Invaded
BR, μg C g^{-1} h^{-1}	30.13[a]	1.28	24.36[a]	2.6 ± 0.8	1.4 ± 0.5	2.1 ± 1.2	1.9 ± 0.4
MBC, μg C g^{-1}	21.82[a]	0.60	6.31[c]	1198.1 ± 311.7	683.9 ± 183.6	983.6 ± 485.9	898.5 ± 204.2
qCO_2, μg C mg^{-1} MBC h^{-1}	0.03	0.08	2.41	2.1 ± 0.5	2.2 ± 0.9	2.1 ± 0.5	2.3 ± 0.8
Nematode abundance	5.46[c]	1.54	0.27	410.5 ± 140.6	262.1 ± 100.7	370.8 ± 133.5	301.9 ± 148.2
Genera diversity index	1.16	3.54	4.63	2.4 ± 0.2	2.5 ± 0.2	2.3 ± 0.2	2.5 ± 0.2
Bacterivores	4.86[c]	0.03	3.55	108.6 ± 63.7	57.3 ± 27.9	84.9 ± 74.8	81.0 ± 27.1
Fungivores	12.95[b]	2.96	0.76	143.8 ± 57.3	66.6 ± 29.0	123.6 ± 64.0	86.8 ± 51.5
Herbivores	1.47	0.39	10.67[b]	145.6 ± 64.2	112.8 ± 74.8	137.6 ± 49.6	120.8 ± 87.7
Omnivores	3.17	0.94	0.14	8.6 ± 7.1	23.5 ± 21.1	20.5 ± 20.9	11.6 ± 11.9
Predators	0.44	0.16	2.91	3.9 ± 4.5	2.0 ± 2.1	4.1 ± 4.6	1.8 ± 1.2
Maturity Index	1.78	2.50	11.75[b]	2.3 ± 0.4	2.5 ± 0.5	2.6 ± 0.5	2.3 ± 0.4
∑Maturity Index	5.12[c]	1.9	11.81[b]	2.3 ± 0.38	2.5 ± 0.3	2.5 ± 0.4	2.3 ± 0.3
Plant Parasite Index	15.15[b]	0.78	8.56[c]	2.2 ± 0.2	2.5 ± 0.2	2.3 ± 0.3	2.4 ± 0.2
Enrichment Index	0.17	0.68	0.25	68.5 ± 10.6	70.6 ± 9.1	67.5 ± 9.9	71.7 ± 9.4
Structure Index	2.14	0.51	6.74[c]	63.2 ± 17.0	73.6 ± 16.1	70.9 ± 17.5	65.9 ± 17.1
Channel Index	0.23	4.77[c]	0.16	31.6 ± 20.1	28.0 ± 11.5	37.9 ± 17.3	21.7 ± 9.3
Basal Index	1.84	0.04	5.5[c]	18.9 ± 8.2	14.7 ± 7.3	17.2 ± 9.3	16.5 ± 6.6

Significance level.
[a] 0.001.
[b] 0.01.
[c] 0.05.

Table 3
Two-way ANOVAs results (F (1,12) values with significance level) for factors ‘ecosystem’ (Forest, Grassland) and ‘invasion status’ (Invaded, Uninvaded) and its combination. Means (n = 8) ± standard deviation of basal respiration (BR), microbial biomass carbon (MBC), metabolic quotient (qCO_2), nematode abundance, genera diversity index, abundance nematodes in trophic groups, ecological and functional indices. Soil sampling in spring 2018.

Evaluated indices	Ecosystem	Invasion	Ecosystem × Invasion	Forest	Grassland	Uninvaded	Invaded
BR, μg C g^{-1} h^{-1}	30.6[a]	0.00	3.12	2.9 ± 1.0	1.5 ± 0.3	2.3 ± 1.3	2.1 ± 0.8
MBC, μg C g^{-1}	37.22[a]	0.51	0.02	1448.4 ± 259.3	821.4 ± 91.2	1171.4 ± 366.5	1098.3 ± 403.6
qCO_2, μg C mg^{-1} MBC h^{-1}	1.10	0.02	5.68[c]	2.0 ± 0.5	1.8 ± 0.4	1.9 ± 0.5	1.9 ± 0.4
Nematode abundance	4.93[c]	12.22[b]	0.02	324.5 ± 70.5	268.4 ± 62.3	340.6 ± 49.2	252.3 ± 61.4
Genera diversity index	2.44	0.94	4.20	2.2 ± 0.3	2.4 ± 0.1	2.2 ± 0.3	2.3 ± 0.2
Bacterivores	43.68[a]	0.46	5.84[c]	124.6 ± 52.9	41.4 ± 11.7	97.4 ± 73.9	68.6 ± 31.3
Fungivores	0.20	1.65	0.47	85.1 ± 37.4	77.4 ± 31.2	92.3 ± 30.7	70.3 ± 34.4
Herbivores	5.10[c]	5.18[c]	1.88	112.6 ± 24.8	143.1 ± 37.0	143.3 ± 38.1	112.5 ± 23.0
Omnivores	2.60	26.85[a]	5.44[c]	1.8 ± 1.4	6.3 ± 7.1	7.1 ± 6.2	0.9 ± 1.4
Predators	0.00	2.00	0.00	0.4 ± 1.1	0.3 ± 0.7	0.6 ± 1.2	0.0 ± 0.0
Maturity Index	18.13[b]	0.23	3.2	1.7 ± 0.2	2.3 ± 0.3	2.0 ± 0.5	2.0 ± 0.3
∑Maturity Index	35.07[a]	0.63	3.24	1.9 ± 0.2	2.4 ± 0.2	2.1 ± 0.4	2.2 ± 0.2
Plant Parasite Index	35.01[a]	10.99[b]	0.22	2.1 ± 0.1	2.4 ± 0.1	2.2 ± 0.2	2.4 ± 0.2
Enrichment Index	11.14[b]	7.28[c]	0.03	70.7 ± 11.1	54.5 ± 11.5	69.2 ± 12.6	56.2 ± 12.2
Structure Index	9.17[c]	4.87[c]	1.56	15.2 ± 8.1	43.9 ± 29.7	40.0 ± 25.0	19.1 ± 23.2
Channel Index	16.47[b]	1.10	0.16	25.8 ± 12.3	53.6 ± 14.3	36.1 ± 22.6	43.3 ± 16.0
Basal Index	0.76	11.5[b]	0.17	27.8 ± 10.1	31.7 ± 13.2	22.15 ± 7.6	37.4 ± 9.7

Significance level.
[a] 0.001.
[b] 0.01.
[c] 0.05.

3.2. Nematode-community analysis

Total nematode abundance was lower in the invaded than the uninvaded plots but significantly only in the spring. Ecosystem, invasion status, and their interaction did not significantly affect the diversity index for nematode genera for either sampling date (Tables 2 and 3).

A total of 47 nematode genera were identified (Table 5). F and G contained 35 and 32 genera, respectively, and FHs and GHs contained 34 and 32 genera, respectively. The genera found in F or G but not FHs or GHs were *Acrobeles*, *Gracilacus*, *Mesorhabditis*, *Teratocephalus*, *Xiphinema* (only in F) *Dorylaimoides*, and *Geocenamus* (only in G). *Aulolaimus*, *Trichodorus*, and *Wilsonema* were found only in FHs, and *Diplogaster*, *Ditylenchus*, *Oxydirus*, and *Thonus* were found only in GHs.

An RDA of the nematode-community data identified the relationships between the nematode taxa and soil properties for each sampling date using the explanatory variables soil pH, C/N, ecosystem, and invasion status (Figs. 1 and 2). The explanatory variables for autumn (spring) accounted for 29.0% (50.3%) of the total variation. Axes 1 and 2, with eigenvalues of

Table 4
Means (n = 4) ± standard deviation for evaluated indices. Results from *t*-tests applied separately for each ecosystem and time period to determine the effect of 'invasion status'. Tested were only indices for which ANOVA confirmed significant interaction of 'ecosystem' and 'invasion status' (see Tables 2 and 3).

Evaluated indices	Forest			Grassland		
In autumn	Uninvaded	Invaded	p - value	Uninvaded	Invaded	p - value
BR, μg C g^{-1} h^{-1}	3.2 ± 0.5	2.0 ± 0.4	0,011 [b]	1.1 ± 0.2	1.9 ± 0.4	0,013 [b]
MBC, μg C g^{-1}	1378.9 ± 357.4	1017.4 ± 109.1	0,101	588.2 ± 80.8	779.6 ± 218.4	0,151
Herbivores	109.8 ± 15.1	181.5 ± 77.2	0,118	165.5 ± 58.6	60.0 ± 46.5	0,030 [b]
Maturity Index	2.2 ± 0.2	2.5 ± 0.5	0,323	2.9 ± 0.2	2.1 ± 0.3	0,003 [a]
∑Maturity Index	2.1 ± 0.1	2.4 ± 0.3	0,181	2.8 ± 0.1	2.3 ± 0.3	0,011 [b]
Plant Parasite Index	2.0 ± 0.0	2.4 ± 0.2	0,012 [b]	2.6 ± 0.1	2.5 ± 0.3	0,273
Basal Index	22.9 ± 9.6	14.8 ± 4.3	0,195	11.2 ± 4.1	18.2 ± 8.6	0,136
Structure Index	56.6 ± 11.5	69.9 ± 20.6	0,302	85.2 ± 5.5	61.9 ± 14.5	0,024 [b]
In spring						
qCO2, μg C mg^{-1} MBC h^{-1}	2.2 ± 0.6	1.8 ± 0.4	0,260	1.5 ± 0.1	2.0 ± 0.3	0,028 [b]
Bacterivores	158.0 ± 52.7	91.3 ± 27.8	0,060	36.8 ± 12.3	46.0 ± 10.6	0,286
Omnivores	2.5 ± 0.6	1.0 ± 1.4	0,078	11.8 ± 5.7	0.8 ± 1.5	0,002 [a]

Significance level.
[a] 0.01.
[b] 0.05.

0.24 (0.41) and 0.12 (0.15), respectively, explained 36% (55%) of the cumulative variance. The permutation test on all axes confirmed their significance (pseudo $F = 2.5$ (4.8), $p = 0.002$). Several genera were positively correlated with *H. sosnowskyi* invasion, e.g. the herbivores *Helicotylenchus* and *Rotylenchus* and the fungivore *Aphelenchus*. In contrast, the fungivore *Filenchus*, the herbivores *Malenchus* and *Psilenchus*, and the omnivore *Eudorylaimus* were more abundant in the uninvaded plots. Several genera were correlated with the C/N ratio: *Gracilacus* and *Prismatolaimus* were positively correlated, and *Aphelenchus*, *Boleodorus*, *Helicotylenchus*, *Psilenchus*, and *Rotylenchus* were negatively correlated (Figs. 1 and 2).

A two-dimensional solution was recommended by Autopilot and confirmed by a Monte Carlo permutation test. The best two-dimensional solution indicated a final stress of 9.35/8.70 ($p = 0.001$) after 61/31 iterations. Percentage of variance explained by the axes was 67/78 and 23/14, respectively. The NMS analysis not presented graphically showed clear separation of 'ecosystem x invasion status' plots mainly in spring samples. In autumn samples, invaded sites (FHs, GHs) were closer to each other than uninvaded sites (F, G).

3.3. *Trophic-group distribution and ecological and functional nematode indices*

Herbivores were the most abundant trophic group in both ecosystems, with significantly higher abundances in the uninvaded than the invaded plots in the spring samples (Table 3) and similar significant trend was observed in grassland in the autumn samples (Table 4).

Omnivores were more abundant in the uninvaded than the invaded plots in the both spring and autumn samples (Tables 2 and 3), but a subsequent *t*-test confirmed a significant effect of invasion only between G and GHs in spring (Table 4).

The bacterivores, fungivores and predators were more abundant in the uninvaded than the invaded plots, but the difference were not significant for either ecosystem or sampling date (Tables 2 and 3). The opposite non-significant trend was recorded on grassland in spring, where bacterivores abundance was greater in invaded than uninvaded plots (Table 4).

MI and ∑MI did not differ significantly between the invaded and uninvaded plots (Table 3). A subsequent *t*-test found that MI and ∑MI were significantly higher in G than GHs in autumn (Table 4). PPI was significantly higher in the invaded than the uninvaded plots in the spring samples (Table 3) and a subsequent *t*-test found that PPI was also significantly higher but only in FHs than F in the autumn samples (Table 4). The functional indices EI, SI, CI, and BI differed between the sampling dates. EI and SI were significantly lower and BI was significantly higher in the invaded than the uninvaded plots in the spring samples (Table 3). CI was significantly lower in the invaded than the uninvaded plots in the autumn samples (Table 2). The subsequent *t*-test indicated that SI was higher in G than GHs in the autumn samples (Table 4).

4. Discussion

The main mechanism of the invasion plants effect on soil microbial, nematode community, its structure and functioning is still not exactly determined due to the several possible influence ways such as change of the domestic plant community composition, decreasing its diversity and a protective cover, inputs of the untypical organic compounds from the litter and rhizosphere of invasive plants, as well as through contributing soil nutrients accumulation, producing the inhibitors and supporting the growth of the pathogenic microflora (Baležentiené and Bartkevičius, 2013; Kuebbing et al., 2014; Dalke et al., 2015; Mishyna et al., 2015; Zhang et al., 2019). There is controversial information in relation to the invasive plants influence on the soil microbial community (Stefanowicz et al., 2016; Gaggini et al., 2018; Wang et al., 2018; Zhang et al., 2019). For instance, the invasive plants (*Impatiens glandulifera, Fallopia japonica*) decreased soil microbial biomass, respiration and urease

Table 5
List of identified nematode genera and their mean total abundance (n = 4) (individual 100 g^{-1} soil; mean ± SD) in autumn 2017 and spring 2018; in ‘ecosystem’ (Forest, Grassland) and ‘invasion status’ (Invaded, Uninvaded). Nematode genera are evaluated to trophic groups, c-p value of coloniser-persister nematode species from 1 to 5 according Bongers (1990); Abbreviation used in RDA analysis.

Nematode genera in trophic group (Abbreviation)	c-p	Forest Autumn		Forest Spring		Grassland Autumn		Grassland Spring	
		Invaded	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded
Bacterivores									
Acrobeles (Acro)	2	–	0.8 ± 1.5	–	0.5 ± 1.0	–	–	–	–
Acrobeloides (Acrb)	2	10.3 ± 6.4	19.0 ± 6.1	26.0 ± 10.3	26.5 ± 17.2	10.3 ± 6.2	4.5 ± 3.5	17.0 ± 7.3	6.8 ± 4.3
Alaimus (Alai)	4	1.0 ± 1.4	1.3 ± 1.5	–	–	1.5 ± 0.6	0.5 ± 1.0	–	–
Aulolaimus (Aulo)	3	1.5 ± 3.0	–	–	–	–	–	–	–
Cephalobus (Ceph)	2	1.5 ± 1.3	2.8 ± 3.4	10.3 ± 8.0	16.0 ± 5.3	3.3 ± 2.8	4.5 ± 5.8	4.0 ± 3.2	3.3 ± 2.9
Cervidellus (Cerv)	2	1.5 ± 1.9	1.3 ± 2.5	–	–	1.8 ± 2.9	–	–	–
Diplogaster (Dipl)	1	–	–	–	–	0.5 ± 1.0	–	–	–
Eucephalobus (Euce)	2	7.8 ± 4.9	3.5 ± 2.4	8.3 ± 6.0	3.3 ± 3.9	4.5 ± 5.1	6.5 ± 8.1	7.3 ± 4.9	6.3 ± 4.3
Chiloplacus (Chil)	2	0.8 ± 1.5	0.8 ± 1.5	0.5 ± 1.0	–	6.8 ± 5.6	0.3 ± 0.5	–	–
Mesorhabditis (Meso)	1	–	1.0 ± 2.0	–	–	–	–	–	–
Pelodera (Pelo)	2	–	–	1.0 ± 1.2	2.5 ± 1.7	2.0 ± 1.8	2.0 ± 1.8	–	3.8 ± 4.9
Plectus (Plec)	2	13.5 ± 14.3	10.0 ± 6.9	4.0 ± 6.2	–	4.0 ± 4.1	1.0 ± 2.0	7.5 ± 2.6	2.8 ± 3.0
Prismatolaimus (Pris)	3	–	9.8 ± 10.7	1.5 ± 1.7	6.0 ± 4.5	–	2.3 ± 2.9	–	–
Rhabditis (Rhab)	1	46.3 ± 29.7	75.3 ± 67.9	39.8 ± 19.4	102.8 ± 49.0	42.8 ± 18.2	15.8 ± 10.8	10.3 ± 6.8	14.0 ± 7.0
Teratocephalus (Tera)	3	–	7.3 ± 8.4	–	0.5 ± 1.0	–	–	–	–
Wilsonema (Wils)	2	0.8 ± 1.5	–	–	–	–	–	–	–
Fungivores									
Aphelenchoides (Aphe)	2	7.5 ± 7.7	26.5 ± 14.1	16.0 ± 14.8	14.3 ± 9.4	7.5 ± 3.7	7.5 ± 4.4	17.8 ± 11.8	5.8 ± 1.5
Aphelenchus (Aphu)	2	14.0 ± 16.5	–	31.8 ± 20.4	17.8 ± 14.5	18.0 ± 4.3	5.3 ± 3.5	11.3 ± 9.9	6.8 ± 4.9
Diphtherophora (Diph)	3	5.0 ± 5.6	1.5 ± 1.7	0.8 ± 1.0	2.8 ± 2.8	–	1.5 ± 1.9	–	1.5 ± 2.4
Ditylenchus (Dity)	2	–	–	–	–	1.3 ± 2.5	–	–	–
Dorylaimoides (Dory)	4	–	–	–	–	–	0.8 ± 1.5	–	–
Filenchus (File)	2	37.0 ± 29.9	109.5 ± 34.3	30.0 ± 16.7	55.3 ± 17.3	16.5 ± 10.9	22.8 ± 12.5	22.8 ± 15.2	51.3 ± 12.7
Tylencholaimus (Tyle)	4	52.5 ± 31.9	34.0 ± 9.9	1.5 ± 1.7	0.3 ± 0.5	14.3 ± 11.4	38.0 ± 19.9	8.8 ± 10.1	29.0 ± 26.9
Herbivores									
Aglenchus (Agle)	2	7.3 ± 7.2	16.0 ± 13.4	4.5 ± 5.3	2.8 ± 2.2	5.0 ± 5.2	8.5 ± 8.7	1.3 ± 1.5	4.8 ± 1.7
Bitylenchus (Bity)	2	–	–	1.3 ± 2.5	–	–	2.0 ± 2.8	1.3 ± 2.5	–
Boleodorus (Bole)	2	45.3 ± 41.7	3.3 ± 1.3	1.3 ± 2.5	–	5.5 ± 7.2	25.0 ± 17.2	26.0 ± 11.2	27.3 ± 7.6
Coslenchus (Cosl)	2	–	–	1.5 ± 3.0	1.0 ± 2.0	1.3 ± 2.5	–	0.8 ± 1.5	–
Geocenamus (Geoc)	3	–	–	–	–	–	0.5 ± 1.0	–	–
Gracilacus (Grac)	2	–	5.3 ± 6.2	–	0.8 ± 1.5	–	–	–	–
Helicotylenchus (Heli)	3	40.8 ± 25.9	–	12.5 ± 11.6	–	30.0 ± 44.0	70.8 ± 43.2	44.3 ± 19.9	38.3 ± 9.1
Malenchus (Male)	2	33.3 ± 19.6	73.5 ± 21.7	14.5 ± 9.7	53.8 ± 19.8	10.3 ± 11.4	16.0 ± 4.2	26.8 ± 11.1	57.8 ± 24.5
Paratylenchus (Para)	2	14.5 ± 17.1	6.3 ± 7.3	59.3 ± 25.8	57.3 ± 22.4	1.5 ± 1.3	7.5 ± 3.9	–	9.8 ± 7.2
Pratylenchus (Prat)	3	10.8 ± 8.2	–	1.5 ± 3.0	0.8 ± 1.5	1.8 ± 2.1	21.8 ± 23.4	9.5 ± 9.5	21.5 ± 7.6
Psilenchus (Psil)	2	22.0 ± 13.5	4.0 ± 5.7	–	1.5 ± 1.9	–	–	–	8.0 ± 11.3
Rotylenchus (Roty)	3	6.8 ± 4.5	–	9.8 ± 8.2	0.5 ± 1.0	3.8 ± 4.5	13.0 ± 5.1	8.8 ± 4.0	0.5 ± 1.0
Tylenchorhynchus (Tyle)	3	1.0 ± 2.0	1.3 ± 2.5	–	–	1.0 ± 2.0	0.5 ± 1.0	–	–
Xiphinema (Xiph)	5	–	0.3 ± 0.5	–	0.5 ± 1.0	–	–	–	–
Trichodorus (Tric)	4	–	–	0.5 ± 1.0	–	–	–	–	–
Omnivores									
Aporcelaimellus (Apor)	5	–	–	–	–	0.5 ± 1.0	3.0 ± 3.2	–	–
Eudorylaimus (Eudo)	4	5.8 ± 6.6	8.3 ± 5.6	0.8 ± 1.5	2.3 ± 1.0	14.5 ± 15.2	25.5 ± 22.7	0.8 ± 1.5	11.8 ± 5.7
Mesodorylaimus (Meso)	4	1.5 ± 1.9	1.8 ± 2.1	–	–	–	2.5 ± 3.3	–	–
Thonus (Thon)	4	–	–	–	–	1.0 ± 1.4	–	–	–
Axonchium (Axon)	5	–	–	0.3 ± 0.5	0.3 ± 0.5	–	–	–	–
Predators									
Anatonchus (Anat)	4	0.3 ± 0.5	2.5 ± 3.8	–	–	0.5 ± 1.0	1.3 ± 2.5	–	–
Mylonchulus (Mylo)	4	1.0 ± 0.8	4.0 ± 2.9	–	0.3 ± 0.5	1.3 ± 1.0	0.3 ± 0.5	–	0.5 ± 1.0
Oxydirus (Oxyd)	5	–	–	–	–	0.3 ± 0.5	–	–	–
Tripyla (Trip)	3	–	–	–	0.5 ± 1.0	0.3 ± 0.5	0.3 ± 0.5	–	–
Number of genera		**28**	**28**	**25**	**26**	**31**	**31**	**18**	**21**

activities, amount of gram-negative bacteria and altered the microbial community structure (Stefanowicz et al., 2016; Gaggini et al., 2018). In contrast, the positive effect of alien plants (*Erigeron annuus* and *Solidago canadensis*) on the abundance, the richness and diversity of soil fungal communities was shown (Wang et al., 2018). The recent meta-analysis of possible pathways influence of invasion plants on soil biota has found the neutral impact on soil microbial biomass carbon (Zhang et al., 2019). Consequently, the positive, negative and neutral effects of exotic plants on soil microbial properties are possible. In our study all these types of effects have caught. In the autumn period, soil BR rate of the invaded plots was lower in forest and higher in grassland compared to the uninvaded. The soil BR is index of the organic matter decomposition rate and characterises the nutrients acquisition and biogeochemical C cycle. It is shown the impact directions of invasion species on soil properties are strongly determined by its initial nutrient status. The significant negative impacts were observed in rich

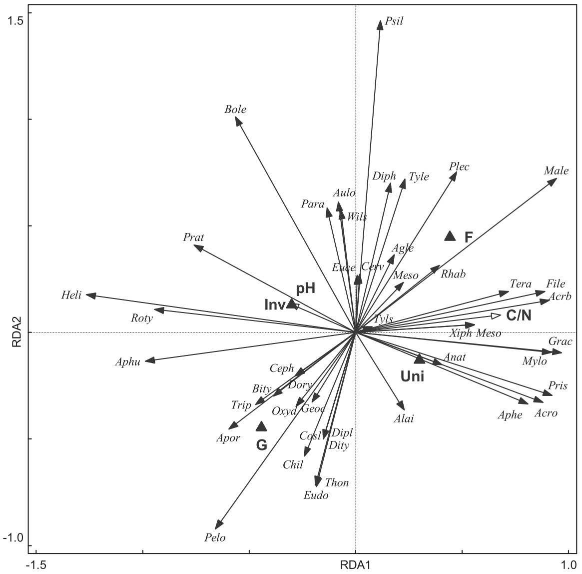

Fig. 1. RDA ordination diagram of the nematode communities in the samples from autumn 2017 with the explanatory variables soil pH, C/N, ecosystem, and invasion status. F, forest; G, grassland; Inv, invaded; Uni, uninvaded. Quantitative and nominal variables are plotted as arrows with white heads and as black triangles, respectively, and nematode genera are plotted as arrows with black heads (see Table 3 for abbreviations). The eigenvalues for axes 1 and 2 are 0.35 and 0.12, respectively (47% of the cumulative variance explained).

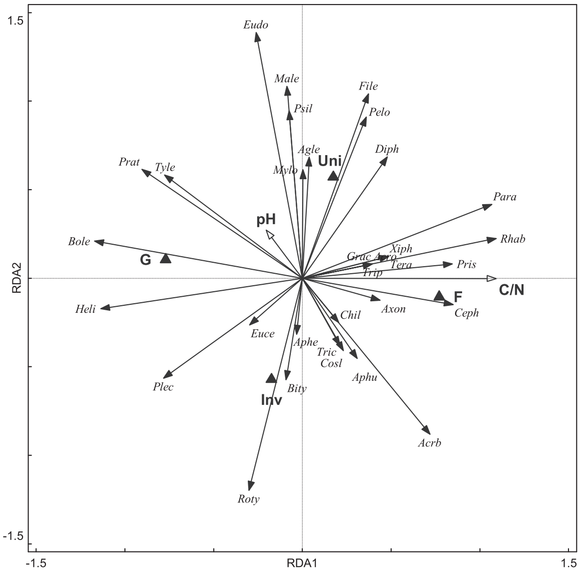

Fig. 2. RDA ordination diagram of the nematode communities in the samples from spring 2018 with the explanatory variables soil pH, C/N, ecosystem, and invasion status. F, forest; G, grassland; Inv, invaded; Uni, uninvaded. Quantitative and nominal variables are plotted as arrows with white heads and as black triangles, respectively, and nematode genera are plotted as arrows with black heads (see Table 3 for abbreviations). The eigenvalues for axes 1 and 2 are 0.41 and 0.15, respectively (55% of the cumulative variance explained).

nutrient sites, while positive impacts appeared at the opposite conditions (Dassonville et al., 2008). The high soil nutrient status and quality of organic matter (high C/N ratio) were observed in the forest ecosystem in contrast to the grassland (Table 1). Also, we suggested that in the autumn period the basal respiration was more sensitive to *H. sosnowskyi* invasion, since at the end of the vegetation season its impact may be stronger compared to the native plant community.

Our study revealed, that the impact of *H. sosnowskyi* invasion was more pronounced on the composition of the nematode than on microbial communities. Nematode abundance decreased by *H. sosnowskyi* invasion, consistent with the results by Renčo and Baležentiené (2015) from three habitats invaded by *H. sosnowskyi*, abandoned land, grassland roadside slope, and forest edge. Nematode diversity was nevertheless not affected by *H. sosnowskyi* in either of our habitats, supporting the results by Renčo et al. (2019) from four habitats invaded by *H. sosnowskyi* in Poland.

The decrease in nematode abundance in the plots invaded by *H. sosnowskyi* was particularly caused by a decrease in the number of several herbivorous nematodes, which 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 can well characterise the variations in nematode communities due to changes in plant communities (Viketoft et al., 2005). Renčo and Baležentiené (2015) and Renčo et al. (2019) similarly found decreases in herbivore abundance in soil after the establishment of *H. sosnowskyi* in some habitats of Latvia and Poland, which were attributed to root systems on which plant parasitic nematodes cannot feed or to the release of toxic furanocoumarins to the surrounding environment (Jahodová et al., 2007a). In contrast, the well-developed root system, high nutrient-use efficiency, and high biomass production of the invasive plant *S. gigantea* (Scharfy et al., 2009) were attributed to the increased abundance of herbivorous nematodes in invaded plots (Čerevková et al., 2019). Some nematode taxa in our study such as *Helicotylenchus*, *Rotylenchus*, and *Paratylenchus* were nevertheless more abundant in the plots invaded by *H. sosnowskyi*, especially in the forest habitat, inconsistent with the results by Renčo and Baležentiené (2015).

The abundances of both omnivorous and predaceous nematodes decreased under *H. sosnowskyi* invasion and were thus responsible for the lower nematode abundance in the invaded than the uninvaded plots, partially supporting the results by Renčo et al. (2019) but contradicting the results by Liang et al. (2007), Renčo and Baležentiené (2015), and Čerevková et al. (2019). Omnivorous and predatory nematodes are considered to be more sensitive to environmental disturbance due to their long generation times and low fecundities (Bongers, 1990; Ferris et al., 2001). De Deyn et al. (2004), however, reported that changes in plant communities, root diversity, and biomass production did not affect the abundance of nematodes of higher trophic groups such as predators and omnivores. Because the predators are feeding on bacterivores or fungivores, and often unknown feeding strategies of omnivores it might explain why the predators and omnivores still show a weak response to plant invasion. Nevertheless, the weaker response of the predators and omnivores than of the herbivores is in line with predictions based on a larger variety of belowground species diversity (Scherber et al., 2010).

Bacterivores and fungivores belong to other trophic groups that should be affected by changes in plant composition. We assumed that these groups were most likely to benefit from plant invasion, because increases in ground litter and decaying vegetation associated with many invasive plants can provide more food and preferred microclimatic conditions (Longcore, 2003; Levin et al., 2006). The rate of litter decomposition can also be higher in invaded areas (Standish et al., 2004), because chemical properties may differ between dead and living vegetation. The abundances of bacterivores and fungivores that feed on soil microbes differed little in our study, supported by only limited differences in microbial properties between the invaded and uninvaded plots. CI, based on the abundance of bacterial- and fungal-feeding opportunistic nematodes, was <50% in all plots (invaded and uninvaded) in our study. This low value of CI (<50%) indicating a stronger bacterial contribution to decomposition in soil under *H. sosnowskyi* invasion and under native vegetation in habitats of Russia. Similar CIs (<50%) for *S. gigantea* invasion were reported by Renčo et al. (2019) and Čerevková et al. (2019).

The low MI and $\sum$MI (2.0–2.6) in our study, with small differences between habitats and invasion status, indicated a disturbed environment (Bongers, 1990). PPI for the herbivorous nematodes was significantly higher in the invaded than the uninvaded plots in the spring samples and in FHs than F in the autumn samples, perhaps because their abundance was determined mostly by the host plants. The low PPIs (2.2–2.4) for all plots was associated with a high proportion of Tylenchidae (c-p2) in the nematode assemblage and indicate nutrient-poor conditions of natural ecosystems (Bongers, 1990). SI was significantly lower in the invaded than the uninvaded plots (except for FHs compared to F in the autumn samples), and EI was relatively high in all plots, indicating an N-enriched, highly disturbed environment with a low C/N ratio (Ferris et al., 2001).

5. Conclusion

This study provides insights into the impact of *H. sosnowskyi* invasion on the soil microbial and nematode communities in two ecosystems, grassland and forest, measured in the spring and autumn. The microbial and nematode communities generally differed considerably between the forest and grassland soils. Invasion by *H. sosnowskyi* into both habitats significantly affected the nematode communities but had less of an effect on soil microbial activity. These changes were much greater in the spring than the autumn samples. Stress-sensitive omnivores and herbivores best represented the changes in the nematode communities under the influence of *H. sosnowskyi* invasion in both habitats. The abundances of several herbivorous genera, *Helicotylenchus*, *Rotylenchus*, and *Paratylenchus*, however, were higher in the invaded than the uninvaded plots (especially in FHs compared F), potentially indicating a host-enemy relationship with *H. sosnowskyi* with the roots of trees and native herbs.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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