

Diversity and structure of soil nematode communities under *Heracleum sosnowskyi* pressure: latitudinal and invasion-driven variations

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Summary. Soil nematode communities under invasion by *Heracleum sosnowskyi* Manden. (Sosnowsky's hogweed) were studied in habitats of different latitudinal locations. The research was conducted in four hogweed sites located between 61° and 55° N, in the Republic of Karelia (Shuya and Essoila villages), and the Leningrad and Moscow Regions. Soil samples were collected beneath dense *H. sosnowskyi* stands and in adjacent control meadows that were not invaded. The structure of soil nematode communities in hogweed habitats was characterised by the dominance of omnivorous nematodes and plant-associated nematodes (Shuya village), as well as bacterial feeders and omnivores (Essoila village) in Karelia; by a high proportion of bacterial feeders and plant parasites in the Leningrad Region; and by the dominance of bacterial- and fungal feeders in the Moscow Region. Plant invasion altered the ratio of trophic groups in the nematode communities: statistically significant changes were detected in the abundance of bacterial feeders (increased under hogweed), fungal feeders, and plant-associated nematodes (both decreased under hogweed). However, the total number of identified nematode taxa remained almost unchanged, indicating that the introduction of a non-native plant species into local ecosystems did not lead to a substantial decrease in diversity of soil nematodes. RDA analysis showed that the studied abiotic and biotic factors – habitat type (hogweed/meadow) as an indicator of invasion impact, pH, total carbon and nitrogen, available phosphorus, and potassium – had a significant influence on nematode community parameters. The combination of these factors explained about 50% of the variation in nematological characteristics. Notably, latitude had no significant effect on the overall variability of nematode indices, emphasising the predominance of invasion effects over geographic position.

Keywords: community structure, environmental factors, latitude gradient, meadow vegetation, plant invasions, population density, RDA analysis, soil nematodes, taxonomic diversity.

The problem of plant invasions and the displacement of native flora and fauna by alien species is a global issue. In Northern and Central Russia, as well as in some European countries, particular attention is given to the invasive Caucasian species *Heracleum sosnowskyi* Manden. (EPPO Bulletin, 2009). Sosnowsky's hogweed is an aggressive invader, representing a clear example of the expansion of non-native species into new habitats and ecological niches (Antipina & Shuiskaya, 2009; Baležentienė & Bartkevičius, 2013). Established colonies of hogweed can almost totally replace the natural vegetation and threaten biodiversity, including fauna associated with native plants, building a 'giant hogweed landscape' (Nielsen *et al.*, 2005). This plant can cause

photochemical dermatitis and poses a serious threat to human health (Vinogradova *et al.*, 2010).

Plant invasion is a major component of environmental change and can significantly alter the soil biological activities that are essential for organic matter decomposition and nutrient cycling in terrestrial ecosystems (Liao *et al.*, 2008; Castro-Díez *et al.*, 2014; Pearson *et al.*, 2024; Negesse *et al.*, 2025). However, the relationship between plant invasion and soil biota remains unclear and often exhibits contrasting trends.

Among multicellular soil biota, nematodes are the most abundant and diverse group. Their ubiquitous distribution, large number of species with various feeding types, and occupation of multiple trophic levels in the soil food web make

nematodes a good indicator of environmental conditions and soil disturbances (Bongers, 1990; Ferris *et al.*, 2001).

In recent years, there has been a growing interest among scientists worldwide in studying soil nematode communities under the influence of plant species invasions; however, the results of these studies often appear to be contradictory. Previous studies have shown that during plant invasions, soil nematode abundance may increase (Chen *et al.*, 2007), decrease (Fitoussi *et al.*, 2016; Čerevková *et al.*, 2020), or remain unchanged (Yeates & Williams, 2001). Likewise, nematode diversity may decrease (Renčo & Baležentienė, 2015; Lozzaro *et al.*, 2018; Tóth & Korponai, 2025) or remain stable (Jakubcsiková *et al.*, 2024). Plant invasions have also been associated with the emergence of new nematode taxa (Yeates & Williams, 2001). The abundance of plant-parasitic nematodes has been reported to either decline or increase under invasion (Yeates & Williams, 2001; Morriën *et al.*, 2012; Renčo & Baležentienė, 2015; Čerevková *et al.*, 2020). The restructuring of nematode communities has been linked mainly to shifts in the proportions of bacterial feeders, omnivores, and plant-associated nematodes or plant parasites (Renčo & Baležentienė, 2015; Čerevková *et al.*, 2020; Tóth & Korponai, 2025). In the conditions of Karelia, we also investigated the response of soil nematode communities to the invasion of *Heracleum sosnowskyi*, but only at two locations; the results revealed no significant differences in nematode abundance or diversity (Sushchuk *et al.*, 2025). Here, we integrate these data with additional sites to allow analysis of a unified dataset, enabling the identification of general patterns in nematode community responses to invasion and the key factors driving them.

The diversity and composition of above- and below-ground communities may change differently along biogeographic gradients. For instance, a study on the invasive plant *Alternanthera philoxeroides* (Mart.) Griseb. across a 1700 km latitudinal gradient demonstrated that differences in soil fungal community composition between adjacent invaded and uninvaded sites increased with increasing latitude, while differences in above-ground arthropod communities remained constant (Gao *et al.*, 2024). The role of latitude in shaping soil nematode communities has been analysed previously, both globally (Procter, 1984; Boag & Yeates, 1998; Nielsen *et al.*, 2014; Kerfahi *et al.*, 2016; Song *et al.*, 2017; van den Hoogen *et al.*, 2019) and regionally (Neher *et al.*, 1998; Sohlenius & Boström, 1999). However, the effects of plant

invasion on native soil nematode communities have mostly been investigated at single localities. In this context, the study of nematode-plant relationships across a 2000 km latitudinal transect involving four range-expanding plant species in Europe (Wilschut *et al.*, 2019) is of particular importance. The authors reported latitudinal differences in nematode community composition, while taxonomic richness and abundance remained unchanged. They also noted that plant species identity was a stronger predictor of nematode community composition than abiotic environmental variables. Thus, the issue of whether communities of below-ground organisms exhibit similar or different responses to plant invasion across biogeographic gradients has received limited attention. The first attempt to analyse latitudinal patterns in soil nematode community changes in habitats invaded by *H. sosnowskyi* was undertaken by our research group (Sushchuk *et al.*, 2024). However, that study focused on a limited set of nematological parameters, did not incorporate soil properties, and lacked a comparative analysis with non-invaded (control) habitats; therefore, the invasion factor itself was not explicitly assessed. The dataset presented in Sushchuk *et al.* (2024) forms the basis of the present study and is here substantially expanded and re-analysed to provide a comprehensive assessment of nematode community responses and to address a broader range of ecological questions.

The diversity of combinations of abiotic environmental factors affecting soil biota, such as soil texture, moisture, pH, and the content of mineral and organic substances, largely determines the behaviour, development and reproduction, composition and structure of soil-dwelling organisms (Solov'eva, 1986). Nevertheless, soil nematode communities often exhibit inconsistent responses to soil properties, suggesting a strong specificity to local conditions (Vonk *et al.*, 2013). Invasive plants are often associated with greater soil pools of organic matter and increased rates of litter decomposition and nutrient cycling than native plant species (Liao *et al.*, 2008; Castro-Díez *et al.*, 2014; Negesse *et al.*, 2025). However, the effect of invasive plants on soil properties is not consistent and the magnitude as well as the direction of the effect can depend on numerous variables related to the plant species and/or ecosystem characteristics. For example, nutrient concentrations have been observed to increase in invaded plots with low initial fertility, and to decrease in sites with high initial nutrient levels (Dassonville *et al.*, 2008).

Thus, the present study aims to answer the

following questions:

- Do soil nematode communities change following the invasion of *Heracleum sosnowskyi* into meadow ecosystems?
- Will be the changes in nematode communities in response to hogweed invasion be consistent among four habitats differing in latitude?
- What is the role of abiotic environmental factors in shaping nematode communities under plant invasion?

MATERIAL AND METHODS

Study area. The study was carried out at four localities representing habitats of *H. sosnowskyi* with different latitudinal positions. An area that was not yet colonised by the invasive plant was chosen in proximity to the corresponding invaded one. Thus, each habitat was characterised by invaded and comparable non-invaded control meadow areas.

The locations for the nematological survey were selected as follows:

Site 1 – Shuya village, roadside (Prionezhsky district, Republic of Karelia; 61°52' N, 34°14' E);

Site 2 – Essoila village, abandoned farmland (Pryazhinsky district, Republic of Karelia; 61°49' N, 33°09' E);

Site 3 – Leningrad Region, roadside near the highway (60°05' N, 32°23' E);

Site 4 – Moscow Region, private abandoned agricultural field (55°37' N, 36°28' E).

In each of the four study locations, *H. sosnowskyi* formed dense monospecific stands with 100% cover. According to the geobotanical description, the herbaceous layer of the control meadow in Essoila village consisted of species belonging to the family Poaceae, as well as *Taraxacum officinale* F.H. Wigg., *Aegopodium podagraria* L., *Trifolium pratense* L., *Vicia cracca* L., and *Ranunculus* sp. The herbaceous layer of the meadow in Shuya village included species of the family Poaceae, *Alchemilla* sp., *Achillea millefolium* L., and *Anthriscus* sp. In the control meadow of the Leningrad Region, species of the Poaceae family dominated, forming a dense turf, while *Cirsium arvense* (L.) Scop., a ruderal plant, occurred sporadically. The meadow in the Moscow Region was composed of Poaceae, *Leucanthemum vulgare* Lam., *Achillea millefolium* L., *Taraxacum officinale* F.H. Wigg., *Galium* sp., and *Stellaria* sp.

Sampling and extraction of nematodes. Soil samples were taken randomly from uniform vegetation plot (2 × 2 m) in the invaded area and the adjacent non-invaded meadow using a soil auger (20 mm diam.) with sampling to 0–15 cm depth with

nine replications in sites 1–3 (both hogweed and meadow) and site 4 (hogweed), and seven replications in site 4 (meadow). Nematodes were extracted from a 30 g soil aliquot by a modified Baermann funnel method over 48 h. Extracted nematodes were fixed in TAF (triethanolamine : formalin : water, 2 : 7 : 91) (van Bezooijen, 2006). Temporary glycerol microslides were made for nematode identification. At least 100 nematode specimens from each sample were identified to genus using light microscopy (Olympus CX41).

Nematological analysis. The taxonomic structure of nematodes was determined in accordance with the classification of De Ley and Blaxter (2004) and Abebe *et al.* (2006). The parameters used for the analysis of the nematode fauna were: taxonomic diversity (number of genera), Shannon index H' gen, Simpson dominance index C (Odum, 1975), nematode population density (abundance) (indiv. (100 g fresh soil)^{−1}), and trophic structure of nematode communities. The feeding grouping of nematodes was based on the classification suggested by Yeates *et al.* (1993a, b), with division into six trophic groups: bacterial feeders (B), fungal feeders (F), omnivores (Om), predators (Pr), nematodes associated with plants (Asp), and plant-parasitic nematodes (Pp).

The maturity index ΣMI was calculated for nematode communities as a metric of the ecosystem condition based on the composition and ratio of nematode taxa. Nematode species have different ecological preferences related to their morphology, biology and ecology, which are expressed as values given to each taxon on the c-p scale of Bongers (1990): from 1 for colonisers, tolerant of adverse habitat conditions, to 5 for persisters, sensitive to environmental impacts.

The analysis also included indices introduced by Ferris *et al.* (2001). Integration of the taxon's feeding group (Yeates *et al.*, 1993a) and the value (1 to 5) on the c-p scale (Bongers, 1990) by authors of this concept resulted in a grouping into 'functional guilds' representing the ecological specialisations of the nematodes within trophic groups. The functional guilds are the basis for calculating the ecological indices that characterise the soil food web and help assess the condition of the habitat for nematodes as soil-inhabiting organisms. These were the Structure (SI) and Enrichment (EI) indices and the index for the predominant pathway for organic matter decomposition in soil (Channel index, CI) (Ferris *et al.*, 2001).

Statistical analysis. The statistical analyses were performed separately for each habitat and data compared between invaded areas and non-invaded

Table 1. Soil properties of habitats invaded by *Heracleum sosnowskyi* and control meadows.

Locations	Biotope	pH H ₂ O	pH KCl	C tot., %	N tot., %	P avail., %	K avail., mg kg ⁻¹	N-NO ₃ ⁻ , mg kg ⁻¹ soil
Republic of Karelia, Shuya village	Hogweed	5.30	5.46	15.76	0.30	0.029	200	66
	Meadow	5.80	5.83	21.82	0.41	0.029	140	39
Republic of Karelia, Essoila village	Hogweed	5.68	5.00	7.98	0.26	0.031	110	24
	Meadow	5.64	5.37	11.92	0.37	0.040	366	41
Leningrad Region	Hogweed	7.23	6.71	2.37	0.23	0.047	774	26
	Meadow	6.89	6.43	3.42	0.27	0.047	392	19
Moscow Region	Hogweed	6.71	6.09	2.76	0.21	0.013	367	29
	Meadow	6.18	5.42	4.23	0.13	0.014	316	9

Note. pH H₂O – soil pH in water; pH KCl – soil pH in potassium chloride; C tot., % – total carbon; N tot., % – total nitrogen; P avail., % – available phosphorus; K avail., mg kg⁻¹ – available potassium; N-NO₃⁻, mg kg⁻¹ soil – nitrate nitrogen.

control meadows. Additionally, pooled samples representing combined data from all studied locations were analysed using the same approach. Statistical data processing was performed using the Mann-Whitney U-test. Differences between groups were considered statistically significant at $P < 0.05$ or $P < 0.01$. Numerical data are given as $M \pm SE$ (mean $\pm$ standard error). Statistical analyses were performed using PAST version 5.3 (Hammer *et al.*, 2001).

Redundancy analysis (RDA) was used to examine the relationships between two datasets: response (nematological parameters) variables and explanatory (environmental factors) variables. The following environmental factors were included in the analysis: habitat type (hogweed-invaded or non-invaded (meadows) plots, 'Location'), latitude (Lat), soil pH (measured in water and KCl extracts; pH_{H₂O} and pH_{KCl}), total carbon (C) and nitrogen (N), available phosphorus (P) and potassium (K), and nitrate nitrogen (N-NO₃). Due to the deviation from normality detected by the Shapiro-Wilk test, all variables were log₁₀-transformed prior to analysis. The significance of canonical axes obtained from RDA was assessed using the `anova.cca()` function in the `vegan` package (R software) with a permutation test (999 permutations) (R Core Team, 2020). Differences were considered statistically significant at $P < 0.05$.

Chemical analysis. Soil properties were analysed by conventional methods (Arinushkina, 1970). The following parameters were estimated: pH (H₂O) and pH (KCl) was determined

potentiometrically (pH meter Hanna), total carbon content (C tot., %) by Tyurin's combustion method with spectrophotometric detection (SF-2000 spectrophotometer, Russia), total nitrogen content (N tot., %) – by Kjeldahl digestion with titrimetric and spectrophotometric detection, available phosphorus (P avail., %) and available potassium (K avail., mg kg⁻¹) by Kirsanov method with spectrophotometric detection (phosphorus) (SF-2000 spectrophotometer, Russia) and with atomic emission detection (potassium) (flame atomic spectrophotometer, Shimadzu AA 7000, Japan), nitrate nitrogen (N-NO₃⁻, mg kg⁻¹ soil) – potentiometrically (Anion-4100, Russia). Chemical analyses were conducted in the Analytical Laboratory of Forest Research Institute, Karelian Research Centre of the Russian Academy of Sciences.

Research on soil nematodes was carried out using equipment of the Core Facility of the Karelian Research Centre of the Russian Academy of Sciences.

RESULTS

Soil chemical properties. Control meadow soils were characterised by higher contents of carbon (in all locations, to varying degrees) and nitrogen (in three locations), as well as lower concentrations of available potassium and nitrate nitrogen (in three locations) compared with soils under *H. sosnowskyi*. The highest carbon and nitrogen contents were recorded in the meadow soil of Shuya village. The lowest pH (KCl) values and potassium

Table 2. Nematode abundance and fauna diversity in habitats invaded by *Heracleum sosnowskyi* and in control meadows.

Parameters	Sites invaded by hogweed	Control meadow	Significance
Republic of Karelia, Shuya village			
Abundance, indiv. (100 g soil) ⁻¹	1639 ± 242	1777 ± 196	—
H'gen	2.94 ± 0.13	2.80 ± 0.07	—
Index C	0.08 ± 0.02	0.10 ± 0.01	—
Republic of Karelia, Essoila village			
Abundance, indiv. (100 g soil) ⁻¹	2758 ± 417	1748 ± 172	—
H'gen	2.47 ± 0.22	2.19 ± 0.11	—
Index C	0.12 ± 0.04	0.17 ± 0.02	—
Leningrad Region			
Abundance, indiv. (100 g soil) ⁻¹	2097 ± 173	1694 ± 325	—
H'gen	2.61 ± 0.08	2.95 ± 0.09	**
Index C	0.12 ± 0.01	0.07 ± 0.01	**
Moscow Region			
Abundance, indiv. (100 g soil) ⁻¹	2393 ± 155	708 ± 111	**
H'gen	2.66 ± 0.06	2.93 ± 0.10	*
Index C	0.11 ± 0.01	0.08 ± 0.01	—
Pooled samples			
Abundance, indiv. (100 g soil) ⁻¹	2222 ± 146	1482 ± 122	**
H'gen	2.67 ± 0.09	2.72 ± 0.08	*
Index C	0.11 ± 0.01	0.10 ± 0.01	—

Note. Data are given as $M \pm SE$ (mean $\pm$ standard error); * $P < 0.05$, ** $P < 0.01$, significant differences between the same control and invaded areas (Mann-Whitney U-test was applied). H'gen – Shannon index; C – Simpson dominance index. Pooled samples represent combined data from all studied locations for each habitat type (applies to Tables 2, 4 & 5).

concentrations were detected in the soils under hogweed stands in Essoyla. In general, soils in Karelia exhibited lower pH values and higher carbon and nitrogen contents compared to other regions under study. Sites in the Leningrad Region were distinguished by higher levels of available phosphorus and potassium, while those in the Moscow Region had the lowest total nitrogen and available phosphorus contents (Table 1).

Nematode population density and taxonomic diversity. The total abundance of soil nematodes was higher under *H. sosnowskyi* than in control meadow soils at three of the four locations; however, the difference was statistically significant only for the Moscow Region (Mann-Whitney U-

test, $P < 0.01$) and in the pooled comparison of all locations ($P < 0.01$) (Table 2). The highest nematode abundance overall was recorded in the hogweed site in Shuya. Soil nematode diversity under *H. sosnowskyi* ranged from 20 (Essoyla, Karelia) to 31 (Shuya, Karelia; Leningrad Region) genera. The number of genera did not differ significantly between hogweed and meadow sites, except in the Moscow Region, where a slight decrease was observed (27 vs 31). However, in the Leningrad and Moscow Regions, nematode taxonomic diversity, measured by the Shannon index (H'gen), was significantly higher in meadows than under *H. sosnowskyi* (Tables 2 & 3). The Shannon index H'gen integrates both species/genus

Table 3. Mean relative abundance (%) of soil nematode taxa in habitats invaded by *Heracleum sosnowskyi* and in control meadows.

Taxa	Functional guild	Sh Hs	Sh Cont	Es Hs	Es Cont	LR Hs	LR Cont	MR Hs	MR Cont
Order Enoplida Filipjev, 1929									
Family Alaimidae Micoletzky, 1922									
<i>Alaimus</i> De Man, 1880	B4	0.9	1.1	1.2	0	0.2	1.5	0.5	0.7
Order Triplonchida Cobb, 1920									
Family Diphtherophoridae Micoletzky, 1922									
<i>Diphtherophora</i> de Man, 1880	F3	2.1	2.6	0	0	5.1	3.4	0	0.2
Family Prismatolaimidae Micoletzky, 1922									
<i>Prismatolaimus</i> de Man, 1880	B3	0	0	0	0	0	0.1	0	0
Order Dorylaimida Pearse, 1942									
Family Tylencholaimellidae Jairajpuri, 1964									
<i>Doryllium</i> Cobb, 1920	F4	2.4	4.6	0	0	0	9.0	0	1.8
Family Dorylaimidae de Man, 1876									
<i>Mesodorylaimus</i> Andrassy, 1959	Om5	4.7	0	0.5	0	0.3	0.6	0.6	1.1
<i>Prodorylaimium</i> Andrassy, 1969	Om4	15.9	0.3	0	0	0	0	0	0
Family Qudsianematidae Jairajpuri, 1963									
<i>Eudorylaimus</i> Andrassy, 1959	Om4	4.1	9.1	20.5	27.0	7.2	6.5	3.1	5.8
<i>Epidorylaimus</i> Andrassy, 1986	Om4	1.9	2.4	0	0	0	0	0	0
Family Aporcelaimidae Heyns, 1965									
<i>Aporcelaimellus</i> Heyns, 1965	Om5	0	0.2	0	0.2	0.2	0.4	0	2.8
Order Mononchida Jairajpuri, 1969									
Family Mononchidae Chitwood, 1937									
<i>Clarkus</i> Jairajpuri, 1970	Pr4	0	1.0	0	0	0	0	2.5	1.4
<i>Prionchulus</i> Cobb, 1916	Pr4	0	0	0	0	0.1	0	0	0
Family Mylonchulidae Jairajpuri, 1969									
<i>Mylonchulus</i> Cobb, 1916	Pr4	1.6	1.3	0	0	0.1	0	0	0.7
Order Chromadorida Chitwood, 1933									
Family Achromadoridae Gerlach & Riemann, 1973									
<i>Achromadora</i> Cobb, 1913	B2	0	0	0	0	0	1.5	0.7	0
Order Desmodorida De Coninck, 1965									
Family Desmodoridae Filipjev, 1922									
<i>Prodesmodora</i> Micoletzky, 1923	B2	0	0	0	0	0	8.2	0	0
Order Monhysterida Filipjev, 1929									
Family Monhysteridae De Man, 1876									
<i>Eumonhystera</i> Andrassy, 1981	B2	0	0.2	0	0	0.3	2.9	0.3	0.4
Order Araeolaimida De Coninck & Stekhoven, 1933									
Family Diplopeltidae Filipjev, 1918									
<i>Cylindrolaimus</i> De Man, 1880	B3	0	0	0	0	0	0	2.8	0
Order Plectida Malakhov, 1982									
Family Plectidae Örley, 1880									
<i>Plectus</i> Bastian, 1865	B2	3.1	5.3	0.7	0.6	4.6	12.5	2.3	6.2
<i>Anaplectus</i> De Coninck & Stekhoven, 1933	B2	0	0	9.8	0.2	0	0	0	0
<i>Wilsonema</i> Cobb, 1913	B2	0	0	0	0	1.2	0.4	0.3	0
Order Rhabditida Chitwood, 1933									
Family Panagrolaimidae Thorne, 1937									
<i>Panagrobelus</i> Thorne, 1939	B1	0.1	0	0	0	0	0	0	0
<i>Panagrolaimus</i> Fuchs, 1930	B1	0.5	1.9	0.5	2.4	0.3	0	1.0	1.7

Table 3 (continued). Mean relative abundance (%) of soil nematode taxa in habitats invaded by *Heracleum sosnowskyi* and in control meadows.

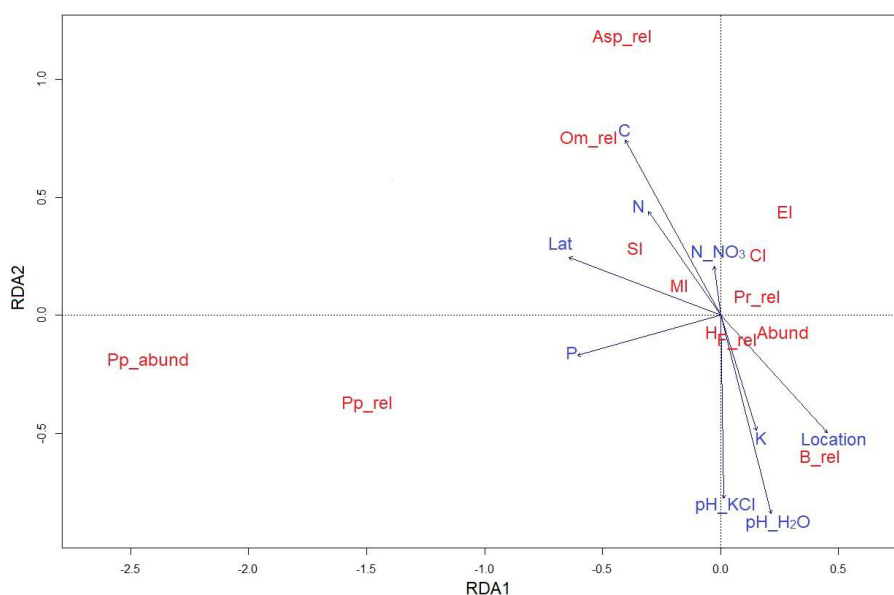
Taxa	Functional guild	Sh Hs	Sh Cont	Es Hs	Es Cont	LR Hs	LR Cont	MR Hs	MR Cont
Family Cephalobidae Filipjev, 1931									
<i>Acrobeloides</i> Cobb, 1924	B2	1.6	0.2	1.1	1.7	21.8	7.3	16.9	10.3
<i>Acrobeles</i> von Linstow, 1877	B2	0	0	0	0	1.7	1.8	0	0
<i>Cephalobus</i> Bastian, 1865	B2	8.0	4.2	3.4	4.1	0	0.4	0.1	0.7
<i>Cervidellus</i> Thorne, 1937	B2	0	0	0	0	5.4	5.7	18.4	0.2
<i>Chiloplacus</i> Thorne, 1937	B2	0.7	1.7	6.4	3.3	1.6	0.3	3.4	0.2
<i>Eucephalobus</i> Steiner, 1936	B2	4.1	3.0	7.4	5.3	9.6	4.7	17.3	6.7
<i>Heterocephalobus</i> Brzeski, 1960	B2	0	0.2	0	0	0	0.1	0	0
Family Rhabditidae Örley, 1880									
<i>Diploscapter</i> Cobb, 1913	B1	0	0	0	0	0	0	0	0.2
<i>Rhabditis</i> Dujardin, 1845	B1	1.5	1.6	11.8	0	3.0	2.0	9.6	0
<i>Mesorhabditis</i> Osche, 1952	B1	0.1	0.2	1.6	2.8	0	0	0	0
Family Diplogastridae Micoletzky, 1922									
Diplogastridae sp. Micoletzky, 1922	B1	0	0	0	0	0	0	1.5	0.3
Family Tylenchidae Örley, 1880									
<i>Boleodorus</i> Thorne, 1941	Asp2	0	0.6	0	0	0	0	0	0
<i>Filenchus</i> Andrassy, 1954	Asp2	8.0	5.3	0.4	1.2	1.1	3.0	1.6	3.4
<i>Malenchus</i> Andrassy, 1968	Asp2	1.8	0.6	1.1	0.4	0.4	0.7	1.0	2.1
<i>Aglenchus</i> Andrassy, 1954	Asp2	8.7	19.2	17.2	26.2	1.2	0.8	0.4	0.3
<i>Coslenchus</i> Siddiqi, 1978	Asp2	1.4	3.5	0	0.9	0.9	0.4	1.6	4.5
<i>Lelenchus</i> Andrassy, 1954	Asp2	0.4	0.7	0	0	0.6	0	0.8	1.4
<i>Tylenchus</i> Bastian, 1865	Asp2	0.7	0	0	0	0	0	0	0
Family Anguinidae Nicoll, 1935									
<i>Ditylenchus</i> Filipjev, 1936	F2	1.1	0.6	1.6	1.2	0.9	1.8	7.3	20.5
Family Dolichodoridae Chitwood in Chitwood & Chitwood, 1950									
<i>Tylenchorhynchus</i> Cobb, 1913	Pp3	1.1	0.3	0	0	22.6	9.7	0	0
Family Merliniidae Siddiqi, 1971									
<i>Geocenamus</i> Thorne & Malek, 1968	Pp3	0	0	0	0	0	0	0	4.5
<i>Nagelus</i> Thorne & Malek, 1968	Pp3	1.6	4.2	0	0	1.0	0.5	0	0
Family Tylenchulidae Skarbilovich, 1947									
<i>Paratylenchus</i> Micoletzky, 1922	Pp2	0.8	0	8.3	1.1	0.4	0	0.2	6.8
Family Pratylenchidae Thorne, 1949									
<i>Pratylenchus</i> Filipjev, 1936	Pp3	0.3	0	3.5	5.8	0.9	2.1	0	3.2
Family Hoplolaimidae Filipjev, 1934									
<i>Helicotylenchus</i> Steiner, 1945	Pp3	14.3	18.7	0	0	2.0	9.0	0	1.3
Family Aphelenchoididae Skarbilovich, 1947									
<i>Aphelenchoides</i> Fischer, 1894	F2	1.5	1.2	0.5	2.0	2.9	2.0	1.0	5.9
Family Aphelenchidae Fuchs, 1937									
<i>Aphelenchus</i> Bastian, 1865	F2	5.0	4.0	2.5	13.6	1.9	0.2	4.5	4.1
Nematoda*	–	0	0	0	0	0.5	0.5	0.3	0.6
Total taxa – 49		31	31	20	19	31	32	27	31

Note. A functional guild (Ferris *et al.*, 2001) is the union of a taxon's trophic group (Yeates *et al.*, 1993a, b) and a value (from 1 to 5) on the c-p scale of Bongers (Bongers, 1990). Trophic groups: B – bacterial feeders; F – fungal feeders; Om – omnivores; Pr – predators; Asp – nematodes associated with plants; Pp – plant parasites. Nematoda* – unidentified individuals due to mechanical damage. «Sh Hs» is Shuya village hogweed habitat; «Sh Cont» is control meadow in the Shuya village; «Es Hs» is Essoyla village hogweed habitat; «Es Cont» is control meadow in the Essoyla village; «LR Hs» is Leningrad Region hogweed habitat; «LR Cont» is control meadow in the Leningrad Region; «MR Hs» is Moscow Region hogweed habitat; «MR Cont» is control meadow in the Moscow Region.

Table 4. The structure of soil nematode communities in habitats invaded by *Heracleum sosnowskyi* and in control meadows.

Locations	Biotope	Relative abundance of nematode trophic groups, %					
		B	F	Om	Pr	Asp	Pp
Republic of Karelia, Shuya village	Hogweed n = 9	20.6 ± 2.3	12.1 ± 2.7	26.6 ± 6.8	1.6 ± 0.5	21.0 ± 3.2	18.1 ± 3.3
	Meadow n = 9	19.6 ± 1.7	13.0 ± 1.9	12.0 ± 2.4	2.3 ± 0.7	29.9 ± 1.9	23.2 ± 1.5
Republic of Karelia, Essoila village	Hogweed n = 9	43.9 ± 3.9**	4.6 ± 2.1**	21.0 ± 5.7	0	18.7 ± 3.6*	11.8 ± 2.9
	Meadow n = 9	20.4 ± 1.7	16.8 ± 2.7	27.2 ± 4.1	0	28.7 ± 3.4	6.9 ± 1.5
Leningrad Region	Hogweed n = 9	50.2 ± 2.6	10.8 ± 1.5	7.7 ± 1.4	0.2 ± 0.1	4.2 ± 0.7	26.9 ± 2.6
	Meadow n = 9	49.9 ± 3.2	16.4 ± 2.0	7.5 ± 1.2	0	4.9 ± 0.9	21.3 ± 2.1
Moscow Region	Hogweed n = 9	75.4 ± 2.6**	12.8 ± 1.6*	3.7 ± 0.7	2.5 ± 0.8	5.4 ± 1.2*	0.2 ± 0.1**
	Meadow n = 7	28.2 ± 3.5	32.5 ± 5.7	9.7 ± 3.8	2.1 ± 1.0	11.7 ± 1.7	15.8 ± 1.6
Pooled samples	Hogweed n = 36	47.5 ± 3.5**	10.1 ± 1.2**	14.8 ± 2.7	1.1 ± 0.3	12.3 ± 1.8*	14.3 ± 2.1
	Meadow n = 34	29.5 ± 2.6	19.7 ± 1.9	14.1 ± 2.0	1.1 ± 0.3	18.8 ± 2.2	16.8 ± 1.4

Note. n – number of samples; B – bacterial feeders, F – fungal feeders, Om – omnivores, Pr – predators, Asp – plant-associated nematodes, Pp – plant-parasitic nematodes. Data are given as $M \pm SE$ (mean $\pm$ standard error); * $P < 0.05$, ** $P < 0.01$, significant differences between the same control and invaded areas (Mann-Whitney U-test was applied).

**Fig. 1.** Redundancy analysis (RDA) ordination plot showing the relationship between environmental factors and nematological parameters.

Note. Environmental factors (blue): N – total nitrogen, C – total carbon, pH_{H₂O} – soil pH in water, pH_{KCl} – soil pH in potassium chloride, P – available phosphorus, K – available potassium, N_{NO₃} – nitrate nitrogen, Lat – latitude (geographical coordinate), Location – habitat type (hogweed/meadow). Nematological parameters (red): Abund – total nematode abundance, B_{rel} – relative abundance of bacterial feeders, F_{rel} – relative abundance of fungal feeders, Pp_{rel} – relative abundance of plant-parasitic nematodes, Pp_{abund} – abundance of plant-parasitic nematodes, Pr_{rel} – relative abundance of predators, Om_{rel} – relative abundance of omnivores, Asp_{rel} – relative abundance of nematodes, associated with plants, H – Shannon diversity index, CI – Channel index, MI – Maturity index, SI – Structure index, EI – Enrichment index.

richness and the evenness of abundance distribution; thus, lower values under hogweed in the Leningrad Region (despite a similar number of genera) may reflect dominance by a single genus, namely *Tylenchorhynchus* (23%). Higher Simpson dominance index values under hogweed in the Leningrad Region than in meadows confirm this finding (Table 2).

It has been established that plant invasion sites exhibit changes in the dominant genera of nematodes. Thus, in the meadow soils of Essoyla village, the genera *Eudorylaimus* (Om) and *Aglenchus* (Asp) dominate, with a high abundance of the genus *Aphelenchus* (F) as well. Under hogweed, the first two dominant genera (*Eudorylaimus*, *Aglenchus*) remain prevalent; however, bacterial feeders of two genera – *Anaplectus* and *Rhabditis* – are abundant here, whereas they are almost entirely absent in meadow soil. In the meadow soil of Shuya village, nematodes of the genera *Aglenchus* (Asp), *Helicotylenchus* (Pp) and *Eudorylaimus* (Om) dominate. Under hogweed, the first two dominant genera (*Helicotylenchus*, *Aglenchus*) are still dominant, although their relative abundance decreases. However, omnivorous nematodes of the genus *Prodorylaimium* become the most numerous, being scarce in meadow soil (0.3% of the total abundance). In hogweed habitats in the Leningrad Region, high abundance of the genera *Acrobeloides* (B) and *Tylenchorhynchus* (Pp) is observed, whereas in meadow soil, nematodes of the genus *Plectus* (B) predominate. Under hogweed in the Moscow Region, bacterial feeders from the family Cephalobidae (*Acrobeloides*, *Cervidellus*, *Eucephalobus*) are also abundant, whereas in meadow soil, fungal-feeding nematodes of the genus *Ditylenchus* dominated (Table 3). When considering dominant taxa along the latitudinal gradient, it is notable that in the northern hogweed habitats, there is an increased abundance of omnivorous nematode genera (*Prodorylaimium*, *Eudorylaimus*), whereas further south, the dominant taxa primarily include bacterial-feeding genera (family Cephalobidae), which are widespread and stable components of nematode communities.

Trophic structure of nematode communities. The structure of soil nematode communities under *H. sosnowskyi* was characterised by dominance of omnivorous and plant-associated nematodes (Shuya), and by bacterial feeders and omnivores (Essoyla) in Karelia; by a high proportion of bacterial-feeding nematodes and plant parasites in the Leningrad Region; and by bacterial- and fungal feeders in the Moscow Region. The trophic groups whose

relative abundances changed significantly under invasion compared to meadows were bacterial- and fungal feeders, and plant-associated nematodes; these shifts were statistically significant in only two of the studied locations and in the pooled comparison of all invasion sites with meadows (Table 4). In general, the relative abundances of fungal feeders and plant-associated nematodes were higher in control meadows. The relative abundance of bacterial-feeding nematodes, despite similar values between hogweed and meadow soils in two locations (Shuya, Karelia; Leningrad Region), was significantly higher under hogweed in the pooled comparison of all invasion sites with meadows ($P < 0.01$; Table 4). By contrast, the abundances of omnivores, predators, and plant parasites exhibited contrasting trends across individual locations, with no significant differences in the pooled comparison of hogweed-invaded and control sites.

Ecological indices of soil nematode communities. The Maturity index (ΣMI) reached maximal values in hogweed soils in Shuya and minimal values in hogweed soils in the Moscow Region. No consistent trend in ΣMI was observed under invasion, as it either increased or decreased depending on the site. Statistically significant differences ($P < 0.01$) between hogweed and meadow soils were detected only in the Moscow Region (Table 5).

The Structure index (SI) exceeded 50 in all meadows and in three of the four hogweed sites, indicating a well-developed, multi-component soil food web. The relationships between the Structure index and the Enrichment index (EI) classified meadow ecosystems and three hogweed sites as slightly or moderately disturbed (quadrants B and C of the faunal profile), except for the Moscow region hogweed site, where the soil ecosystem was under stress (SI < 50 , quadrant D). No significant differences in SI or EI were found between hogweed and meadow soils (Table 5), suggesting that these indices may be of limited use as bioindicators for detecting plant-invasion-induced transformations of nematode communities and soil ecosystems.

The Channel index (CI), reflecting the dominant decomposition pathway, was generally higher in meadow soils (three locations) than under hogweed, but the difference was statistically significant only in the Moscow Region (Mann-Whitney U-test, $P < 0.01$; Table 5). Overall, the results suggest that plant invasion promotes a shift toward bacterial dominance in organic matter decomposition (lower CI), whereas meadow soils show a greater contribution of fungal pathways (higher CI).

Table 5. Ecological indices of soil nematode communities in habitats invaded by *Heracleum sosnowskyi* and in control meadows.

Parameters	Sites invaded by hogweed	Control meadow	Significance
Republic of Karelia, Shuya village			
ΣMI	2.9 ± 0.2	2.7 ± 0.1	–
SI	88.4 ± 4.8	84.7 ± 2.7	–
EI	39.9 ± 6.1	49.9 ± 4.2	–
CI	45.6 ± 14.3	28.4 ± 10.3	–
Republic of Karelia, Essoila village			
ΣMI	2.4 ± 0.2	2.7 ± 0.2	–
SI	80.3 ± 4.8	84.2 ± 3.6	–
EI	64.3 ± 13.5	53.9 ± 4.2	–
CI	7.7 ± 15.8	44.9 ± 6.8	–
Leningrad Region			
ΣMI	2.3 ± 0.1	2.6 ± 0.1	–
SI	53.9 ± 4.3	65.7 ± 3.6	–
EI	26.6 ± 2.6	19.2 ± 3.0	–
CI	29.8 ± 5.8	33.0 ± 6.4	–
Moscow Region			
ΣMI	1.8 ± 0.1	2.3 ± 0.2	**
SI	36.0 ± 3.9	58.9 ± 9.3	–
EI	45.8 ± 2.5	41.1 ± 3.0	–
CI	21.1 ± 3.6	78.3 ± 10.8	**
Pooled samples			
ΣMI	2.4 ± 0.1	2.6 ± 0.1	–
SI	64.7 ± 3.9	73.4 ± 3.2	–
EI	44.2 ± 3.9	41.0 ± 3.1	–
CI	26.1 ± 5.6	46.2 ± 5.1	–

Note. ΣMI – Maturity index, SI – Structure index, EI – Enrichment index, CI – Channel index. Data are given as M ± SE (mean ± standard error); ** $P < 0.01$, significant differences between the same control and invaded areas (Mann-Whitney U-test was applied).

Environmental factors affecting soil nematode community variability. The set of abiotic and biotic variables explained approximately 50% of the variance in nematode community parameters ($F = 6.65$, $P = 0.001$). Most factors, except for nitrate nitrogen (N_{NO_3}) and latitude (Lat), had a significant effect ($P < 0.05$) on nematological parameters (Table 6). The most influential factors were soil pH (H_2O), total carbon and nitrogen (C and N), and habitat type (Location, hogweed vs meadow) (Fig. 1). RDA indicated that soil acidity (pH in water and KCl extracts), available potassium, and habitat type were strongly correlated and positively associated with each other. Carbon and nitrogen contents, and latitude also showed positive correlations. Plant-associated nematodes (Asp_rel), omnivores (Om_rel), and, to a lesser extent, SI were positively correlated with soil C and N contents, and latitude, and negatively correlated with soil pH, available K, and habitat type. Bacterial-feeding nematodes (B_rel) exhibited the opposite trend. The

abundance of plant parasites (Pp_rel and Pp_abund) was positively associated with soil phosphorus content. Other nematological variables (e.g., total abundance, ecological indices) showed weak correlations with the analysed environmental factors.

DISCUSSION

A comparative analysis of the abundance and taxonomic diversity of soil nematodes in areas with hogweed growth and in control meadows revealed that these parameters remain virtually unchanged across the studied sites. The fact that soil nematode diversity remains consistent under plant invasion conditions aligns with some references (Renčo *et al.*, 2019; Čerevková *et al.*, 2020), yet contradicts other studies that reported a decline in diversity (Renčo & Baležentienė, 2015). Thus, the invasion of a new alien plant species into natural communities within the region does not lead to a significant decline in the abundance or diversity of soil

Table 6. Results of redundancy analysis (RDA) and permutation tests (ANOVA) for assessing the effects of environmental factors on nematode community characteristics.

Variable	Variance	F-statistic	P-value
Canonical axes			
RDA1	3.937 (31.3%)	37.5	0.001***
RDA2	1.217 (9.5%)	11.6	0.001***
RDA model	6.279 (49.9%)	6.65	0.001***
Abiotic and biotic factors			
Location	1.5312	14.586	0.001***
pH H ₂ O	1.0866	10.351	0.001***
pH KCl	0.4814	4.586	0.003**
C	0.4190	3.991	0.008**
N	0.7419	7.067	0.001***
P	1.6218	15.449	0.001***
K	0.2870	2.734	0.027*
N NO ₃	0.0460	0.438	0.794
Lat	0.0638	0.607	0.660

Note. Variance – the amount of variation explained by each canonical axis or environmental factors, F-statistic – the F-value from permutation tests (999 permutations), P-value – significance level of the permutation test (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, non-significant values are not marked). RDA model represents the total variance explained by all canonical axes. Location – habitat type (hogweed/meadow), pH_H₂O – soil pH in water, pH_KCl – soil pH in potassium chloride, C – total carbon, N – total nitrogen, P – available phosphorus, K – available potassium, N_NO₃ – nitrate nitrogen, Lat – latitude (geographical coordinate).

nematode fauna, contrary to expectations for monodominant plant stands. According to the available literature, the total abundance of soil nematodes under hogweed has been reported to decline (Renčo & Baležentienė, 2015; Čerevková *et al.*, 2020), while other studies have documented variable trends – either decreasing or slightly increasing – depending on the location (Renčo *et al.*, 2019). The total abundance of soil nematodes also did not show statistically significant differences with increasing plant cover diversity (De Deyn *et al.*, 2004). Thus, to understand the ecological consequences of plant invasion for soil nematode communities, a comprehensive analysis of nematological parameters is required.

In this study, shifts in the trophic structure of nematode communities due to plant invasion are associated with an increase in the relative abundance of fungal feeders and nematodes associated with plants. According to the concept proposed by De Deyn *et al.* (2004), changes in plant communities mainly influence primary consumers (plant parasites and nematodes associated with plants) and secondary consumers (bacterial and fungal feeders), while nematodes of higher trophic groups, such as predators and omnivores, remain largely unaffected. Our findings largely align with the proposed concept. Notably, a trend toward an increased relative abundance of bacterial feeders under

hogweed was observed in two studied locations. It is known that the above-ground parts of *H. sosnowskyi* are characterised by a high content of easily mineralisable compounds, particularly sugars. Additionally, its root system contains significant amounts of labile, easily oxidisable compounds, serving as a primary source of readily available organic matter in soils (Lapteva *et al.*, 2021). These traits of the invasive species may indirectly benefit bacterial-feeding nematodes, promoting an increase in their abundance. Simultaneously, they may negatively affect fungal-feeding nematodes, whose trophic relationships are more closely linked to soil fungi – the primary decomposers of refractory organic matter. The relative abundance of plant-associated nematodes also decreases in areas where hogweed dominates, although the differences are not statistically significant in all locations. A similar pattern was observed in our study of agroecosystems: the abundance of plant-associated nematodes significantly decreased in agroecosystems compared to meadows due to increased agricultural intensity (Matveeva *et al.*, 2023). A decrease in the number of plant-associated nematodes was also observed under the influence of the shrub *Ulex europaeus* L., which is an aggressive invasive species in New Zealand (Yeates & Williams, 2001). However, the group also dominated under the invasion of *H. sosnowskyi* in

central Lithuania (Renčo & Baležentienė, 2015). The ecological plasticity of plant-associated nematodes may be related to their broad feeding spectrum: they are facultatively connected with plants and can feed on both the epidermal cells of the roots and the contents of fungal hyphae (Yeates *et al.*, 1993a; Okada & Harada, 2007).

Overall, according to the literature data, the trophic structure of nematode communities in sites where hogweed dominates varied considerably. Several studies reported the dominance of bacterial feeders and plant parasites (Renčo & Baležentienė, 2015; Renčo *et al.*, 2019, 2021), nematodes associated with plants (or root-fungal feeders) (Renčo & Baležentienė, 2015), and herbivores in general (Čerevková *et al.*, 2020). A distinctive feature of our study is the higher abundance of omnivores recorded in soils of northern hogweed habitats. An increase in the number of omnivorous nematodes with increasing latitude has been previously reported in regional studies of agroecosystems (Matveeva *et al.*, 2023) as well as at the global scale (Song *et al.*, 2017).

The EMI index typically exhibits high values in natural and low-disturbance ecosystems, which characterises the soil nematode communities in these habitats as mature and diverse, with a wide range of species sensitive to environmental conditions (K-strategists). The Structure index (SI), like the Σ MI index, is also an indicator of the degree of ecosystem disturbance. High SI values indicate complex, multi-component food webs and generally stable habitats (Bongers, 1990; Ferris *et al.*, 2001). It has been reported that both the Structure and Maturity indices decrease under the influence of *H. sosnowskyi* (Renčo & Baležentienė, 2015; Čerevková *et al.*, 2020) and other invasive species, such as *Solidago gigantea* Aiton (Jakubcsiková *et al.*, 2024). However, these studies suggest that the response of the indices depends on the type of ecosystem invaded by the alien plant, the season of sampling, and other factors. On the other hand, several studies have reported no significant differences in the SI between invaded sites and controls for *H. sosnowskyi* (Renčo *et al.*, 2019) and *Heracleum mantegazzianum* Sommier & Levier (Renčo *et al.*, 2021). Our findings are consistent with these studies: the Σ MI exhibited variable trends under the influence of invasion, while the SI index showed no statistically significant changes.

The Enrichment index reflects the availability of organic resources in soil (Ferris *et al.*, 2001). However, although plant invasions often lead to increased availability of nutrients (Castro-Díez *et al.*, 2014; Negesse *et al.*, 2025), the EI response to

invasion has varied: some studies reported increased values (Renčo *et al.*, 2019), others observed a decrease (Jakubcsiková *et al.*, 2024), and some found no significant differences compared to control sites (Renčo *et al.*, 2021), consistent with our findings.

According to the literature, sites of plant invasions are typically characterised by low values of the Channel index (Renčo *et al.*, 2019, 2021; Čerevková *et al.*, 2020). The CI values obtained in our study at hogweed-invaded sites confirm that the bacterial component plays a dominant role in the process of organic matter decomposition in these soils. The CI is calculated based on the abundance of bacterial- and fungal feeders in the community – groups trophically linked to primary detritus consumers, soil bacteria and soil fungi (Ferris *et al.*, 2001). Numerous studies report an increase in the abundance of bacterial feeders due to invasions by *H. sosnowskyi* (Renčo & Baležentienė, 2015; Renčo *et al.*, 2019), *H. mantegazzianum* (Renčo *et al.*, 2021), *Spartina alterniflora* Loisel. (Chen *et al.*, 2007), and *Solidago gigantea* (Jakubcsiková *et al.*, 2024). Additionally, increased occurrence and diversity of bacterial feeders have been observed during *Solidago canadensis* L. invasion (Tóth & Korponai, 2025). On the other hand, a reduction in the abundance of fungal feeders due to invasive plant species has been reported in fewer studies (Yeates & Williams, 2001; Renčo *et al.*, 2019). Overall, based on the data described above, it can be inferred that plant invasion exerts a significant impact on soil microbial communities, which in turn affects organisms at higher trophic levels, including nematodes.

The RDA analysis revealed statistically significant relationships between specific nematological parameters – particularly those related to the trophic structure of nematode communities – and the studied ecological factors. The analysis identified key factors that create favourable conditions for nematode communities, including soil acidity and the availability of nitrogen, carbon, and phosphorus. These parameters play a critical role in sustaining the vitality of all soil organisms.

A strong positive correlation was observed between soil carbon and nitrogen content and the abundance of plant-associated nematodes, omnivores, and the Structure index – which is calculated based on the abundance of nematodes at higher trophic levels (omnivores, predators) and reflects the complexity and stability of the soil food web. In this study, particularly in the northern habitats, an increase in carbon and nitrogen levels

was observed in meadow biocenoses (Table 1), which are generally characterised by a stable carbon cycle, balanced nutrient content, good water permeability, and aeration. These stable conditions provide a rich food base for nematodes at higher trophic levels, which is also reflected in the Structure index. The increased proportion of omnivores in soils with stable, mature ecosystems rich in organic matter is supported by the literature (Neher, 2001; Ferris & Bongers, 2006). Higher latitudes also appear to favour omnivorous and plant-associated nematodes (an insignificant positive correlation), *i.e.*, nematodes that possess competitive advantages due to their broad ecological plasticity. These nematodes, capable of utilising a wide range of food sources (bacteria, fungi, organic residues, and other nematodes), exhibit high adaptability to unstable environmental conditions, which enables them to efficiently make use of limited resources. Although latitude did not have a significant effect on the overall variability of nematological parameters, it showed a positive correlation with soil carbon and nitrogen content. This highlights its role in shaping soil conditions and the distribution of biocenoses on a large geographical scale.

In our study, nematodes at lower trophic levels are more sensitive to soil acidity, as indicated by a direct correlation between bacterial feeders and pH level. Although the content of organic matter in the soil plays a significant, albeit indirect, role in sustaining nematode populations, it is not the only factor determining their distribution and activity. The results of several studies indicate that soil nematodes tend to prefer environments with a neutral pH level of the soil solution (Solov'eva *et al.*, 1976; Raty & Huhta, 2003). An acidic environment can reduce the biological activity of soils, inhibit bacterial reproduction, and decrease their involvement in the decomposition of organic matter, thereby limiting the food resources available to bacterial feeders (Robson & Abbott, 1989). At the same time, bacterial feeders (mainly general-opportunistic nematodes classified as c-p-2), characterised by broad ecological plasticity and high resistance to various disturbances, are capable of adapting to a decrease in soil organic matter content (negative correlation with C and N). The abundance and proportion of plant parasites are positively correlated with the level of phosphorus in the soil. It is known that phosphorus is one of the main elements in plant nutrition, and it stimulates the formation of lateral roots and root hairs, increasing the area of nutrient absorption in response to the local distribution of phosphorus in the soil, thus

increasing the root mass in areas with high phosphorus content (Teuchezh, 2018; Ma *et al.*, 2019). This, in turn, can stimulate an increase in the abundance of plant parasites.

Overall, this study highlights that a comprehensive assessment of the changes occurring within nematode communities and their relationships with the invasive plant should include a broader set of abiotic and biotic environmental factors, incorporating those not accounted for in the present study.

CONCLUSION

Many reports on invasive plants focus on their negative impacts on soil organisms; however, the ecological consequences of such invasions are complex and do not always follow a single pattern. Our data show that the structure of soil nematode communities changes in hogweed-invaded sites, with increased abundance of bacterial feeders and decreased abundance of fungal-feeding and plant-associated nematodes, while the total number of nematode taxa remains unchanged. At the same time, individual locations demonstrated contrasting trends across many parameters, and no consistent differences were detected in most nematological parameters between habitats with invasive plants and control meadows. This underscores the risk of hasty generalisations when predicting the ecological impacts of invasive plants. Therefore, to better quantify the impact of plant invasions on soil ecosystems, further research should incorporate a broader range of biotic and abiotic factors. These may include the timing and duration of plant invasion in a new habitat, climatic variables (such as temperature and precipitation), and additional soil characteristics (*e.g.*, moisture, porosity). This would enable a more accurate interpretation of the drivers behind changes in soil nematode communities.

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REFERENCES

- ABEBE, E., ANDRASSY, I. & TRAUNSPURGER, W. 2006. *Freshwater Nematodes: Ecology and Taxonomy*. Wallingford, UK, CAB International. 752 pp.
- ANTIPINA, G.S. & SHUISKAYA, E.A. 2009. [Seed productivity of invasive species Sosnowskyi's hogweed (*Heracleum sosnowskyi* Manden.) in Southern Karelia]. *Uchenye zapiski Petrozavodskogo*

- gosudarstvennogo universiteta 5: 23-25 (in Russian).
- ARINUSHKINA, E.V. 1970. [Manual on Chemical Analysis of Soils]. Russia, Moscow, Mosk. Gos. Univ. 487 pp. (in Russian).
- BALEŽENTIENĖ, L. & BARTKEVIČIUS, E. 2013. Invasion of *Heracleum sosnowskyi* (Apiaceae) at habitat scale in Lithuania. *Journal of Food, Agriculture and Environment* 11: 1370-1375.
- BOAG, B. & YEATES, G.W. 1998. Soil nematode biodiversity in terrestrial ecosystems. *Biodiversity and Conservation* 7: 617-630. DOI: 10.1023/A:1008852301349
- BONGERS, T. 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83: 14-19. DOI: 10.1007/BF00324627
- CASTRO-DÍEZ, P., GODOY, O., ALONSO, A., GALLARDO, A. & SALDAÑA, A. 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecology Letters* 17: 1-12. DOI: 10.1111/ele.12197
- ČEREVKOVÁ, A., IVASHCHENKO, K., MIKLISOVÁ, D., ANANYEVA, N. & RENČO, M. 2020. Influence of invasion by Sosnowsky's hogweed on nematode communities and microbial activity in forest and grassland ecosystems. *Global Ecology and Conservation* 21: 1-11. DOI: 10.1016/j.gecco.2019.e00851
- CHEN, H., LI, B., FANG, C., CHEN, J. & WU, J. 2007. Exotic plant influences soil nematode communities through litter input. *Soil Biology and Biochemistry* 39: 1782-1793. DOI: 10.1016/j.soilbio.2007.02.011
- DASSONVILLE, N., VANDERHOEVEN, S., VANPARYS, V., HAYEZ, M., GRUBER, W. & MEERTS, P. 2008. Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia* 157: 131-140. DOI: 10.1007/s00442-008-1054-6
- DE DEYN, G.B., RAAIJMAKERS, C.E., VAN RUIJVEN, J., BERENDSE, F. & VAN DER PUTTEN, W.H. 2004. Plant species identity and diversity effects on different trophic levels of nematodes in the soil food web. *Oikos* 106: 576-586. DOI: 10.1111/j.0030-1299.2004.13265.x
- DE LEY, P. & BLAXTER, M. 2004. A new system for Nematoda: combining morphological characters with molecular trees, and translating clades into ranks and taxa. In: *Nematology Monographs and Perspectives* (R. Cook & D.J. Hunt. Eds). pp. 633-653. Leiden, The Netherlands, Brill.
- EPPO (EUROPEAN AND MEDITERRANEAN PLANT PROTECTION ORGANIZATION). 2009. *Heracleum mantegazzianum*, *Heracleum sosnowskyi* and *Heracleum persicum*. EPPO data sheet on invasive alien plants. *Bulletin OEPP/EPPO Bulletin* 39: 489-499.
- FERRIS, H. & BONGERS, T. 2006. Nematode indicators of organic enrichment. *Journal of Nematology* 38: 3-12. DOI: 10.1111/epp.70049
- FERRIS, H., BONGERS, T. & DE GOEDE, R.G.M. 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Applied Soil Ecology* 18: 13-29. DOI: 10.1016/S0929-1393(01)00152-4
- FITOUSSI, N., PEN-MOURATOV, S. & STEINBERGER, Y. 2016. Soil free-living nematodes as bio-indicators for assaying the invasive effect of the alien plant *Heterotheca subaxillaris* in a coastal dune ecosystem. *Applied Soil Ecology* 102: 1-9. DOI: 10.1016/j.apsoil.2016.02.005
- GAO, L., FAN, F., HE, Y., WEI, C., XU, H., LIU, X., LU, X. & BARDGETT, R.D. 2024. Contrasting responses of plant, soil fungal and above-ground arthropod communities to plant invasion across latitudes. *Journal of Ecology* 112: 2333-2343. DOI: 10.1111/1365-2745.14398
- HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. 2001. Past: paleontological statistics software package for education and data analysis. *Paleontological Electronica* 4: 1-9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- JAKUBCSIKOVÁ, M., DEMKOVÁ, L., RENČO, M. & ČEREVKOVÁ, A. 2024. Impact of *Solidago gigantea* invasion on nematode communities in grasslands. *Nematology* 26: 779-793. DOI: 10.1163/15685411-bja10338
- KERFAHI, D., TRIPATHI, B.M., PORAZINSKA, D.L., PARK, J., GO, R. & ADAMS, J.M. 2016. Do tropical rain forest soils have greater nematode diversity than High Arctic tundra? A metagenetic comparison of Malaysia and Svalbard. *Global Ecology and Biogeography* 25: 716-728. DOI: 10.1111/geb.12448
- LAPTEVA, E.M., ZAKHOZHII, I.G., DALKE, I.V., SMOTRINA, Y.A. & GENRIKH, E.A. 2021. [Influence of *Heracleum sosnowskyi* Manden. invasion on postagrogenic soil fertility in European North-East]. *Teoreticheskaya i prikladnaya ehkologiya* 3: 66-73 (in Russian).
- LIAO, C., PENG, R., LUO, Y., ZHOU, X., WU, X., FANG, C., CHEN, J. & LI, B. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* 177: 706-714. DOI: 10.1111/j.1469-8137.2007.02290.x
- LOZZARO, L., MAZZA, G., D'ERRICO, G., FABIANI, A., GIULIANI, C., INGHILESI, A.F., LAGOMARSINO, A., LANDI, S., LASTRUCCI, L., PASTORELLI, R., ROVERSI, P.F., TORRINI, G., TRICARICO, E. & FOGGI, B. 2018. How ecosystems change following invasion by *Robinia pseudoacacia*: insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. *Science of the*

- Total Environment* 622-623: 1509-1518. DOI: 10.1016/j.scitotenv.2017.10.017
- MA, X., MASON-JONES, K., LIU, Y., BLAGODATSKAYA, E., KUZAYAKOV, Y., GUBER, A., DIPPOLD, M.A. & RAZAVI, B.S. 2019. Coupling zymography with pH mapping reveals a shift in lupine phosphorus acquisition strategy driven by cluster roots. *Soil Biology and Biochemistry* 135: 420-428. DOI: 10.1016/j.soilbio.2019.06.001
- MATVEEVA, E.M., SUSHCHUK, A.A. & KALINKINA, D.S. 2023. Soil nematodes of northern meadows and agrocoenoses as bioindicators of the transformation degree in soil ecosystems. *Russian Journal of Ecology* 54: 311-321. DOI: 10.1134/S1067413623040070
- MORRIËN, E., DUYTS, H. & VAN DER PUTTEN, W.H. 2012. Effects of native and exotic range-expanding plant species on taxonomic and functional composition of nematodes in the soil food web. *Oikos* 121: 181-190. DOI: 10.1111/j.1600-0706.2011.19773.x
- NEGESSE, Z., PAN, K., GUADIE, A., FRANCIS JUSTINE, M., AZENE, B., PANDEY, B., WU, X., SUN, X. & ZHANG, L. 2025. Plant invasions alter soil biota and microbial activities: a global meta-analysis. *Plant and Soil* 513: 1031-1050. DOI: 10.1007/s11104-025-07227-7
- NEHER, D.A. 2001. Role of nematodes in soil health and their use as indicators. *Journal of Nematology* 33: 161-168.
- NEHER, D.A., EASTERLING, K.N., FISCUS, D. & CAMPBELL, C.L. 1998. Comparison of nematode communities in agricultural soils of North Carolina and Nebraska. *Ecological Applications* 8: 213-223. DOI: 10.2307/2641323
- NIELSEN, C., RAVN, H.P., NENTWIG, W. & WADE, M. 2005. *The Giant Hogweed Best Practice Manual. Guidelines for the management and control of an invasive weed in Europe*. Hoersholm, Denmark, Forest and Landscape Denmark. 44 pp.
- NIELSEN, U.N., AYRES, E., WALL, D.H., LI, G., BARDGETT, R.D., WU, T. & GAREY, J.R. 2014. Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. *Global Ecology and Biogeography* 23: 968-978. DOI: 10.1111/geb.12177
- OKADA, H. & HARADA, H. 2007. Effects of tillage and fertilizer on nematode communities in a Japanese soybean field. *Applied Soil Ecology* 35: 582-598.
- ODUM, E. 1975. [*Fundamentals of Ecology*]. Russia, Mir. 740 pp. (in Russian).
- PEARSON, B.M., MINOR, M.A., ROBERTSON, A.W. & MCCORMICK, A.L.C. 2024. Plant invasion down under: exploring the below-ground impact of invasive plant species on soil properties and invertebrate communities in the Central Plateau of New Zealand. *Biological Invasions* 26: 4215-4228. DOI: 10.1007/s10530-024-03441-z
- PROCTER, D.L.C. 1984. Towards a biogeography of free-living soil nematodes. I. Changing species richness, diversity and densities with changing latitude. *Journal of Biogeography* 11: 103-117. DOI: 10.2307/2844684
- R CORE TEAM. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL: <http://www.r-project.org/index.html>
- RATY, M. & HUHTA, V. 2003. Earthworms and pH affect communities of nematodes and enchytraeids in forest soil. *Biology and Fertility of Soils* 38: 52-58. DOI: 10.1007/s00374-003-0614-5
- RENČO, M. & BALEŽENTIENĖ, L. 2015. An analysis of soil free-living and plant-parasitic nematode communities in three habitats invaded by *Heracleum sosnowskyi* in central Lithuania. *Biological Invasions* 17: 1025-1039. DOI: 10.1007/s10530-014-0773-3
- RENČO, M., KORNOBIS, F.W., DOMARADZKI, K., JAKUBSKA-BUSSE, A., JUROVÁ, J. & HOMOLOVÁ, Z. 2019. How does an invasive *Heracleum sosnowskyi* affect soil nematode communities in natural conditions? *Nematology* 21: 71-89. DOI: 10.1163/15685411-00003196
- RENČO, M., JUROVÁ, J., GÖMÖRYOVÁ, E. & ČEREVKOVÁ, A. 2021. Long-term Giant hogweed invasion contributes to the structural changes of soil nematofauna. *Plants* 10: 2103. DOI: 10.3390/plants10102103
- ROBSON, A.D. & ABBOTT, L.K. 1989. The effect of soil acidity on microbial activity in soils. In: *Soil Acidity and Plant Growth* (A.D. Robson. Ed.). pp. 139-165. Sydney, Australia, Academic Press.
- SOHLENIUS, B. & BOSTROM, S. 1999. Effects of climate change on soil factors and metazoan microfauna (nematodes, tardigrades and rotifers) in a Swedish tundra soil – a soil transplantation experiment. *Applied Soil Ecology* 12: 113-128. DOI: 10.1016/S0929-1393(98)00168-1
- SOLOV'EVA, G.I., VASIL'EVA, A.P. & GRUZDEVA, L.I. 1976. [*Free-living and plant-parasitic nematodes of the Northwest USSR*]. Leningrad, Russia, Nauka. 367 pp. (in Russian).
- SOLOV'EVA, G.I. 1986. [*Ecology of Soil Nematodes*]. Leningrad, Russia, Nauka. 247 pp. (in Russian).
- SONG, D., PAN, K., TARIQ, A., SUN, F., LI, Z., SUN, X., ZHANG, L., OLUSANYA, O.A. & WU, X. 2017. Large-scale patterns of distribution and diversity of terrestrial nematodes. *Applied Soil Ecology* 114: 161-169. DOI: 10.1016/j.apsoil.2017.02.013
- SUSHCHUK, A., KALINKINA, D., IVANOVA, V. & MATVEEVA, E. 2024. The effect of geographical latitude of the habitats invaded by *Heracleum sosnowskyi* on soil nematode communities. *BIO Web of Conferences* 118: 02012. DOI: 10.1051/bioconf/202411802012

- SUSHCHUK, A.A., KALINKINA, D.S. & MATVEEVA, E.M. 2025. How does the invasion of *Heracleum sosnowskyi* (Umbelliferae) affect soil nematode communities in meadow ecosystems? *Russian Journal of Biological Invasions* 16: 661-673. DOI: 10.1134/S2075111725600326
- TEUCHEZH, A.A. 2018. [The value of phosphorus as an important element in the development of living organisms]. *Ehkologicheskij Vestnik Severnogo Kavkaza* 14: 50-53 (in Russian).
- TÓTH, Z. & KORPONAI, K. 2025. Diversity patterns and trait-specific variations in soil nematode communities associated with *Solidago* invasion. *Ecological Indicators* 175: 113598. DOI: 10.1016/j.ecolind.2025.113598
- VAN BEZOOIJEN, J. 2006. *Methods and Techniques for Nematology*. Wageningen, The Netherlands, Wageningen University Press. 112 pp.
- VAN DEN HOOGEN, J., GEISEN, S., ROUTH, D. et al. 2019. Soil nematode abundance and functional group composition at a global scale. *Nature* 572: 194-198. DOI: 10.1038/s41586-019-1418-6
- VINOGRADOVA, YU.K., MAYOROV, S.R. & KHORUN, L.V. 2010. [The Black Book of Flora of Central Russia: Alien Plant Species in Ecosystems of Central Russia]. Russia, GEOS. 512 pp. (in Russian).
- VONK, J.A., BREURE, A.M. & MULDER, C. 2013. Environmentally-driven dissimilarity of trait-based indices of nematodes under different agricultural management and soil types. *Agriculture, Ecosystems and Environment* 179: 133-138. DOI: 10.1016/j.agee.2013.08.007
- WILSCHUT, R.A., GEISEN, S., MARTENS, H., KOSTENKO, O., DE HOLLANDER, M., TEN HOOVEN, F.C., WESER, C., SNOEK, L.B., BLOEM, J., ČAKOVIĆ, D., ČELIK, T., KOOREM, K., KRIGAS, N., MANRUBIA, M., RAMIREZ, K.S., TSIAFOULI, M.A., VREŠ, B. & VAN DER PUTTEN, W.H. 2019. Latitudinal variation in soil nematode communities under climate warming-related range-expanding and native plants. *Global Change Biology* 25: 2714-2726. DOI: 10.1111/gcb.14657
- YEATES, G.W., BONGERS, T., DE GOEDE, R.G.M., FRECKMAN, D.W. & GEORGIEVA, S.S. 1993A. Feeding habits in soil nematode families and genera: An outline for soil ecologists. *Journal of Nematology* 25: 315-331.
- YEATES, G.W., WARDLE, D.A. & WATSON, R.N. 1993B. Relationships between nematodes, soil microbial biomass and weed-management strategies in maize and asparagus cropping systems. *Soil Biology and Biochemistry* 25: 869-876.
- YEATES, G.W. & WILLIAMS, P.A. 2001. Influence of three invasive weeds and site factors on soil microfauna in New Zealand. *Pedobiologia* 45: 367-383.

А. А. Сущук, Д. С. Калинкина и Е. М. Матвеева. Разнообразие и структура сообществ почвенных нематод под влиянием *Heracleum sosnowskyi*: широтные различия и эффекты инвазии.

Резюме. Изучены сообщества почвенных нематод в условиях инвазии борщевика Сосновского *Heracleum sosnowskyi* Manden. с учетом широтного положения местообитаний. Исследование выполнено в четырех местах произрастания борщевика, расположенных от 61° до 55° с.ш.: Республика Карелия (поселки Эссойла и Шуя), Ленинградская и Московская области. Отбор почвенных проб проводился под сплошными зарослями *H. sosnowskyi* и в контрольных лугах, не подвергшихся инвазии. Показано, что структура сообществ почвенных нематод в местах произрастания борщевика характеризовалась доминированием политрофов и нематод, ассоциированных с растениями (п. Шуя), а также бактериотрофов и политрофов (п. Эссойла) в Карелии, высокой долей бактериотрофов и паразитов растений – в Ленинградской области, бактерио- и микотрофов – в Московской области. Растительная инвазия изменила соотношение трофических групп в сообществах нематод: статистически значимо изменилось обилие бактериотрофов (увеличение под влиянием борщевика), микотрофов и нематод, ассоциированных с растениями (снижение под влиянием борщевика). Однако общее число выявленных таксонов нематод осталось практически без изменений, то есть внедрение нового для региона вида растения в природные сообщества не привело к значительному снижению разнообразия фауны нематод. RDA-анализ показал, что следующие абиотические и биотические факторы – тип местообитания (борщевик/луг) как показатель действия фактора инвазии, pH, общий углерод и азот, подвижный фосфор и калий – оказали значимое влияние на параметры сообществ нематод. Совокупность оцененных факторов объясняет около 50% варьирования нематологических параметров. Примечательно, что влияние широты как фактора не значимо для общей изменчивости нематологических параметров исследованных местообитаний, что подчеркивает главенствующую роль фактора инвазии над географическим положением.