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THE INVASIVE EFFECT OF *SOLIDAGO CANADENSIS* L. ON THE STRUCTURAL CHARACTERISTICS OF SOIL NEMATODE COMMUNITIES IN THE ECOSYSTEMS OF THE EU-MESOPHYTIC MEADOWS

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Aim. To compare the eco-trophic structure of soil nematode communities in the ecosystems of the eu-mesophytic meadows in plots non-invaded and invaded by *Solidago canadensis* L. **Methods.** Soil samples from the rhizosphere of native meadow plants and those with *S. canadensis* were collected in September 2021 in two meadow ecosystems located on the outskirts of the villages Shostovytsia and Ladinka of the Chernihiv region. The nematodes were extracted by a modified Baermann's method from the 20 g samples. The exposure time was 48 h. The extracted nematodes were fixed in the triethanolamine–formalin (TAF, 2 % triethanolamine, 7 % formaldehyde solution, 91 % water), and mounted on the temporary hydroglyceric slides. The nematode abundance was expressed as specimens per 100 g of dry soil. The following parameters were analysed: abundance, taxonomic composition, dominance, trophic structure of soil nematode communities. The taxonomic wealth index, Menhinick's, Berger–Parker indexes, Jaccarda's index of similarity, and the maturity index were also calculated. **Results.** The average abundance of nematodes in the soil nematode communities was 1,075 individuals/100 g in the rhizosphere of native meadow plants and 636 individuals/100 g in the rhizosphere of *S. canadensis*. A total of 52 species were identified in the soil of meadow ecosystems: 44 — in the non-invaded plots and 29 — in the invaded plots; Menhinick's diversity index was 1.34 and 1.15, respectively. The taxonomic wealth index of nematode communities in the rhizosphere of native plants was also higher — ST = 116; in the rhizosphere of Canadian goldenrod — ST = 84. Such families as *Tylenchidae*, *Cephalobidae*, *Tylencholaimidae* and *Panagrolaimidae* were more numerous in the soil samples of the native meadow plants (25 %, 18.4 %, 12.9 %, 10.3 % of the total number, respectively). *Paratylenchidae*, *Tylenchidae*, *Cephalobidae* and *Aphelenchidae* were more numerous in the plots with *S. canadensis* (37.1 %, 15.1 %, 14.3 %, 10.1 %, respectively). The taxonomic wealth index was higher in non-invaded plots (2.98) than those, invaded by Canadian goldenrod (2.75). The bacterivores and fungivores predominated quantitatively in nematode communities in the rhizosphere of native meadow plants. The proportion in the community amounted to 76.4 %. The plant parasites and fungivores were the most numerous in the plots with *S. canadensis*. The abundance of nematodes in other tropic groups were limited or not affected. **Conclusions.** It was determined that the species wealth and abundance, the taxonomic and trophic diversity of soil nematode communities were lower in the plots with the invasion by Canadian goldenrod. The abundance of plant parasites was higher (2.3 times); the ratio of fungivores to bacterivores was also higher in the invaded plots (1.2 times). The maturity index was lower in the invaded plots compared to the non-invaded ones (2.1 and 2.4) which demonstrates a more disturbed environmental conditions in the plots of the meadow with the invasion of the *S. canadensis*. The studies emphasize the need to monitor invasive species and develop strategies for their control in order to preserve soil biodiversity and support sustainable grassland management.

Keywords: eu-mesophytic meadows, *Solidago canadensis* L., invasion, soil nematode communities, taxonomic diversity, trophic group.

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INTRODUCTION

Invasions of adventive plants are among the most relevant threats to biological biodiversity (Protopopova et al., 2002; EPPO, 2024). The European and Mediterranean Plant Protection Organization (EPPO) recommends control measures regarding such plants due to their high potential to disrupt ecosystems, change the composition and structure of phytocenoses, and replace ecosystem services (EPPO, 2024). In 2004, the list of invasive foreign plants of EPPO was added two species of *Solidago* L. genus — *S. canadensis* L. (Canadian goldenrod) and *S. gigantea* Aiton (tall goldenrod). According to our observations, initiated in 2005, in Ukraine, *S. gigantea* is sometimes as common as a wild plant. It has not been mentioned in the list of foreign plants that have actively spread in Ukraine in the 19^{th}–21^{st} centuries (Zavialova et al., 2021). As for *S. canadensis*, this invasive plant is common in Ukraine; it quickly establishes itself in meadows, pastures, reclaimed marshes, wastelands, forests, forest glades, clearings, fallow lands, and along roads (Zavialova, 2017). *S. canadensis* contains compounds that can change soil structure and its nutrients and thus affect the growth, germination, and survival of local species (Poljuha et al., 2024). Goldenrods are stable regardless of the rate of soil humidity, illumination, the content of nutrients, temperature, and pH of the soil (Jakobs et al., 2004). These plants produce a large amount of biomass, decrease the pH of soil and the number of soil bacteria, and increase the C : N ratio (Chapuis-Lardy et al., 2006; Scharfy et al., 2010; Bobul'ská et al., 2019; Jakubcsiková et al., 2023). It may affect not only the phytodiversity but the biodiversity of the ecosystems in general.

The problem of the impact of invasive plants on the soil biota structure has attracted considerable attention in recent times. It was reported that under the impact of *S. gigantea*, observable changes have occurred within Collembola accumulations and their density in some parts of riparian wet meadows in Poland (Sterzyńska et al., 2017). In wet meadows, located in southern-eastern suburbs of Krakow, a negative impact on the species wealth and composition of genus Myrmica was noted in the parts with goldenrods (*S. canadensis* and *S. gigantea*) (Kajzer-Bonk et al., 2016; Trigos-Peral et al., 2018). There was a noted decrease in the taxonomic wealth of *Carabidae* in the meadow fields, which were invaded by goldenrods (*S. canadensis* and *S. gigantea*) (Baranová et al., 2014).

The most numerous group of soil microfauna is comprised of nematodes, which occupy all the trophic levels in the food network of soil (De Ruiter et al., 2005; Ferris, 2010). Due to a large number, diversity, and sensitivity to changes in the environment, nematode communities are considered to be valuable indicators of soil ecosystem state (Bongers, 1990; Neher, 2001; Yeates, 2003; Lu et al., 2020; Du Preez et al., 2022). The studies, conducted in natural conditions, demonstrated that the invasion of *S. canadensis* and *S. gigantea* was changing the structure of the communities of soil nematodes. Xiangqi et al. (2011) found that, first of all, the invasion of *S. canadensis* affected the trophic diversity of soil nematodes and the ratio of trophic groups. Quist et al. (2014) noted that under the impact of *S. gigantea*, there was an increase in the density of soil nematodes from *Aphelenchoididae* family. Cerevková et al. (2019b) demonstrated that *S. gigantea* decreased the species diversity of nematodes in both meadow and forest ecosystems and increased the number of plant parasitic nematodes.

S. canadensis is among a few invasive species, which are believed to be both a threat to biodiversity and to potential producers of economic and ecosystem services. For instance, in the late phase after the Chornobyl accident, in order to obtain products with standardized content of heavy metals and radionuclides, it is possible to use *S. canadensis* as a honey resource of meadow ecosystems of Polissia invaded with this species (Lukash et al., 2021). Poljuha et al. (2024) consider the invasive specificities of *S. canadensis* and highlight the chemical characteristics and potential of this species for ecosystem services. In our opinion, the objective evaluation of the use of *S. canadensis* in bioeconomy should consider the entire spectrum of the effects of *S. canadensis* on ecosystems, including the eco-trophic structure of soil nematode communities.

S. canadensis, as an invasive species, is widely common in Ukraine: it is present in Polissia, the Forest-Steppe, Prykarpattia, and Zakarpattia. The invasions of this species change the structure of communities of the class of *Molinio-Arrhenatheretea* Tx. 1937 completely, causing a reduction in the meadow area (Zavialova et al., 2021). True mesophytic meadows (union of *Arrhenatherion elatioris* Luquet 1926), which belong to the class of *Molinio-Arrhenatheretea* Tx, are not just the feeding foundation for the field and meadow-pasture feed production, they also play a relevant role in preserving the habitat of many plant and animal species (Myklestad and Sætersdal, 2004). In terms of composition and structure, the true mesophytic meadows in the Chernihiv region without the invasion of *S. canadensis* are communities of the union of Arrhenatherion elatioris, typical for Ukraine (Kuzemko, 2019). The mesophytic riparian meadows, invaded by *S. canadensis*, represent the stage of transit community formation (Danko et al., 2021).

One of the tasks of meadow formation is to increase the performance of natural fodder fields, their rational use, and improvement. This task cannot be solved without considering many factors, including determining the role of pedobionts. Nematodes are an integral component of microfauna, as are their numbers and biomass. They are involved in maintaining the circulation of nutrients and regulating the amount of soil microflora; phytoparasitic species may cause a decrease in meadow productivity. Soil nematode communities are sensitive to any changes, including the invasion of invasive plant species into the meadow ecosystems.

The impact of the invasive species, *S. canadensis*, on the structure of soil nematode fauna in Ukraine has not been studied sufficiently enough.

The aim of the study was to compare the ecotrophic structure of soil nematode communities in the ecosystems of mesophytic meadows in the non-invaded parts and in the ones invaded by *S. canadensis*, in the context of determining one of the factors, affecting the productivity of fodder meadows.

MATERIALS AND METHODS

The study was conducted on September 5 and 24, 2021, in two meadow ecosystems, located near the villages of Shestovytsia and Ladynka, the Chernihiv region. Both ecosystems had even landscapes. The soil in the investigated land plots was turf-medium podzolic, light clay. The soil was defined using the "Field Guide for Soils" (Polupan et al., 1981). The horizon (Ho) was presented with turf, it was 3–5 cm deep, the humus-eluvial horizon (HE) was 5–25 cm, of gray color and lumpy structure, and pierced with the roots of plants. The true mesophytic meadows were formed in both fields. The phytocenoses of the studied ecosystems belong to the association of *Festucetum pratensis* Soó 1938. Twenty-nine plant species take part in the formation of standing grass, which accounts for approximately 95 % of the total. The dominating species are *Lolium pratense* (Huds.) Darbysh. (35 %), *Alopecurus pratensis* L. (30 %) and *Agrostis capillaris* L. (25 %). In the areas with 6-year-old invasions, *S. canadensis* covers about 20 % and is sometimes found in flowerbeds of 100–200 productive plants per one sq. m (**Fig.1**) (Danko et al., 2021).

Three experimental plots (10 × 10 m) were selected in the ecosystems. At each test site, 10 point (individual) soil samples were taken at a depth of 20 cm in the rhizosphere of natural meadow plants and in the rhizosphere of *S. canadensis*, with a volume of 200–300 g. After thorough mixing, two average samples of 300–500 g were formed. Soil was placed into plastic bags and delivered to the laboratory. The acidity of the soil solution in the experimental plots was determined using the portable pH-meter, ADWA AD12 (Hungary). In terms of acidity, these soils were mostly close to the neutral ones, pH 5.5–6.1. The humus content was 1.77 % on average (Yatsuk et Lishchuk, 2014).

The nematodes were isolated on the following day, using the common Baermann funnel technique and the weighed quantity of 20 g in two repeats. The exposure lasted 48 h, after which nematodes were fixed with TAF (triethanolamine + formalin + water in the 2:7:91 ratio) (Courtney et al., 1955). Temporary water-glycerine micropreparations were made. The nematodes were counted in the sample under the MBS-1 microscope. If the sample contained less than 100 nematodes, all of them were transferred to the specimen slide into the drop of water-glycerine mixture with the blue using the preparation needle. If the samples contained over 100 nematodes, 100 of them were taken, others were counted (Southey, 1986). The species composition of nematodes was determined using the guides (Goodey, 1963; Jairaj-

Fig. 1. The plot of mesophytic meadow with the invasion of *Solidago canadensis* L.

puri and Ahmad, 1992; Siddiqi, 2000). The biological microscope Delta Optical Genetic Pro was used (Poland). The number of nematodes was calculated as per 100 g of absolutely dry soil.

The number of nematodes (N) and the total number of species (S) were determined. The taxonomic wealth (ST) was evaluated as the sum of taxa of the communities (Emelyanov et al., 1999). The analysis of the species diversity involved the Menhinick index ($M = S/\sqrt{N}$). To characterize the structure of nematode fauna, we calculated the domination coefficient (the share of involvement) of each species in the fauna composition (D) as a ratio (%) between the number of representatives of this species and the total number of nematodes. According to this trait, nematodes were united into five groups: eudominant (ed) — over 10 % from all the detected ones, dominant (d) — 5.1–10.0 %, subdominant (sd) — (2.1–5.0 %), recedent (r) — 1.1–2.0 %, subrecedent (sr) — below 1.1 % (Tischler, 1949). The relative significance of the most abundant species was calculated by the Berger-Parker index: $d = 1/(N_{max}/N)$, where N_{max} — the number of nematodes of the most abundant species (Berger et al., 1970). The similarity coefficient of Jaccarda was determined by the formula: $J = c / a + b - c$, where *a* and *b* — the number of species in the compared communities; *c* — the number of common species.

Soil nematodes were divided into five trophic groups: bacterivores, fungivores, plant parasites, predators, and omnivores (Wasilewska, 1971; Yeates et al., 1993; Wasilewska, 1997; McSorley and Frederick, 1999). The index of trophic diversity was used: $Td = 1 / \Sigma p_i^2$, where p_i — relative number of the trophic group i in the community (Yeates and Bongers, 1999); the ratio between the number of fungivores and bacterivores f / b in the communities, where *f* — the relative number of fungivores; *b* — the relative number of bacterivores (Ruess, 2003). A relevant index to characterize fauna is the Bongers' maturity index for nematode communities: $MI = \Sigma\, v(i) \cdot f(i)$, where $v(i)$ — the *c-p* value for the taxon *i*, and $f(i)$ — the taxon share in the sampling (Bongers, 1999). According to the life strategy, the author arranged nematode species within the five-point scale. Typical colonizers, i.e. species with short life cycles, are capable of rapid population increase, resistant to unfavorable environmental conditions, and their *c-p* value on the scale is 1. Typical persistent ones have low reproduction ability and a long life cycle; they are sensitive to environmental conditions and located on the *c-p* scale with an index value of 5.

The statistical analysis involved the Statistica 13.3 package (TIBCO Software, Palo Alto, CA, the USA), the results were expressed as the average value ± standard deviation. The significance of differences between variants was evaluated using Student's *t*-test.

RESULTS

The average number and species wealth of soil nematodes were different (**Table 1**). In the rhizosphere of natural meadow plants, the number of nematodes in 100 g of soil was 1,075±163, and in the rhizosphere of Canadian goldenrod — 636±146. A total of 52 spe-

Table 1. The taxonomic diversity of soil nematodes in meadow ecosystems with the invasion of *Solidago canadensis* (Sc) and without the invasion (K)

Characteristics	K	Sc	Significance, Student's *t*-test
Species	44 ± 16	29 ± 14	*
Genus	39 ± 11	27 ± 12	**
Families	25 ± 4	21 ± 3	—
Orders	8	7	—
Abundance in ind./100 g of soil	1075 ± 163	636 ± 146	**
ST (taxonomic wealth index)	116 ± 25	84 ± 18	**
M (Menhinick's diversity index)	1.34 ± 0.10	1.15 ± 0.15	*
d (Berger-Parker diversity index)	4.5 ± 0.58	2.7 ± 0.33	*

* $P < 0.05$; ** $P < 0.01$.

cies were registered: 44 species in the non-invaded plots, and 29 in the plots with goldenrod.

The taxonomic wealth of nematode communities was found to be lower in the rhizosphere of Canadian goldenrod (ST = 84). In general, their diversity in the invaded plots decreased, and the dominance index increased, which was confirmed by the values of Menhinick's and Berger-Parker diversity indexes.

Nineteen species were common for the compared nematode communities. The Jaccarda similarity index was 0.4. Eight species were noted only in the soil of the plots, invaded by *S. canadensis*: *T. mirabilis*, *E. filiformis*, *C. symmetricus*, *P. pseudoparietinus*, *T. arcuatus*, *B. thylactus*, *D. dipsaci*, *Macroposthonia* sp.

In terms of species diversity, three orders were presented more abundantly in the soil of the meadow ecosystem: *Tylenchida*, *Rhabditida*, and *Dorylaimida* (**Fig. 2**).

The rhizosphere of goldenrod contained 12 species from Tylenchida order (41.4 % of the total species list), Rhabditida — 7 species (24.1 %), Dorylaimida — 5 species (17.2 %). The species diversity of Tylenchida in the rhizosphere of rooted meadow plants was almost not different — 11 species, but in the percentage ratio, they were only 25 % of all the species, detected here. Rhabditida and Dorylaimida were represented in 10 species (22.7 %) and 8 species (18.2 %), respectively.

It should be noted that for species of Plectida order, the best habitat was found in the soil of non-invaded plots: 7 species were detected (15.9 %), whereas in the invaded plots, there was one species (3.4 %). The species diversity of Aphelenchida, Enoplida, Monchysterida, and Triplonchida was insignificant in the studied plots and did not exceed 6.9 %. The species of Enoplida order were detected only in the rhizosphere of natural meadow plants.

In the nematode communities of the meadow ecosystem, the most numerous ones were the representatives of two orders, namely, Tylenchida and Rhabditida (**Fig. 3**). It was found that in the non-invaded plots with natural meadow plants, Tylenchida representatives were 1.5 times more numerous than Rhabditida. In the plots, invaded by *S. canadensis*, Tylenchida nematodes had exceeding numbers, and this ratio was 3:4.

The number of nematodes from orders Monhysterida, Plectida and Triplonchida in 100 g of soil was insignificant (fewer than 10 nematodes/100 g of soil).

The registered species of soil nematodes belonged to 29 families: 25 families in the non-invaded plots and 21 families in the plots, invaded by *S. canadensis*. The representatives of 18 families occurred everywhere (**Table 2**).

The total number of nematodes in the soil of non-invaded plots was formed by four families: *Tylenchi-*

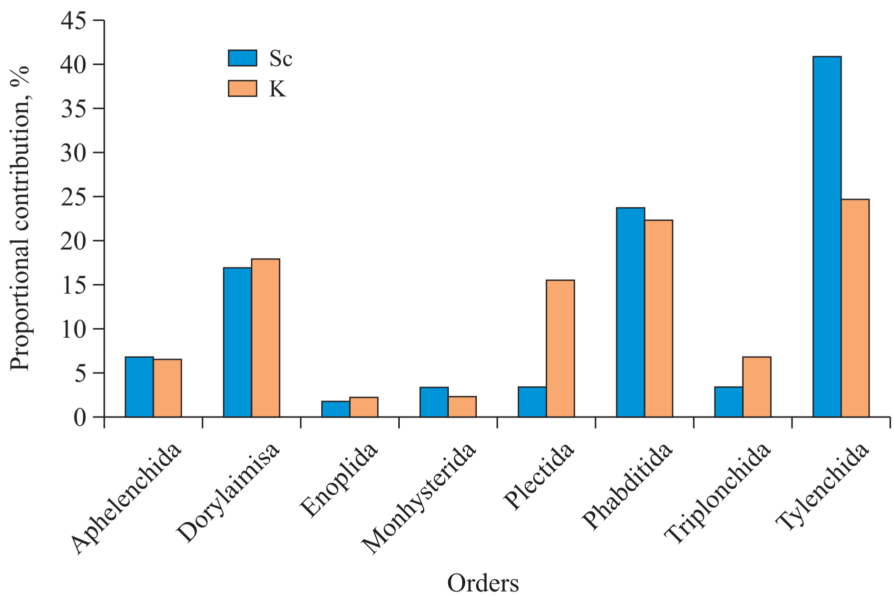

Fig. 2. The share of species of different orders in soil nematode communities of meadow ecosystems: invaded by *Solidago canadensis* (Sc) and not invaded by *S. canadensis* (K)

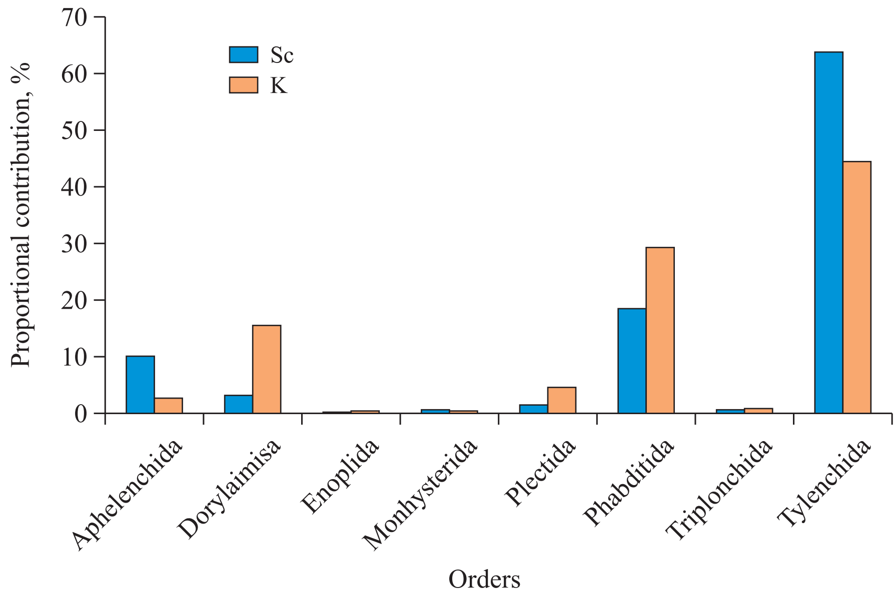

Fig. 3. The share of involvement of different orders in the soil nematode communities of the meadow ecosystems with the invasion of *Solidago* canadensis (Sc) and without the invasion of *S. canadensis* (K)

Table 2. The share of involvement (%) of the representatives of different families in soil nematode communities in the meadow ecosystems with the invasion of *Solidago* canadensis (Sc) and without the invasion of *S. canadensis* (K)

No	Family	Share in the community, %	
		Sc	K
1	*Alaimidae*	0	0.2
2	*Anguinidae*	2	0.2
3	*Aphelenchidae*	10.1	1.5
4	*Aphelenchoididae*	0	1.3
5	*Aporcelaimidae*	0.3	1.8
6	*Belonolaimidae*	1.3	1.6
7	*Cephalobidae*	14.3	18.4
8	*Criconematidae*	0.5	0
9	*Diphterophoridae*	0.5	0.3
10	*Dorylaimidae*	0	0.3
11	*Heteroderidae*	3.5	2.9
12	*Hoplolaimidae*	0.9	1
13	*Leptolaimidae*	0	0.3
14	*Monhysteridae*	0.3	0.2
15	*Neotylenchidae*	1.9	0
16	*Nordiidae*	0.6	0.2

End of the Table 2

No	Family	Share in the community, %	
		Sc	K
17	*Nygolaimidae*	0	0.1
18	*Trichodoridae*	0	0.2
19	*Panagrolaimidae*	0.9	10.3
20	*Paraphelenchidae*	0.3	0
21	*Paratylenchidae*	37.1	7.3
22	*Plectidae*	1.7	4.3
23	*Pratylenchidae*	2.4	7.3
24	*Prismatolaimidae*	0	0.4
25	*Qudsianematidae*	0.3	0.7
26	*Rhabditidae*	3.8	1.3
27	*Tylenchidae*	15.1	25
28	*Teratocephalidae*	0	0
29	*Tylencholaimidae*	2.2	12.9
Total		**100**	**100**

dae (25 % of all detected nematodes), *Cephalobidae* (18.4 %), *Tylencholaimidae* (12.9 %) and *Panagrolaimidae* (10.3 %). In the rhizosphere of *S. canadensis*, these were such families as *Paratylenchidae* (37.1 %), *Tylenchidae* (15.1 %), *Cephalobidae* (14.3 %) and *Aphelenchidae* (10.1 %).

The analysis of species by the criterion of dominance demonstrated that the main number of species belonged to the recedent and subrecedent groups (D ≤ 2.0 %) (**Table 3**). These species amounted to almost 80 % in the nematode communities of natural meadow plants, and 66 % — in plots with Canadian goldenrod. The living conditions in the rhizosphere of meadow plants may be more favorable for a larger number of nematode species than those in the rhizosphere of goldenrod.

In the investigated meadow ecosystems, only six species reached a considerable number and entered the eudominant group (D > 10 %). Only four such species were present in the non-invaded plots (9 %): *T. teres* (12.9 %), *A. bűtschlii* (14.8 %), *P. rigidus* (10.3 %), A. agricola (22 %). In the plots, invaded with *S. canadensis*, there were three eudominant species (10 %): *A. avenae* (10.1 %), A. agricola (10.7 %), *P. nanus* (37.1 %). Therefore, only one species, *A. agricola*, occurred in large numbers regardless of plant species.

Five species (11 %) in the plots of natural meadow plants and seven species (24 %) in the invaded plots belonged to the dominant and subdominant groups (D = 2.1...10.0 %). There were no common dominant species in the investigated plots, and only one subdominant species was registered — *Heterodera* sp.

In terms of trophic characteristics, soil nematode communities of the meadow ecosystems were presented with five trophic groups: bacterivores, fungivores, plant parasites, predators, and omnivores (**Fig. 4**).

Among the nematodes in the rhizosphere of the natural meadow plants, the bactivores showed the most remarkable species diversity — 20 species (or 45.5 % from all the detected ones), the fungivores were twice fewer — ten species (22.7 %), there were seven species of plant parasites (15.8 %), five species of omnivores (11.4 %), and two species of predators (4.6 %).

Table 3. The ecotrophic structure of the nematode fauna in the soil of meadow ecosystems with the invasion of *Solidago canadensis* (Sc) and without the invasion of *S. canadensis* (K)

No.	Nematode species and trophic groups	*c-p*	D	
			K	Sc
	BACTERIVORES			
1	*Acrobeles ciliatus* von Linstow, 1877	2	sr	0
2	*Acrobeloides bűtschlii* (de Man, 1884) Steiner et Buhrer, 1933	2	ed	sd
3	*Alaimus primitivus* de Man, 1880	4	sr	0
4	*Anaplectus granulosus* (Bastian, 1865) De Coninck et Sch. Stekhoven, 1933	2	sd	0
5	*Bastiania* sp.	3	sr	0
6	*Cephalobus persegnis* Bastian, 1865	2	sr	d
7	*Cervidellus cervus* Thorne, 1925	2	sr	sr
8	*Chiloplacus symmetricus* (Thorne, 1925) Thorne, 1937	2	0	r
9	*Eucephalobus mucronatus* (Kozlowska et Roguska-Wasilewska, 1963) Andrassy, 1967	3	r	0
10	*Eucephalobus oxyuroides* (de Man, 1880) Steiner, 1936	3	sr	sd
11	*Heterocephalobus elongatus* (de Man, 1880) Andrassy, 1967	2	sr	0
12	*Mesorhabditis monhystera* (Bütschli, 1873) Dougherty, 1955	1	r	0
13	*Monhystera filiformis* Bastian, 1865	1	0	sr
14	*Monhystrella bulbifera* (de Man, 1880) Schneider, 1939	1	sr	0
15	*Panagrolaimus rigidus* (Schneider, 1866) Thorne, 1937	1	ed	sr
16	*Rhabditis* sp.	1	sr	sd
17	*Rhabdolaimus terrestris* de Man, 1880	3	sr	0
18	*Plectus parietinus* Bastian, 1865	2	sr	r
19	*Plectus parvus* (Bastian, 1865) Paramonov, 1964	2	sr	0
20	*Plectus rhizophilus* (de Man, 1880) Paramonov, 1964	2	sr	0
21	*Tylocephalus auriculatus* (Bütschli, 1873) Anderson, 1966	2	sr	0
22	*Wilsonema otophorum* (de Man, 1880) Cobb, 1913	2	sr	0
	FUNGIVORES			
23	*Aglenchus agricola* (de Man, 1921) Andrassy, 1954	2	ed	ed
24	*Aphelenchoides composticola* Franklin, 1957	2	sr	0
25	*Aphelenchoides bicaudatus* (Immamura, 1931) Filipjev et Sch. Stekhoven, 1941	2	sr	0
26	*Aphelenchus avenae* Bastian, 1865	2	r	ed
27	*Boleodorus thylactus* Thorne, 1941		0	r

End of the Table 3

No.	Nematode species and trophic groups	*c-p*	D	
			K	Sc
28	*Diphtherophora communis* de Man, 1880	3	sr	sr
29	*Ditylenchus* sp.	2	sr	0
30	*Filenchus filiformis* (Butschli, 1873) Andrassy, 1954	2	sr	sd
31	*Paraphelenchus pseudoparietinus* (Micoletzky, 1922) Micoletzky, 1925	2	0	sr
32	*Psilencus* sp.	2	sr	0
33	*Tylencholaimus mirabilis* (Bütschli, 1873) de Man, 1876	4	0	sr
34	*Tylencholaimus teres* Thorne, 1939	4	ed	r
35	*Tylenchus arcuatus* sp.	2	0	sr
36	*Tylenchus* sp.	2	sd	sr
OMNIVORES				
37	*Dorylaimus* sp.	4	sr	0
38	*Eudorylaimus centrocercus* de Mann, 1880	4	sr	0
39	*Eudorylaimus* sp.	4	sr	sr
40	*Longidorella parva* Thorne, 1939	4	sr	sr
41	*Mesodorylaimus bastiani* Bütschli, 1873	4	sr	0
PREDATORS				
42	*Aporcelaimellus obtusicaudatus* (Bastian, 1865) Heyns, 1965	5	r	sr
43	*Nygolaimus* sp.	5	sr	0
PLANT PARASITES				
44	*Ditylenchus dipsaci* (Kuhn, 1857) Filipjev, 1935	2		r
45	*Helicotylenchus dihystera* (Cobb, 1893) Sher, 1961	3	sr	sr
46	*Heterodera* sp.	3	sd	sd
47	*Hirschmaniella* sp.	3	sr	0
48	*Macroposthonia* sp.	3	0	sr
49	*Paratylenchus nanus* Cobb, 1923	2	d	ed
50	*Pratylenchus pratensis* (De Man, 1880) Filipjev, 1936	3	d	sd
51	*Trichodorus primitivus* (de Man, 1880) Micoletzky, 1922	4	sr	0
52	*Tylenchorhynchus dubius* (Butschli, 1873) Filipjev, 1936	3	r	r

Note: c-p — five-point scale, corresponding to the life strategy of the species. D — dominance: ed — eudominant ; d — dominant; sd — subdominant; r — recedent; sr — subrecedent.

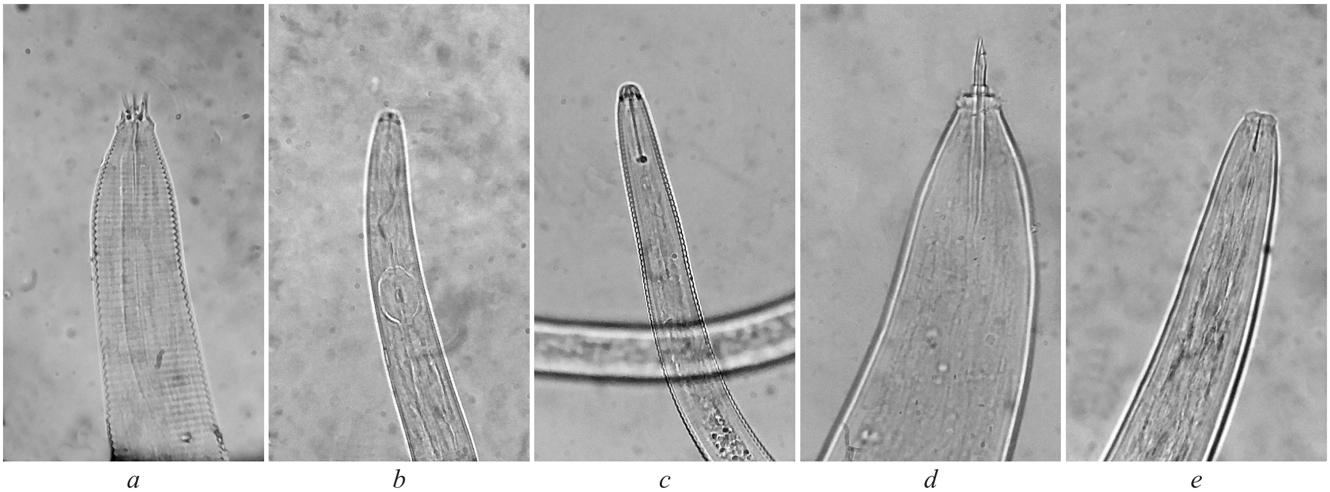

Fig. 4. Anterior ends of soil nematodes from different feeding groups in the meadow ecosystem: *a* — bacterivores (*Acrobeles*); *b* — fungivores (*Aphelenchoides*); *c* — plant parasites (*Helycotylenchus*); *d* — predators (*Aporcelaimellus*); *e* — omnivores (*Mesodorylaimus*)

Two trophic groups were notable in the rhizosphere of *S. canadensis* in terms of their species wealth, namely, fungivores and bacterivores (10 and 9 species or 34.5 % and 31.1 %, respectively, from all the detected ones). There were seven species of plant parasites but their percentage was higher in the total fauna of nematodes as compared to the non-invaded plots of meadow plants, which made up 24.1 % of all the detected species.

The omnivores and predators were presented with two and one species (6.9 % and 3.4 %, respectively) (**Fig. 5**).

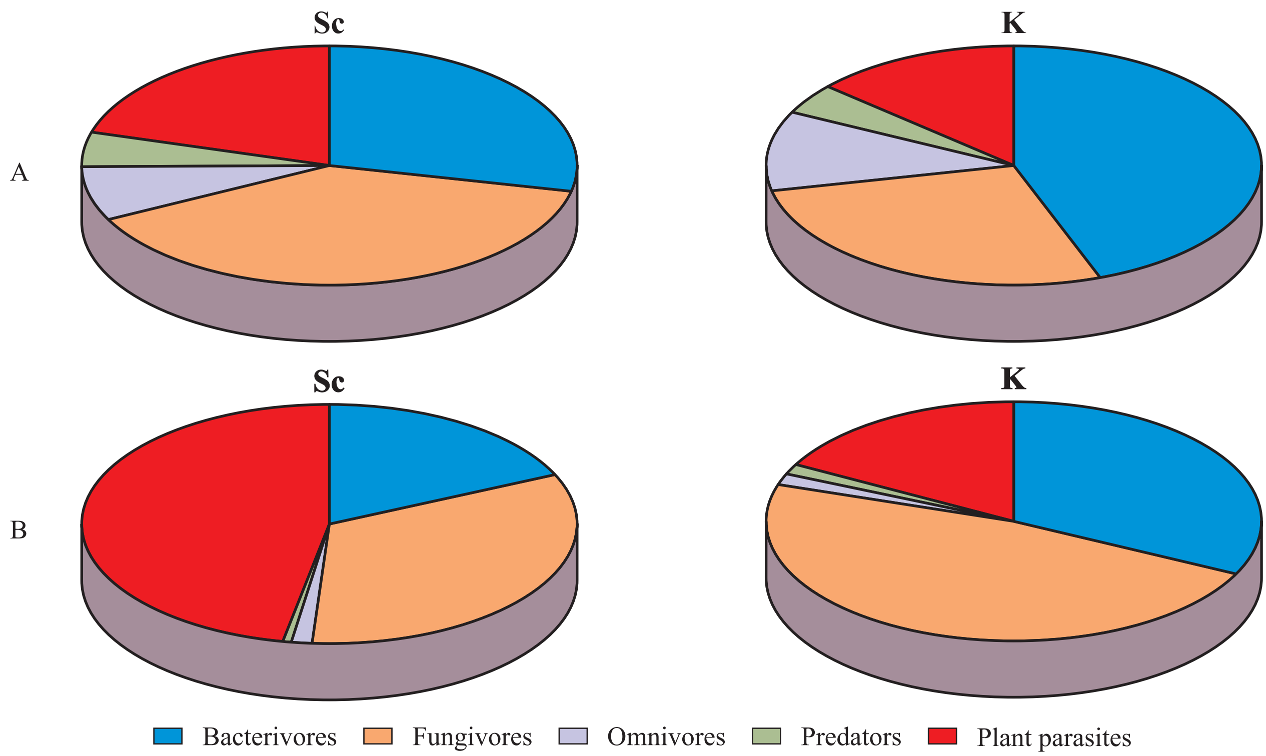

Fig. 5. The trophic structure of the soil nematode fauna of the plots in the meadow ecosystems with the invasion by *Solidago canadensis* (Sc) and without the invasion by *S. canadensis* (K): A — in terms of species representation (%), B — in terms of numbers (%)

Table 4. The ecotrophic indices of soil nematode fauna in the meadow ecosystems with the invasion by *Solidago* canadensis (Sc) and without the invasion by *S. canadensis* (K)

Index	K	Sc
f/b	1.16±0.6**	1.43±1.1**
Td	2.98±0.18*	2.75±0.15*
MI	2.4±0.15*	2.1±0.14*
Structure of domination	Fungivores → Bacterivores → Plant parasites → Predators → Omnivores	Plant parasites → Fungivores → Bacterivores → Omnivores → Predators

* $P<0.05$; ** $P<0.01$.

Bacterivores and fungivores had predominant numbers in the rhizosphere of natural meadow plants. The share of the involvement of these two groups in nematode communities was 76.4 %. The f/b index was 1.16 (**Table 4**). The number of plant parasites was 20.5 % of the total number, which was 3.7 times fewer than that of bacterivores and fungivores. The most numerous parasitic species were *P. nanus* and *P. pratensis*. The shares for the involvement of these two species did not differ considerably, approximating 7 %. Other species of plant parasites were less numerous (2.9 %–0.3 %). Only the rhizosphere of natural meadow plants was found to have such parasitic species as *T. primitivus* and *Hirschmaniella* sp. The group of nematodes-predators was larger in number than that of omnivores (1.9 % against 1.2 %).

In the plots of meadow ecosystems with *S. canadensis*, the share of plant parasites increased considerably (2.3 times), their number in the nematode communities reached 47.7 % of the total number. This group was composed of *D. dipsaci*, *H. dihystera*, *Heterodera* sp., *Macroposthonia* sp., *P. nanus*, *P. pratensis*, *T. dubius*. It was found that the abundant species was *P. nanus*, and its share of involvement was 37.1 %. The percentage of other species of phytoparasitic nematodes in the invaded plots fluctuated from 0.5 % to 3.5 %.

The second and third-ranked trophic groups in terms of numbers were fungivores and bacterivores (the cumulative share of involvement was 51.1 %), the *f/b* ratio was 1.43 (**Table 4**). In general, the trophic diversity index (Td) was higher for nematode communities inhabiting non-invaded sites (2.98) than for sites with invasion (2.75).

The analysis of soil nematodes by life strategy showed that in terms of species representation and abundance in the studied areas of meadow ecosystems, colonizers (*c-p* on scales 1 and 2), i.e. species with short life cycles that are resistant to adverse habitat conditions, prevailed (24 species or 54.5 % of all detected species in non-invaded meadow plots and 17 species or 58.6 % in plots with *S. canadensis*). It should be noted that in the soil with natural meadow plants, these are nematodes from the bacterivores group, and in the rhizosphere of the invasive plant *S. canadensis* — fungivores. The percentage of persistent species (*c-p* on the scales 4 and 5) in soil nematode communities of the natural meadow plants was 22.7 %. Only 17.2 % of such species were found in the invaded areas.

The maturity index of soil nematode communities in the studied ecosystems was generally low. The MI was 2.4 for the nematode communities in the plots with native flora and 2.1 for the nematode communities of invaded plots.

DISCUSSION

Nematodes are an important component of soil biota (Neher, 2010; Ferris, 2010). This is proven by their wide spreading, diversity, high abundance, biomass, and diverse biological relations with all the groups of the soil biota. Every change in the soil habitat of nematodes is reflected in the biodiversity of their communities (Bongers, 1990; Bongers and Ferris, 1999; Zhang et al., 2007; Mahboob et al., 2023). This group is widely used for soil state indication. The nematode species differ in their sensitivity to pollutants and disruptions in the environment. This information was used to develop indices, integrating the reactions of different taxa and trophic groups on disruptions. Therefore, the analysis of soil nematode fauna may serve as a systemic evaluation of the environment (Yeates, 2003; Mulder et al., 2005; Lu Q et al., 2020; Du Preez et al., 2022).

The impact of invasive plants on the soil environment may be evaluated by the changes in the taxonomic, trophic, and functional structure of the nematode communities. This was demonstrated in studies of different invasive plants. Fitoussi et al. (2016) determined that the trophic diversity and composition of taxa in nematode communities, inhabiting Israel's Mediterranean coastal dunes, changed considerably under the impact of the invasive plant *Heterotheca subaxillaris* (Lam.) Britton & Rusby. There was an increase in the number of bacterivores and fungivores, whereas the number of predators and omnivores did not change. Renčo and Baležentiené (2015) studied the composition of soil nematodes in central Latvia, in three environments, inhabited by *Heracleum sosnowskyi* Manden. It was shown that this invasive species reduced the number and species diversity of nematodes; the populations of bacterivores and fungivores were significantly higher in hogweed-infested habitats. In Slovakia, it was also found that the invasion of *Reynoutria japonica* Houtt. changed the structure of roundworm communities; their total number, number of species and biomass were significantly lower in areas infested by *R. japonica* (Renčo et al., 2021). At the same time, Jurova et al. (2020) reported that the invasion by *Asclepias syriaca* L. did not have a negative impact on soil nematode populations in the south of the Slovak Republic.

The eco-biological impact of goldenrod on soil nematode communities is also a subject of research by scientists from different countries. The results are not always unambiguous. This is largely due to the fact that the nematode fauna was studied in different natural and climatic zones and different ecological and cenotic conditions. According to Čerevková et al. (2019b), the number of nematodes was higher, and the number of identified species and their diversity were lower in areas with *S. gigantea* invasion than in uninhabited meadows. Xiangqi et al. (2011) reported that the number of genera and diversity of phytonematodes did not differ under *S. canadensis* and the natural species *Phragmites australis* (Cav.) Trin. ex Steud. In our study, the number, species diversity, and taxonomic wealth of soil nematodes in the rhizosphere of *S. canadensis* decreased by 1.4–1.7 times compared to the natural phytocoenosis.

Regarding the trophic structure of nematode communities, scientists unanimously noted that under the influence of the invasive species, there were changes in the diversity of trophic groups, their composition and number, especially in plant parasites and fungivores.

In the study by Čerevková et al. (2019b), the number of plant parasites in the soil was higher under *S. gigantea* invasion than in uninhabited areas of meadows. The authors explain it by the characteristics of this plant. *S. gigantea* often grows in bumps, forming mainly single-species stands. Therefore, the number of some plant parasite species will be higher, as nutrient use efficiency and biomass production are high in these areas. The plant has a well-developed root system, where some phytoparasitic nematodes can find their food. On the contrary, Xiangqin et al. (2011), based on their observations, claim that *S. canadensis* is less vulnerable to parasitic nematodes than the local species *P. australis*. The authors note a decrease in the share of plant parasites in the soil dominated by *S. canadensis*. In the investigated meadow ecosystems, the number of plant parasites increased 2.3 times under the influence of *S. canadensis*. Thus, our results are in line with the reports of Slovak scientists (Čerevková et al., 2019b). We agree with their opinion that this phenomenon is related to the characteristics of the plant, which has a well-developed root system with fibrous creeping rhizomes. This creates conditions for the development and feeding of endoparasitic, ectoparasitic and semi-endoparasitic root-feeding nematodes. In areas, invaded by *S. canadensis*, we have recorded 7 species of plant parasites. According to the type of their feeding, four species belonged to ectoparasites (*Macropostonia* sp., *T. dubius*, *P. nanus*, *H. dihystera*), 2 species — to endoparasites (*P. pratensis*, *D. dipsaci*), and one species — to semiendoparasites (*Heterodera* sp.). The recorded species are polyphagous. *P. nanus* was a particularly abundant parasitic species. Its number in 100 g of soil was 236 nematodes (37.1 %). This trophic group can complicate the functioning of meadow ecosystems and contribute to the replacement of meadow species (Verschoor et al., 2002).

It is known that bacterivores and fungivores are involved in nitrogen mineralization, and their ratio is an indicator of the pathway via which organic material decomposes (Ruess, 2003; Ruess and Ferris, 2004). Scharfy et al. (2010) observed a significant decrease in bacterial biomass and an increase in fungal biomass in plant communities dominated by *S. gigantea*. Quist et al. (2014) and Harkes et al. (2021) attributed the high abundance of fungivores to an increase in the number of soil myxomycetes that fungivores feed on. A similar trend toward an increase in the number of fungivores in the soil under Canadian goldenrod was observed by Xiangqin et al. (2011). *S. gigantea* invasion significantly affected the number of fungivores in the studies conducted in meadow ecosystems in Slovakia (Cerevková et al., 2019b).

We found that in the meadow ecosystems in non-invaded plots and the ones, invaded by *S. canadensis*, the representatives of the trophic group of fungivores were more numerous in nematode communities (41.1 % and 30.1 %, respectively) than bacterivores (35.3 % and 21 %, respectively). The ratio of these groups (f/b) was higher in the invaded plots (1.43) than in the plots of natural meadow plants (1.16). Based on the works of Ruess and Ferris (2004); Scharfy et al. (2010) and our own results, it can be assumed that fungi play a significant role in the decomposition of organic material in the soil of mesophytic meadows under Canadian goldenrod.

The quantitative indicators of trophic groups of predators and omnivores in soil nematode communities differ in the invasion by different plant species. Cerevková et al. (2019a) indicate that the number of omnivores was significantly higher in plots, uninhabited by *Fallopia japonica* (Houtt.) Ronse Decr., than in the invaded ones; no differences in predator abundance were found. *S. gigantea* invasion in meadow ecosystems in Slovakia did not affect the density of nematode omnivores and predators (Cerevková et al., 2019b). Our results show that the invasion by *S. canadensis* reduced the number of predators and omnivores compared to non-invaded areas (by 6.3 and 1.3 times, respectively). This is consistent with the data published by Renčo et al., 2021, who studied the impact of *R. japonica* invasion on soil nematode communities.

The nematode community maturity index (MI) was proposed to assess soil condition by the composition of the free-living nematode community (Bongers, 1990). Higher index values are characteristic of a less disturbed and stable environment. The maturity index in the investigated ecosystems was lower in areas with invasion (2.1 vs. 2.4).

Similar results were obtained in areas, invaded by *H. sosnowskyi*, in central Lithuania (Renčo et al., 2015). In the invaded areas of meadow ecosystems of roadside slopes, the MI was 2.40, while in the control, it was 2.85. With *R. japonica* invasion, the MI was lower (1.99 on average) than in non-invaded plots (2.27), regardless of the years of study (Renčo et al., 2021). MI values in plots with *S. gigantea* invasion in meadow ecosystems in Slovakia did not differ significantly, averaging 2.0–2.4 (Cerevková et al., 2019b). Lower values of the maturity index indicate impaired conditions of the invaded ecosystems (Ferris et al., 2001).

Low MI values also indicate the predominance of colonizer species (c-p on scales 1 and 2), which are more adapted to unfavorable habitat conditions and have short life cycles. In the meadow plots with *S. canadensis* invasion in our study, such species accounted for 58.6 % of the total species list, and by number they made up 84 %. This is 1.1 times more in terms of the number of species and 1.2 times more in terms of the number of species than in non-invaded areas.

Thus, the results of our study indicate that the invasion of *S. canadensis* in the ecosystems of true mesophytic meadows had negative consequences on the structure of soil nematode communities. Compared to the areas of natural meadow plants, there was a decrease in their number, species, and trophic diversity; the number of two trophic groups increased, namely, plant parasites and fungivores. Indicators of trophic wealth and maturity of the nematode community decreased during the invasion of Canadian goldenrod.

Due to the fact that *S. canadensis* is widespread in meadows, pastures, reclaimed marshes, forests, forest glades, and clearings of Polissia, further study of its impact on the soil environment of different ecosystems is needed, depending on many factors (soil, season, climate, and species composition of local plant communities). Soil nematode communities can serve as an indicator group of general trends in changes in soil processes during the invasion of Canadian goldenrod. Therefore, phytonematological studies are a promising direction.

CONCLUSIONS

The obtained results give an idea of the influence of the invasive species of Canadian goldenrod on the structure of soil nematode communities in the ecosystem of true mesophytic meadows of the association Festucetum pratensis Soó 1938, which were formed on turf-medium podzolic light clay soils of Ukrainian Polissia.

A total of 52 species of soil nematodes were registered in the meadow ecosystems. The index of taxonomic wealth of nematode communities in plots, invaded by *S. canadensis*, was 1.4 times lower. On the plots of natural meadow plants, 44 species were registered, on the invaded ones — 29, which is 1.5 times less. The core of the soil nematode communities of the meadow ecosystem in both non-invaded plots and plots with *S. canadensis* invasion was made up of representatives of the orders Tylenchida and Rhabditida, but their proportion in the communities was different. In the invaded plots, Tylenchida significantly prevailed in the number of detected species (1.7 times) and in number (3.4 times).

In the areas with *S. canadensis* invasion, three species belonged to the eudominant group: *A. avenae* (proportion in the community — 10.1 %), *A. agricola* (10.7 %), P. nanus (37.1 %). Only four such species were present in the non-invaded plots: *T. teres* (12.9 %), *A. bűtschlii* (14.8 %), *P. rigidus* (10.3 %), *A. agricola* (22 %).

The trophic structure of nematode communities in the plots with Canadian goldenrod also had its own peculiarities. The index of trophic diversity was higher for nematode communities inhabiting non-invaded plots (2.98) than for plots with invasion (2.75). In terms of species wealth, bacterivores and fungivores dominated the plots of natural meadow plants and plots with invasion. These two groups were also more numerous in non-invaded areas of the meadow ecosystem. The cumulative share of the involvement of bacterivores and fungivores in the nematode communities was 76.4 %. The f/b index was 1.16. While plant parasites dominated in the areas of meadow ecosystems with *S. canadensis* infestation, their number in the nematode communities reached 47.7 % of the total. Fungivores and bacterivores were the next most abundant (the share of participation was 51.1 %), with an f/b ratio of 1.43.

The Bongers maturity index (MI) of the nematode community was lower in plots with *S. canadensis* (2.1) than in plots with natural meadow plants (2.4). In the areas with goldenrod invasion, the species with short life cycles and more adapted to unfavorable habitat conditions prevailed in terms of species representation and abundance. Such species accounted for 58.6 % of the detected ones, and their number was 84 % of the total. These indicators demonstrate the instability of soil conditions in areas with Canadian goldenrod invasion for nematode communities.

The results emphasize the importance of monitoring the impact of invasive plant species on the functioning of soil biocenoses, as such changes can have long-term consequences for biodiversity and ecosystem services of grasslands. Further research should be aimed at establishing the mechanisms by which *S. canadensis* affects the structure of nematode communities, in particular, via possible changes in soil chemistry, the release of allelopathic compounds, or changes in the microbial composition of the rhizosphere.

These studies emphasize the need to monitor invasive species and develop strategies for their control in order to preserve soil biodiversity and maintain sustainable grassland management.

Adherence to ethical principles. This article does not contain the results of any studies involving human participants and animals performed by any of the authors.

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ІНВАЗИВНИЙ ЕФЕКТ *SOLIDAGO CANADENSIS* L. НА СТРУКТУРНІ ХАРАКТЕРИСТИКИ УГРУПОВАНЬ ҐРУНТОВИХ НЕМАТОД В ЕКОСИСТЕМАХ СПРАВЖНІХ МЕЗОФІТНИХ ЛУКІВ

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Мета. Порівняти еко-трофічну структуру угруповань ґрунтових нематод екосистем справжніх мезофітних луків на неінвазованих ділянках і з інвазією *Solidago canadensis* L. **Методи.** Зразки ґрунту з ризосфери природних лучних рослин та *S. canadensis* були зібрані у вересні 2021 року у двох лучних екосистемах, розташованих на околицях сіл Шостовиця та Ладинка Чернігівської області. Виділення нематод проводили лійковим методом Бермана з наважки 20 г. Експозиція становила 48 год., після чого нематод фіксували ТАФом (триетаноламін+формалін+вода у співвідношенні 2:7:91). Перерахунок чисельності здійснювали на 100 г абсолютно сухого ґрунту. Аналізували чисельність, таксономічний склад, домінування, трофічну структуру угруповань нематод. Розраховували індекси таксономічного багатства, різноманітності Менхініка, Бергера–Паркера, індекс подібності Жаккара та індекс зрілості угруповання нематод Бонгерса. **Результати.** Середня чисельність нематод у 100 г ґрунту становила 1075 особин у ризосфері природних лучних рослин та 636 особин у ризосфері *S. canadensis*. Всього зареєстровано 52 види: 44 — на ділянках з місцевими рослинами, 29 — в купинах золотушника канадського; індекс Менхініка відповідно дорівнював 1,34 та 1,15. Таксономічне багатство угруповань нематод у ризосфері місцевих рослин також вище; ST = 116; у ризосфері золотушника канадського ST = 84. Загальна чисельність нематод природних лучних рослин формувалася за рахунок чотирьох родин: *Tylenchidae*, *Cephalobidae*, *Tylencholaimidae* та *Panagrolaimidae* (25 %; 18,4 %; 12,9 %; 10,3 % всіх виявлених особин відповідно). В ризосфері *S. canadensis* переважали: *Paratylenchidae*, *Tylenchidae*, *Cephalobidae* та *Aphelenchidae* (37,1 %; 15,1 %; 14,3 %; 10,1 % відповідно). Індекс трофічної різноманітності виявився вищим для угруповань нематод, які населяли неінвазовані ділянки (2,98), ніж ділянки з інвазією золотушником канадським (2,75). В угрупованнях нематод ризосфери корінних лучних рослин кількісно переважали сапробіонти та мікогельмінти. Частка участі цих двох груп разом становила 76.4 %. На ділянках лучних екосистем з інвазією *S. canadensis* найбільш чисельними виявилися фітогельмінти та мікогельмінти. Чисельність нематод інших трофічних груп була невеликою і не зазнала змін. **Висновки.** Встановлено, що на ділянках з інвазією золотушника канадського видове багатство, чисельність, таксономічна та трофічна різноманітність угруповань ґрунтових нематод зменшились. Зросла чисельність фітогельмінтів (в 2,3 раза); співвідношення мікогельмінтів і сапробіонтів на інвазованих ділянках було вище (в 1,2 раза). Індекс зрілості угруповання нематод Бонгерса нижче на інвазованих ділянках у порівнянні з неінвазованими (2,1 і 2,4) і вказує на погіршення умов середовища на лучних ділянках з інвазією *S. canadensis*. Проведені дослідження підкреслюють необхідність моніторингу інвазивних видів і розробки стратегій їхнього контролю з метою збереження ґрунтового біорізноманіття та підтримки сталого луківництва.

Ключові слова: справжні мезофітні луки, *Solidago canadensis*, інвазія, угруповання ґрунтових нематод, таксономічна різноманітність, трофічна група.