

ORIGINAL PAPER

Diversity and trophic structure of litter-dwelling nematodes show significant differences between declining spruce monocultures and natural old-growth stands in Ukrainian Carpathians

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ABSTRACT

Critical decline of managed spruce monocultures health in the Beskids presents a challenge for all segments of forest management, thus understanding all aspects of this process is crucial to address this threat. While numerous factors contributing to the degradation of spruce monocultures in the Carpathians have been investigated, there is limited knowledge regarding possible connections between this phenomenon and alterations in soil nematode communities. Thus, analysis of the structural and functional organization of nematode communities is of scientific and practical importance because by comparing nematode communities between natural and managed temperate forests it is possible to determine the degree of transformation of the latter ecosystems, as anthropogenic activities lead to changes in nematode communities. The aim of our study was to analyze and compare nematode communities found in different layers of forest litter in managed spruce monocultures with visible signs of decline and unmanaged old-growth mixed forest. The research was conducted in the area of the 'Skole Beskids' National Nature Park in Ukraine. An analysis of collected samples of forest litter revealed 104 species belonging to 5 nematode communities (plant parasites, fungivores, bacterivores, predators, and omnivores). The species diversity of nematodes was twice as high in an unmanaged old-growth mixed forest (91 species) compared to managed spruce monocultures (47 and 51 species in forest aged 60-70 years and 70-80 years, respectively). The significantly higher species diversity in the old-growth mixed forest than in spruce monocultures applied to predatory, bacterivorous, and omnivorous species, while species diversity of fungivorous and plant-parasitic species was similar in the old-growth mixed forest and spruce monocultures. The abundance of nematodes belonging to all trophic groups differed significantly between the old-growth mixed forest and spruce monocultures. In contrast, both investigated spruce monocultures were similar to each other in this regard. The abundance of plant-parasitic and fungivorous nematodes per square meter of forest litter was significantly lower in the old-growth mixed forest than in spruce monocultures. In contrast, the abundance of bacterivorous, predatory, and omnivorous nematodes showed the opposite pattern and was significantly higher in the old-growth mixed forest than in managed

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spruce monocultures. Described changes in nematode communities with the conversion of natural old-growth mixed forest into managed spruce monocultures may contribute to deterioration of spruce forests health.

KEY WORDS

litter-dwelling nematode communities, old-growth mixed forest, spruce monocultures

Introduction

The Ukrainian Carpathians form an integral component of the broader Eastern Carpathian mountain range. They feature distinctive altitudinal vegetation belts, encompassing the foothill deciduous forest zone, the lower mid-altitude mixed forest zone, the upper coniferous forest zone, and the high-altitude subalpine and alpine zones. Before the 16th century, the Carpathians were predominantly covered by beech-fir forests with a limited presence of spruce (Hlásny and Sitková, 2010). Over past centuries, certain natural ecosystems in the Ukrainian Carpathians have encountered substantial human-induced influences, which have molded their landscape and vegetation. At first, the foothill forests were logged and utilized for livestock grazing. As time passed and settlements expanded along with the cultivation of adjoining lands, the surrounding forests saw further reduction. The summer pastures on the alpine meadows, known as ‘polonynas,’ were enlarged through the clearance or setting fire to the subalpine open woodlands and shrubs forming the upper forest limit. From the mid-19th century until World War I, the thriving oil mining and refining industry, which had its roots in the Carpathian region, profoundly impacted the environment and landscape of the Eastern Carpathians. The Carpathian mountain forests have been subjected to intense exploitation due to the surging need for timber, which is primarily used in drilling towers, wells, pipelines, tanks, and barrels. Subsequently, in the areas of clearcuts, the old-growth natural beech and fir-beech forests were replaced by artificially planted, highly productive yet ecologically precarious Norway spruce monocultures. Nowadays, the spruce forests in the Beskids region have become one of the central areas experiencing a spruce decline across Europe. This phenomenon commenced around 2002, although initial indications of reduced tree health had been noted in certain locations as early as the late 1990s (Hlásny and Sitková, 2010). Symptoms of spruce decline encompass needle loss and discoloration, shortened needles and shoots, decreased stem and height growth, stem necrosis and resin leakage. Several factors responsible for spruce forest decline have been identified, with fungal pathogens playing an important role. Studies in Slovak Beskids dating back to 1972 shows a notable rise in the occurrence of fungal diseases, particularly in the period after 2002 (Kunca *et al.*, 2007, 2009). Fungi that parasitize the roots of living trees are of particular concern due to their ability to cause substantial harm. Their presence leads to notable production losses as they weaken root systems, hinder growth, and sap the vitality of the trees. In the Beskids, the genus *Armillaria* is widely recognized as a significant representative of such fungi (Holuša and Liška, 2002, Jankovský *et al.*, 2003, Grodzki, 2007). A multitude of environmental and human-induced factors within managed spruce forests in the Beskids region can trigger widespread forest infestations by parasitic fungi that cause root and wood decay. Trees experiencing physiological stress as a result of water imbalances have been identified as highly susceptible to fungal infections (Černý, 1989). Additionally, prolonged air pollution is another contributing factor in heightening the virulence of pathogenic fungi (Kodrik, 2003). For instance, a two- to three-fold greater area damaged by *Armillaria* spp. was noted in the 1980s within the industrial regions of Poland when compared

to areas located farther away and experiencing lower pollution levels (Grzywacz and Ważny, 1973). In regions characterized by acidified soils with a pH level below 4.5, deficiency of essential mineral nutrients like potassium, magnesium, and calcium, which play a crucial role in plant water absorption, is observed. Consequently, even trees situated in relatively moist areas may be susceptible to water shortages which has the potential to enhance the aggressiveness of pathogenic fungi (Larcher, 1995; Maňkowska, 2004; Kurjak, 2009), being more prevalent and conspicuous in second-generation forests (Jančařík and Jankovsky, 1999). A fungal infection is typically accompanied by a beetle infestation. The emission of volatile compounds by distressed trees, triggered by factors like drought or acute attack by *Armillaria* spp., makes them alluring targets for colonization by bark beetles *Ips typographus* (L.) (Madziara-Borusiewicz and Strzelecka, 1977). Pfeffer (1950) observed that more than 90% of spruces attacked by bark beetles were infected by *Armillaria* spp. Physiologically compromised, large-scale managed spruce forests located in the Beskids beyond the natural range of spruce, coupled with ongoing climate change, create conditions favorable for the emergence of unprecedented bark beetle infestations. The combined impact of insects and wood-decaying fungi exerts synergistic pressure, serving as a contributing and primary factor leading to the decline of spruce forests, which can occur as early as 40-50 years of age (Vakula *et al.*, 2009). In ecosystems that operate within their natural balance, *I. typographus* is not typically an aggressive or primary factor causing the death of healthy trees. However, when its populations reach a critical threshold, they can successfully attack nearly any mature tree, whether healthy or not. Such outbreaks can occur particularly swiftly in spruce forests that have been damaged by wind, snow, or stressed by factors like drought or air pollution (Schroeder and Eidmann, 1993; Grodzki *et al.*, 2004). Deterioration in the health status of spruce stands was also caused by worsened soil condition (Hlásny and Sitková, 2010).

Critical decline of forest health in the Beskids presents a challenge for all segments of forest management, thus understanding all aspects of this process is crucial to address this threat. While numerous factors contributing to the degradation of spruce monocultures in the Carpathians have been investigated, there is limited knowledge regarding possible connections between this phenomenon and alterations in soil nematode communities. Soil nematodes are considered an important component for preserving and enhancing the stability of ecosystem functions (Bardgett and van der Putten, 2014). Forest soil nematodes exhibit ubiquity, abundance, functional diversity, and a high susceptibility to environmental changes. They play roles in every significant trophic level of the soil food chain and are accountable for numerous essential processes crucial to the proper functioning of soil ecosystems (van den Hoogen *et al.*, 2019, Wilschut and Giesen 2020). Examining the composition of nematode fauna provides a foundation for the ecological evaluation of soil (de Goede and Bongers, 1994).

Nematodes' contribution to ecosystems can be examined across various organizational levels, including the individual, population, species, and community. It appears reasonable to assess their role within a systems analysis framework at the community level. Nematode communities consist of a variety of species categorized into five major groups based on their dietary preferences, including plant parasites, bacterial and fungal consumers, predators, and omnivores (Wasilewska, 1997). In natural forest soil, the most prevalent nematode groups primarily consume bacteria, and in conjunction with nematodes that feed on fungi, they have a pivotal role in breaking down organic materials and facilitating the nutrient cycle in the soil (Ingham *et al.*, 1985; Wasilewska, 1997; Ferris *et al.*, 2012). Herbivorous nematodes consume and harm plant roots, potentially exerting an adverse influence on plant development. An upsurge in their population or a pronounced prevalence of herbivorous species can occur in biotopes with characteristics similar to

those in long-term monocultures and is typically linked to soil deterioration (Wasilewska, 1997; Ferris *et al.*, 2012). On the other hand, predators and omnivores belong to the highest trophic level of soil microfauna. An elevation in the prevalence of them might serve as an indicator of the ecological naturalness of the environment (Yeates *et al.*, 1993; Wasilewska, 1997). The examination of nematode communities offers insights into ecological succession, alterations in the decomposition pathways within soil food webs, nutrient levels, soil fertility, acidity, and the impacts of soil pollutants (Bongers and Ferris, 1999). Thanks to their ecological significance and their ability to respond to environmental changes nematodes serve as valuable soil condition indicators (Yeates *et al.*, 1993; Bongers and Ferris, 1999; Wilschut and Giesen 2020).

Previous studies have suggested that changes in aboveground vegetation could affect soil nematode communities (de Goede *et al.*, 1993). Both in controlled pot experiments and field studies, the type of tree species had discernible effects on the compositions of soil nematode communities (Keith *et al.*, 2009; Cesarz *et al.*, 2013). Within forest ecosystems, tree species can be a particularly significant factor in shaping nematode communities since it constitutes the primary component of the forest. Thus, analysis of the structural and functional organization of nematode communities is of scientific and practical importance because by comparing nematode communities between natural and managed temperate forests it is possible to determine the degree of transformation of the latter ecosystems, as anthropogenic activities lead to changes in nematode communities. The aim of our study was to analyze and compare nematode communities found in different layers of forest litter in managed spruce monocultures with visible signs of decline and unmanaged old-growth mixed forest (beech-fir-spruce *Piceeto-Abieto-Fageta*).

Methods

The research was conducted in the area of the 'Skole Beskids' National Nature Park in Ukraine. Three study plots, each with an area of 400-500 square meters, were designated: 1) an unmanaged old-growth mixed forest (beech-fir-spruce *Piceeto-Abieto-Fageta*) located at 48.984530, 23.462157; 2) a managed spruce monoculture *Piceeta* aged 60-70 years (48.907398, 23.429908) and 3) a managed spruce monoculture *Piceeta* aged 70-80 years (48.917614, 23.409201).

At each study plot, samples of the forest litter were collected beneath spruce trees from the L, F, and H horizons. The L horizon represents the uppermost layer of the forest litter, composed of fallen leaves and plant residues. This layer plays a crucial role in maintaining moisture and regulating soil temperature. The F horizon is the fermentation layer, where microorganisms begin to break down leaves and other organic compounds present in the forest litter. The H horizon is the humus layer, where the final breakdown of organic matter takes place. This layer enriches the soil with nutrients.

Throughout the vegetation season, samples were collected three times at each location: in spring (mid-May), summer (mid-June), and autumn (mid-September). The research was conducted over two vegetation seasons, in the years 2014 and 2015. A total of 270 forest litter samples were collected and subsequently analyzed for the presence of nematodes. The samples were collected using a biocenometer with a surface area of 25 cm².

The nematodes were extracted from the collected forest litter samples using the Baermann method. This method takes advantage of the nematodes' ability to move towards water. The forest litter samples were placed on a sieve with a 1 mm mesh size lined with filter paper. The sieve was positioned in a funnel filled with water to a level that submerged the forest litter sample. Nematodes migrated into the water and gathered at the bottom of the tube connected to the funnel with a rubber tube. The water separation of nematodes took 2 days at room temperature.

Subsequently, the tube was heated to 60°C, two-thirds of the water was removed, and the remaining volume was replenished with a 3% formalin solution or 70% ethanol. The Baermann funnel method, which relies on nematode mobility may not be effective for isolating specimens of the Criconematidae family due to their low mobility. Thus for extraction of specimens from this family we modified funnel method. After the other nematodes left the sample we immersed the sample in the funnel in water. We gently agitated the sample to release nematodes and allowed them to settle into the water below the funnel. Then we collected the water containing nematodes. Further procedure was the same as with the other nematodes collected in Baermann funnel method.

Next, 1 ml of the extracted sample suspension with the nematodes were transferred to a Petri dish and examined under a microscope at 400× magnification. The nematodes were identified both to the species and trophic group. Species identification was carried out based on De Man indices and was limited to sexually mature individuals. The determination of trophic group membership relied on literature information about the feeding habits of each species, as well as the morphology of the mouthparts, which is a key morphological characteristic defining nematode feeding types. G. Yeates method (Yeates *et al.*, 1993) was also employed for trophic group determination.

The numbers of nematodes of each trophic group was converted to a unit of area [m²], using a formula:

$$N = (v_2 / v_1 \cdot n_1) \cdot 10000/\text{surf nematodes per m}^2 \quad (1)$$

where:

- n_1 – a number of nematodes in v_1 ,
- v_1 – volume [ml] of the counted suspension obtained from v_2 ,
- v_2 – volume [ml] of the extracted sample total suspension,
- surf – sample surface [cm³] (van Bezooijen, 2006).

Differences in the abundance of individuals representing nematode communities (plant parasites, fungivorous, bacterivorous, predatory and omnivorous) between an unmanaged old-growth mixed forest and managed spruce monocultures were analyzed using the Mann-Whitney U test.

The differences in species diversity between the old-growth mixed forest and spruce monocultures as well as between two types of spruce monocultures were analyzed using proportion test.

Results

ANALYSIS OF NEMATODE SPECIES IN AN UNMANAGED OLD-GROWTH MIXED FOREST AND MANAGED SPRUCE MONOCULTURES. An analysis of collected samples of forest litter revealed 104 species belonging to 5 nematode communities (Table 1). Noteworthy, the species diversity of nematodes was twice as high in an unmanaged old-growth mixed forest (91 species) compared to managed spruce monocultures (47 and 51 species in forest aged 60-70 years and 70-80 years, respectively). The differences between the old-growth mixed forest and spruce monocultures were statistically significant (proportion test: $p < 0.001$), while both types of spruce forest did not differ statistically (proportion test: $p = 0.572$). The significantly higher species diversity in the old-growth mixed forest than in spruce monocultures applied to predatory, bacterivorous, and omnivorous species, while species diversity of fungivorous and plant-parasitic species was similar in the old-growth mixed forest and spruce monocultures (Fig. 1).

Table 1.

A list of species identified in samples of forest litter and their classification to trophic groups (× – present)

Nº	Taxon	Nematode community type	Old-growth mixed forest	Spruce monoculture 60-70 years	Spruce monoculture 70-80 years
Chromadorida					
1	<i>Odontolaimus chlorurus</i> de Man 1880	bacterivorous	×		
Enoplida					
2	<i>Tripula affinis</i> de Man 1880	predatory	×	×	×
3	<i>T. filicaudata</i> de Man 1880	predatory	×		×
4	<i>T. longicaudata</i> de Man 1880	predatory	×		
5	<i>Trischistoma monochystera</i> de Man 1880	predatory	×		
6	<i>Cryptonchus</i> sp.	bacterivorous	×		
7	<i>Tobrilus</i> sp.	predatory	×		
8	<i>Ironus filicaudatus</i> Daday 1899	predatory	×		
9	<i>Alaimus editorus</i> Siddiqi et Husain 1967	bacterivorous	×	×	×
10	<i>A. primitivus</i> de Man, 1880	bacterivorous	×		×
11	<i>Amphidellus dolichurus</i> Siddiqi et Husain 1967	bacterivorous	×		×
12	<i>Amphidellus</i> sp.	bacterivorous	×		
Monchysterida					
13	<i>Monhystera aenariensis</i> Meyl 1953	bacterivorous	×		
14	<i>Prismalaimus dolichurus</i> de Man 1880	bacterivorous	×	×	×
Teratocephalida					
15	<i>Teratocephalus terrestris</i> Bütschli 1873	bacterivorous	×	×	×
Plectida					
16	<i>P. armatus</i> Bütschli 1873	bacterivorous	×	×	×
17	<i>P. cirratus</i> Bastian 1865	bacterivorous	×		
18	<i>P. parietinus</i> Bastian 1865	bacterivorous	×		
19	<i>P. parvus</i> Bastian 1865	bacterivorous	×		
20	<i>P. longicaudatus</i> Bütschli 1873	bacterivorous	×	×	×
21	<i>P. rizophilus</i> de Man 1880	bacterivorous	×	×	×
22	<i>Anaplectus granulatus</i> Bastian 1865	bacterivorous	×	×	×
23	<i>Wilsonema otophorum</i> de Man 1880	bacterivorous	×	×	×
24	<i>Tylocephalus auriculatus</i> Bütschli 1873	bacterivorous	×	×	×
Araolaimida					
25	<i>Bastiana gracilis</i> de Man 1880	bacterivorous	×		
Mononchida					
26	<i>Clarcus papillatus</i> Bastian 1865	predatory	×	×	×
27	<i>C. parvus</i> de Man 1880	predatory	×		
28	<i>Prionchulus muscorum</i> Dujardin 1845	predatory	×		
29	<i>Mononchulus brachyuris</i> Bütschli 1873	predatory	×		
30	<i>Mylonchulus striatus</i> Thorne 1924	predatory	×		
31	<i>Anatonchus tridentatus</i> de Man 1880	predatory	×		
32	<i>Iotonchus zschokkei</i> Menzel 1913	predatory	×		
Dorylaimida					
33	<i>Laimydorus filiformis</i> Bastian 1865	omnivorous	×	×	×
34	<i>L. vixamictus</i> Andrassy 1969	omnivorous	×		
35	<i>Mesodorylaimus bastiani</i> Bütschli 1873	omnivorous	×	×	×
36	<i>M. meylli</i> Andrassy 1958	omnivorous	×		
37	<i>M. mesonyctius</i> Kreis 1930	omnivorous	×		

Table 1. continued

N ^o Taxon	Nematode community type	Old-growth mixed forest	Spruce monoculture 60-70 years	Spruce monoculture 70-80 years
38 <i>M. recurvus</i> Andrassy 1964	omnivorous	x		
39 <i>Eudorylaimus acuticaudatus</i> de Man 1876	omnivorous	x		
40 <i>E. bryophilus</i> de Man 1880	omnivorous	x	x	x
41 <i>E. bureshi</i> Andrassy 1958	omnivorous	x	x	x
42 <i>E. carteri</i> Bastian 1865	omnivorous	x		
43 <i>E. ettersbergensis</i> de Man 1885	omnivorous	x		
44 <i>E. krygeri</i> Ditlevsen 1928	omnivorous	x		
45 <i>E. maritus</i> Andrassy 1959	omnivorous	x	x	x
46 <i>E. microdorus</i> de Man 1880	omnivorous	x		
47 <i>E. monohystera</i> de Man 1880	omnivorous	x		
48 <i>E. paraobtusicaudatus</i> Micol 1929	omnivorous	x		
49 <i>E. simmus</i> Andrassy 1959	omnivorous	x		x
50 <i>E. sp.</i>	omnivorous	x		
61 <i>Aporcelaimus superbus</i> de Man 1880	omnivorous	x	x	x
62 <i>Aporcelaimellus obtusicaudatus</i> Bastian 1865	omnivorous	x		x
63 <i>A. obscurus</i> Thorne et Swanger 1936	omnivorous	x		
64 <i>Nygolaimus brachyuris</i> de Man 1880	predatory	x		
65 <i>Enchodellus macrodorus</i> de Man 1880	omnivorous	x		
66 <i>Tylencholaimus mirabilis</i> Bütschli 1873	fungivorous	x	x	x
67 <i>T. stecki</i> Steiner 1914	fungivorous	x		
68 <i>Tylencholaimellus coronatus</i> Thorne 1939	fungivorous	x	x	x
69 <i>Dipherophora communis</i> de Man 1880	fungivorous		x	
70 <i>Triplonchium minor</i> Cobb 1920	fungivorous	x	x	x
<i>Rhabditida</i>				
71 <i>Rhabditis brevispina</i> Claus 1863	bacterivorous	x	x	x
72 <i>Rh. Filiformis</i> Bütschli 1875	bacterivorous	x		
73 <i>Parasitorhabditis piniperde</i> Fuchs 1937	bacterivorous	x		
74 <i>Parasitorhabditis</i> sp.	bacterivorous		x	x
75 <i>Diploscapter coronata</i> Cobb 1893	bacterivorous	x		
76 <i>Bunonema reticulata</i> Richters 1905	bacterivorous	x		
77 <i>Eucephalobus elongatus</i> de Man 1880	bacterivorous	x	x	x
78 <i>E. latus</i> Cobb 1937	bacterivorous	x		
79 <i>E. mucronatum</i> Kozlovska et Wasilewska 1963	bacterivorous	x	x	x
80 <i>Acrobeles ciliatus</i> von Linstow 1877	bacterivorous	x	x	x
81 <i>Ceroidellus serratus</i> Thorne 1925	bacterivorous	x	x	x
82 <i>Chiloplacus propinguus</i> de Man 1921	bacterivorous	x		
83 <i>Acrobeloides buetschli</i> de Man 1884	bacterivorous	x	x	x
84 <i>A. nanus</i> de Man 1880	bacterivorous	x	x	x
85 <i>Panagrolaimus rigidus</i> Schneider 1866	bacterivorous	x	x	
<i>Tylenchida</i>				
86 <i>Tylenchus davaini</i> Bastian 1865	plant parasites*	x	x	x
87 <i>T. exiguus</i> de Man 1876	plant parasites*	x	x	x
88 <i>T. filiformis</i> Bütschli 1873	plant parasites*	x	x	x
89 <i>T. fusiformis</i> Thorne et Malek 1968	plant parasites*	x	x	x
90 <i>T. limichus</i> Nesterov 1973	plant parasites*	x		x
91 <i>T. minutus</i> Cobb 1893	plant parasites*	x		

Table 1. continued

N ^o	Taxon	Nematode community type	Old-growth mixed forest	Spruce monoculture 60-70 years	Spruce monoculture 70-80 years
92	<i>Rotylenchus uniformis</i> Thorne 1949	plant parasites	×	×	×
93	<i>Helicotylenchus pseudorobustus</i> Steiner 1914	plant parasites	×	×	×
94	<i>Crossonema menzeli</i> Stefański 1924	plant parasites		×	×
95	<i>xenocriconemella macrodora</i> Taylor 1936	plant parasites	×	×	×
96	<i>Gracilacus audriellus</i> Brown 1959	plant parasites	×	×	×
97	<i>Aphelenchus</i> sp.	fungivorous	×	×	×
98	<i>Aphelenchooides asterocaudatus</i> Das 1960	fungivorous	×	×	×
99	<i>A. composticola</i> Franklin 1957	fungivorous	×	×	×
100	<i>A. helophilus</i> de Man 1880	fungivorous	×	×	×
101	<i>A. parietinus</i> Bastian, 1865	fungivorous	×	×	×
102	<i>A. pusillus</i> Thorne 1949	fungivorous	×	×	×
103	<i>A. saprophilus</i> Franklin 1957	fungivorous	×	×	×
104	<i>Aphelenchooides</i> sp.	fungivorous	×	×	×

*plant parasitic nematodes feeding on root-knots

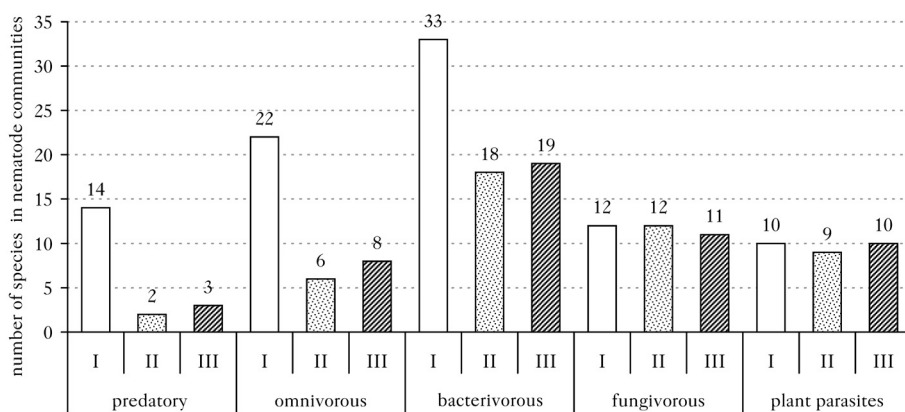


Fig. 1.

Forest litter nematode species diversity in different communities in the old-growth mixed forest and in spruce monocultures

I – old-growth mixed forest, II – spruce monoculture 60-70 years, III – spruce monoculture 70-80 years

ANALYSIS OF NEMATODE COMMUNITIES IN AN UNMANAGED OLD-GROWTH MIXED FOREST AND MANAGED SPRUCE MONOCULTURES. The abundance of nematodes belonging to all trophic groups (*i.e.*, plant parasites, fungivores, bacterivores, predators, and omnivores) differed significantly between the old-growth mixed forest and spruce monocultures (Table 2-6). In contrast, both investigated spruce monocultures were similar to each other in this regard (Table 2-6).

The abundance of plant-parasitic nematodes per square meter of forest litter was significantly lower in the old-growth mixed forest than in spruce monocultures (Fig. 2), and this difference was statistically significant for each season and each of the three layers of the forest litter investigated (Table 2).

Similarly, the abundance of fungivorous nematodes per square meter of forest litter was significantly lower in the old-growth mixed forest than in spruce monocultures (Fig. 3), and this

Table 2.

Mean number of plant parasite nematodes in three study plots and U Mann-Whitney test for differences in the abundance of plant parasite nematodes between the three study plots; significant differences are indicated in bold

Forest litter layer	Season of the year	Mean number of nematode individuals/m ² ±SD			Difference between forests		
		I. Old-growth mixed forest	II. Spruce monoculture 60-70 years	III. Spruce monoculture 70-80 years	I/II	I/III	II/III
L	spring	2240 ±5070	23680 ±6256	28800 ±12998	U=1.5 P<0.001	U=0.0 P<0.001	U=43.5 P=0.622
L	summer	4320 ±11514	35360 ±10863	35520 ±13655	U=6.5 P=0.001	U=6.5 P=0.001	U=49.0 P=0.939
L	autumn	6080 ±13168	28960 ±8447	30080 ±15943	U=11.0 P=0.002	U=12.0 P=0.003	U=44.5 P=0.674
F	spring	2400 ±2745	39200 ±8167	38560 ±10705	U=0.0 P<0.001	U=0.0 P<0.001	U=48.5 P=0.909
F	summer	3360 ±2552	47360 ±11954	44800 ±12866	U=0.0 P<0.001	U=0.0 P<0.001	U=43.5 P=0.622
F	autumn	2720 ±5893	41600 ±8158	37760 ±13068	U=0.0 P<0.001	U=0.0 P<0.001	U=32.5 P=0.185
H	spring	4800 ±5170	56160 ±18998	45920 ±12599	U=0.0 P<0.001	U=0.0 P<0.001	U=27.5 P=0.089
H	summer	8160 ±6101	69120 ±20080	67840 ±16459	U=0.0 P<0.001	U=0.0 P<0.001	U=50.0 P=1.0
H	autumn	3840 ±4957	67360 ±15317	55040 ±13538	U=0.0 P<0.001	U=0.0 P<0.001	U=28.5 P=0.103

Table 3.

Mean number of fungal-feeding nematodes in three study plots and U Mann-Whitney test for differences in the abundance of plant parasite nematodes between the three study plots; significant differences are indicated in bold

Forest litter layer	Season of the year	Mean number of nematode individuals/m ² ±SD			Difference between forests		
		I. Old-growth mixed forest	II. Spruce monoculture 60-70 years	III. Spruce monoculture 70-80 years	I/II	I/III	II/III
L	spring	960 ±2023	23360 ±9305	22240 ±8447	U=0.0 P<0.001	U=0.0 P<0.001	U=47.5 P=0.849
L	summer	1440 ±2318	28960 ±9818	26080 ±5746	U=0.0 P<0.001	U=0.0 P<0.001	U=39.0 P=0.426
L	autumn	2240 ±2634	25760 ±8312	25280 ±10714	U=0.0 P<0.001	U=0.0 P<0.001	U=45.5 P=0.732
F	spring	5120 ±5583	30240 ±11224	31680 ±11557	U=2.5 P<0.001	U=2.5 P<0.001	U=47.0 P=0.820
F	summer	7200 ±5293	40000 ±11586	37120 ±8853	U=0.0 P<0.001	U=0.0 P<0.001	U=41.5 P=0.494
F	autumn	6720 ±10280	38720 ±13146	33920 ±12706	U=4.0 P<0.001	U=7.0 P=0.001	U=39.5 P=0.426
H	spring	4000 ±5656	44160 ±15331	41600 ±14009	U=0.0 P<0.001	U=0.5 P<0.001	U=48.0 P=0.879
H	summer	2400 ±4216	54400 ±12370	51520 ±11752	U=0.0 P<0.001	U=0.0 P<0.001	U=48.0 P=0.878
H	autumn	5760 ±6838	51680 ±14111	48320 ±13862	U=0.0 P<0.001	U=0.0 P<0.001	U=44.5 P=0.676

Table 4.

Mean number of bacterivorous nematodes in three study plots and U Mann-Whitney test for differences in the abundance of plant parasite nematodes between the three study plots; significant differences are indicated in bold

Forest litter layer	Season of the year	Mean number of nematode individuals/m ² ±SD			Difference between forests		
		I. Old-growth mixed forest	II. Spruce monoculture 60-70 years	III. Spruce monoculture 70-80 years	I/II	I/III	II/III
L	spring	23040 ±8540	3360 ±2552	4000 ±3040	U=0.5 P<0.001	U=1.0 P<0.001	U=44.5 P=0.670
L	summer	92320 ±61811	11680 ±4832	5120 ±3270	U=2.0 P<0.001	U=0.0 P<0.001	U=13.5 P=0.005
L	autumn	40800 ±18980	8640 ±4005	3680 ±2139	U=1.0 P<0.001	U=0.0 P<0.001	U=8.5 P=0.001
F	spring	20800 ±9113	5440 ±2842	5600 ±4478	U=5.0 P=0.001	U=6.0 P=0.001	U=50.0 P=1.000
F	summer	75520 ±48587	13600 ±4283	7520 ±4065	U=11.0 P=0.003	U=7.5 P=0.001	U=14.5 P=0.006
F	autumn	57600 ±19347	11520 ±4991	6400 ±3287	U=1.0 P<0.001	U=0.0 P<0.001	U=17.5 P=0.012
H	spring	27680 ±18947	10880 ±5532	9120 ±4528	U=16.5 P=0.011	U=12.0 P=0.004	U=41.5 P=0.516
H	summer	67520 ±37476	19520 ±6652	13920 ±6534	U=15.5 P=0.009	U=12.0 P=0.004	U=25.5 P=0.061
H	autumn	60960 ±25549	18080 ±5989	10240 ±4899	U=9.0 P=0.002	U=1.0 P<0.001	U=15.0 P=0.008

Table 5.

Mean number of predatory nematodes in three study plots and U Mann-Whitney test for differences in the abundance of plant parasite nematodes between the three study plots; significant differences are indicated in bold

Forest litter layer	Season of the year	Mean number of nematode individuals/m ² ±SD			Difference between forests		
		I. Old-growth mixed forest	II. Spruce monoculture 60-70 years	III. Spruce monoculture 70-80 years	I/II	I/III	II/III
L	spring	12160 ±7699	2880 ±2590	2240 ±2524	U=7.0 P=0.001	U=4.5 P<0.001	U=41.5 P=0.504
L	summer	26880 ±20207	7040 ±3860	4000 ±4079	U=9.5 P=0.002	U=3.5 P<0.001	U=28.5 P=0.101
L	autumn	19680 ±10036	5920 ±2269	3360 ±3326	U=7.0 P=0.001	U=3.0 P<0.001	U=26.0 P=0.064
F	spring	25920 ±10872	7200 ±4603	3360 ±2867	U=2.5 P<0.001	U=0.0 P<0.001	U=24.5 P=0.047
F	summer	59680 ±21506	12320 ±2926	7520 ±5118	U=0.0 P<0.001	U=0.0 P<0.001	U=20.0 P=0.022
F	autumn	53120 ±24796	10240 ±2842	5280 ±3460	U=7.0 P<0.001	U=2.0 P<0.001	U=13.5 P=0.005
H	spring	24320 ±13146	9440 ±5357	7360 ±3035	U=9.5 P=0.002	U=4.0 P<0.001	U=40.5 P=0.468
H	summer	51680 ±12845	20960 ±6101	12960 ±8447	U=2.0 P<0.001	U=0.0 P<0.001	U=25.5 P=0.062
H	autumn	39040 ±20534	17120 ±5795	8000 ±4829	U=22.0 P=0.034	U=13.0 P=0.005	U=11.5 P=0.003

Table 6.

Mean number of omnivorous nematodes in three study plots and U Mann-Whitney test for differences in the abundance of plant parasite nematodes between the three study plots, significant differences are indicated in bold

Forest litter layer	Season of the year	Mean number of nematode individuals/m ² ±SD			Difference between forests		
		I. Old-growth mixed forest	II. Spruce monoculture 60-70 years	III. Spruce monoculture 70-80 years	I/II	I/III	II/III
L	spring	130720 ±48366	40000 ±17720	51680 ±30103	U=2.0 P<0.001	U=7.0 P=0.001	U=31.0 P=0.150
L	summer	164480 ±75521	52960 ±24117	54880 ±31459	U=5.5 P=0.001	U=7.0 P=0.001	U=47.0 P=0.820
L	autumn	128480 ±38812	51520 ±26940	55200 ±30799	U=6.5 P=0.001	U=3.0 P<0.001	U=42.5 P=0.570
F	spring	138400 ±54055	51200 ±13386	60320 ±33705	U=0.0 P<0.001	U=0.0 P<0.001	U=36.5 P=0.305
F	summer	213600 ±116093	70880 ±20337	73600 ±39048	U=3.0 P<0.001	U=4.0 P<0.001	U=40.0 P=0.448
F	autumn	147040 ±42085	66720 ±20821	64640 ±34306	U=3.0 P<0.001	U=0.0 P<0.001	U=49.5 P=0.970
H	spring	174240 ±56726	67520 ±12795	76000 ±40091	U=4.5 P=0.001	U=7.5 P=0.001	U=32.0 P=0.173
H	summer	361600 ±230635	93600 ±23530	87680 ±45516	U=10.0 P=0.002	U=10.0 P=0.002	U=43.5 P=0.623
H	autumn	226400 ±109488	83360 ±27147	78720 ±40930	U=8.5 P=0.002	U=10.0 P=0.002	U=145.5 P=0.733

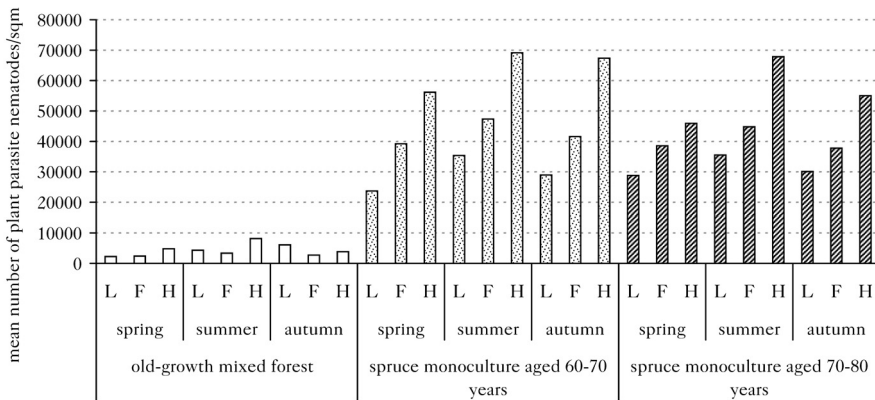


Fig. 2.

Abundance of plant parasitic nematodes in the old-growth mixed forest and spruce monocultures of different ages; L, F, and H are the layers of forest litter

difference was statistically significant for each season and each of the three layers of the forest floor investigated (Table 3).

In contrast, the abundance of bacterivorous, predatory, and omnivorous nematodes showed the opposite pattern. The abundance of nematodes belonging to these trophic groups was significantly higher in the old-growth mixed forest than in managed spruce monocultures (Fig. 4-6, Table 4-6).

The proportions of nematode trophic groups present in the forest litter significantly differed between the old-growth mixed forest and managed spruce monocultures in terms of all studied

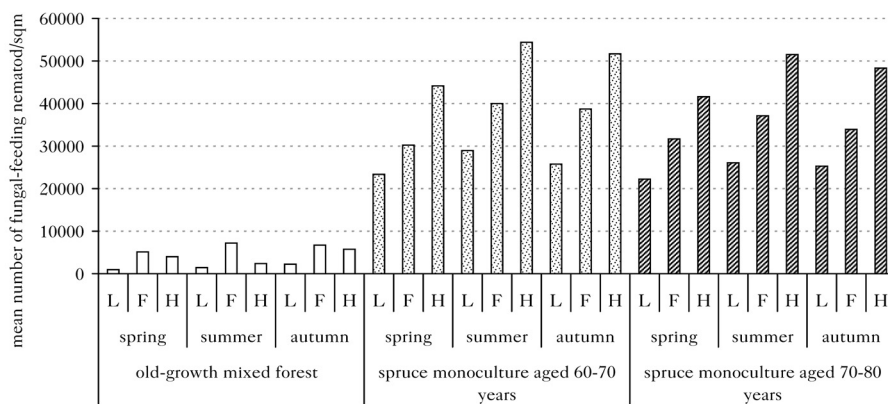


Fig. 3.

Abundance of fungivorous nematodes in the old-growth mixed forest and spruce monocultures of different ages; L, F, and H are the layers of forest litter

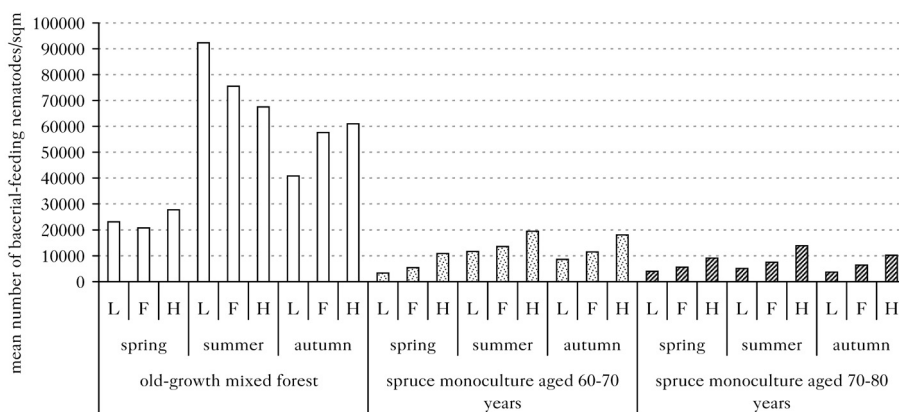


Fig. 4.

Abundance of bacterivorous nematodes in the old-growth mixed forest and spruce monocultures of different ages; L, F, and H are the layers of forest litter

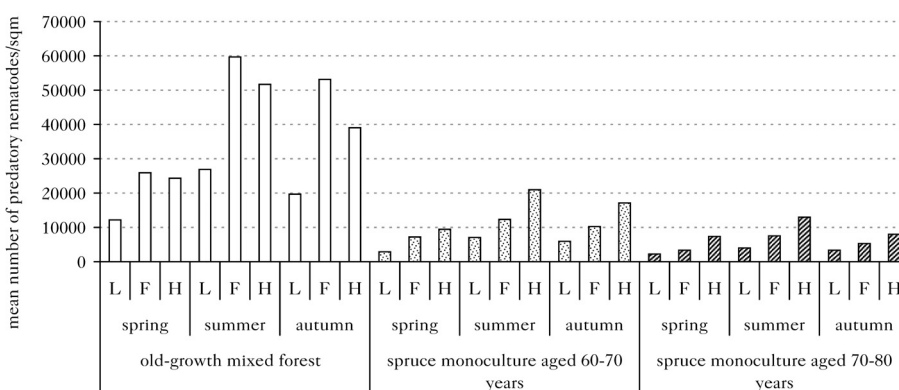


Fig. 5.

Abundance of predatory nematodes in the old-growth mixed forest and spruce monocultures of different ages; L, F, and H are the layers of forest litter

nematode communities (Fig. 7). The most noticeable difference is a very low proportion of plant parasitic and fungivorous nematodes in the old-growth mixed forest as opposed to managed spruce monocultures. Also, the old-growth mixed forest had a much higher proportion of bacterivorous, predatory and omnivorous nematodes in comparison to managed spruce forests.

Discussion

Nematodes form a substantial segment of the soil microfauna, accounting for about 80% of all multicellular organisms in the terrestrial biosphere (Bardgett and Putten, 2014). Because of their swift and taxon-specific reaction to alterations in the environment, nematodes may serve as bioindicators (Yates, 2003). The diversity of nematofauna is predominantly affected by factors such as soil texture, moisture, and the availability of food. Soil properties in forests, in turn, are shaped by trees through leaf fall, litter input on the soil surface, deposition of root exudates, dead roots, *etc.* (Prescott and Grayston, 2013). Trees have the potential to significantly affect the structural

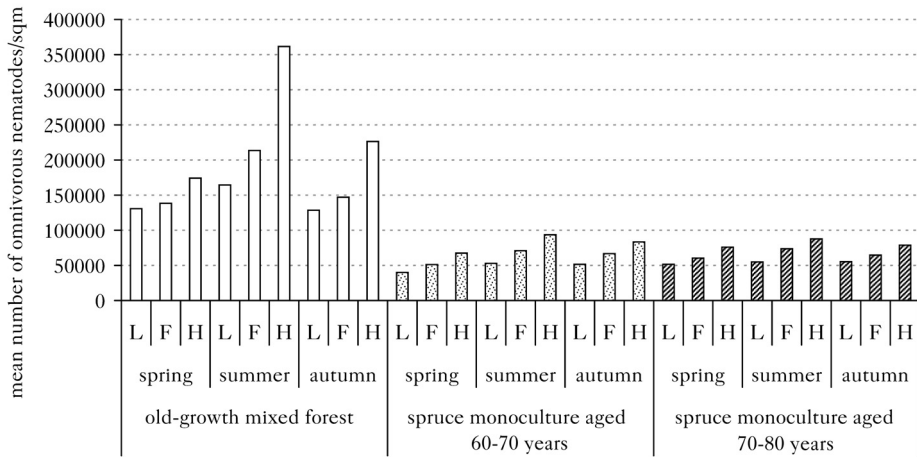


Fig. 6.

Abundance of omnivorous nematodes in the old-growth mixed forest and spruce monocultures of different ages; L, F, and H are the layers of forest litter

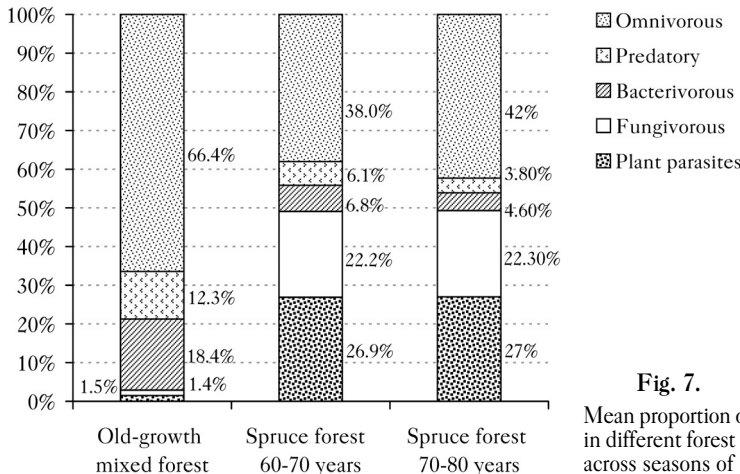


Fig. 7.

Mean proportion of nematode communities in different forest types; data were averaged across seasons of the year and litter layers

composition of the soil, the movement of water, the pH levels of the soil, and the concentrations of soil organic matter and nutrients which can consequently impact the living conditions for soil biota, resulting in shifts in their abundance, biomass, activity, and community structure (Aponte *et al.*, 2013). As the presently declining spruce monocultures in Skole Beskids in Ukraine were planted in areas previously cleared of old-growth mixed forests that originally covered these lands, we were interested in understanding the extent to which this kind of anthropopressure affected soil nematode communities.

Our study revealed that the type of forest had a significant effect on nematode communities. The number of nematode species was twice as high in an unmanaged old-growth mixed forest compared to managed spruce monocultures. This may be explained by the fact that plant richness is positively correlated with diversity of nematodes (Bastida *et al.*, 2020). Another study found that soil biota resistance to disturbance increased with plant diversity, highlighting the importance of plant species richness for belowground communities (Bennett *et al.*, 2020). Consequently, previous works reported a higher nematode abundance and diversity in old-growth forests (Panesar *et al.*, 2001; Yeates, 2007), what is consistent with the results of our research.

We also found that the proportion of nematode trophic groups was healthier in the natural mixed forest than in managed spruce forests. Low proportion of plant-parasitic nematodes found in the former is beneficial as these organisms feed on roots, negatively affecting the health of trees. This may potentially be a cause of the decline of spruce monocultures, in addition to factors such as climate warming, drought, and pollution. Beneficial free-living nematodes (including bacterivores, fungivores, omnivores, and predators), surpass plant-parasites in both abundance and diversity. They fulfil crucial functions in ecosystem operation by occupying vital ecological niches in belowground food webs. They are engaged in carbon sequestration, energy transfer, and nutrient mineralization, thereby enhancing nutrient availability to plants and ultimately improving soil fertility (Ferris, 2010). Thus, the twentyfold increase in the abundance of plant-parasitic nematodes in managed spruce forests compared to old-growth mixed forest (Fig. 7) could explain the decline in the condition of spruce monocultures. Additionally, this increase occurs at the expense of beneficial nematode communities, namely bacterivores, predators, and omnivores (Fig. 7), which may further lead to a deterioration of ecosystem functioning because healthy soils typically have a high abundance of free-living nematodes and a low proportion of herbivores (Bongers and Ferris, 1999). Previous studies revealed that a high ratio of bacteria- to fungal-feeding nematodes suggests predominant organic matter decomposition by bacteria, indicating rapid nutrient cycling (Sánchez-Moreno and Ferris, 2018), which is beneficial for trees. We found such a proportion in the old-growth mixed forest and a reversed one in declining spruce monocultures. The dominance of fungivorous nematodes over bacterivores indicates slow turnover of organic matter (Sánchez-Moreno and Ferris, 2018), which may, in the longer term, lead to a deterioration of managed spruce forests health. Finally, other studies confirmed that high numbers of omnivores and predators indicate that the system is biologically complex and resilient, and has some natural ability to suppress plant-parasitic nematodes and other soil-borne pathogens (Sánchez-Moreno and Ferris, 2018). This is consistent with our results, which indicate a high abundance of the aforementioned nematode communities in a healthy old-growth mixed forest, but not in deteriorating spruce monocultures. Other authors also found that the abundance and diversity of predatory nematodes were higher in unmanaged than managed forests (Cerevková *et al.*, 2021).

Interestingly, the increase of fungivores as well as the decrease of omnivores and predators in monocultures compared to natural forests was also observed in other climatic zones (Krashevsk

et al., 2019), suggesting the prevalence of this phenomenon. Another study revealed that the conversion of natural rainforest to cultivated monocultures affected the nematode community structure similarly to what we observed in our study – a reduction in the predator footprint and an increase in herbivory disservice (Karuri, 2021).

Conclusions

- ✦ Our research has revealed significant differences in nematode community proportions between unmanaged old-growth mixed forest and managed spruce monocultures.
- ✦ In the old-growth mixed forest there was a very low proportion of plant parasitic and fungivorous nematodes and a high proportion of bacteriophages, predatory and omnivorous nematodes compared to managed spruce forests.
- ✦ Observed differences in nematode community proportions between natural and managed forests may be one of the reasons for the decline of spruce monocultures in the Skole Beskids in Ukraine.

Authors' contributions

I.R. – collecting field data, laboratory analyzes of collected samples, species identification of nematodes, assigning nematodes to trophic groups; A.K. – data analyzing; E.W. – conception of the study, data analyzing, statistical analyses, writing the manuscript.

Conflict of interest

There is no conflict of interest in this study.

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STRESZCZENIE

Różnorodność gatunkowa i struktura troficzna nicieni zasiedlających ściółkę wykazują istotne różnice między zamierającymi monokulturami świerkowymi a naturalnymi lasami mieszanymi w ukraińskich Karpatach

Krytyczny spadek zdrowotności użytkowanych gospodarczo monokultur świerkowych w Beskidach stanowi wyzwanie dla wielu segmentów zarządzania lasem, dlatego zrozumienie wszystkich aspektów zamierania świerczyn jest kluczowe w zwalczaniu tego zagrożenia. Pomimo że opisano dotychczas liczne czynniki przyczyniające się do degradacji monokultur świerkowych w Karpatach, niewiele badań dotyczy możliwych związków między tym zjawiskiem a zmianami w grupach troficznych nicieni glebowych. Nicienie glebowe wspierają i wzmacniają stabilność ekosystemu. Pełnią ważną rolę na każdym poziomie troficznym w łańcuchu pokarmowym gleby i odpowiadają za procesy niezbędne do prawidłowego funkcjonowania ekosystemów glebowych. Badanie składu fauny nicieni stanowi podstawę dla ekologicznej oceny gleby, która z kolei ma wpływ na kondycję drzewostanu. Celem przeprowadzonych badań było przeanalizowanie i porównanie grup troficznych nicieni znajdujących się w różnych warstwach ściółki leśnej w użytkowanych gospodarczo monokulturach świerkowych wykazujących widoczne objawy zamierania oraz w pierwotnym lesie mieszanym. Co ważne, monokultury świerkowe objęte badaniami zostały nasadzone w miejsce uprzednio wyciętego pierwotnego lasu mieszanego, dlatego też wyniki przeprowadzonych badań wskazują na zmiany, jakie zaszły w grupach troficznych nicieni glebowych w związku z przekształceniem naturalnego lasu mieszanego w gospodarcze monokultury świerkowe.

Badania przeprowadzono na terenie Parku Narodowego „Beskidy Skolskie” w Ukrainie. Wyznaczono 3 poletka badawcze o powierzchni 400-500 m²: 1) naturalny las mieszany (*Piceeto-Abieto-Fageta*, lokalizacja: 48.984530, 23.462157), 2) użytkowana gospodarczo monokultura świerkowa w wieku 60-70 lat (*Piceeta*, lokalizacja 48.907398, 23.429908) oraz 3) użytkowana gospodarczo monokultura świerkowa w wieku 70-80 lat (*Piceeta*, lokalizacja 48.917614, 23.409201). Na każdym badanym obszarze pod świerkami pobierano próbki ściółki leśnej z 3 poziomów: L, F i H. Próbkę były pobierane trzykrotnie w każdym miejscu: wiosną, latem i jesienią. Badania prowadzono w latach 2014 i 2015. Łącznie zebrano 270 próbek ściółki leśnej. Nicienie były sepa-

rowane z zebranych próbek za pomocą metody Baermanna. Następnie 1 ml uzyskanej zawiesiny z nicieniami nanoszono na płytkę Petriego i badano pod mikroskopem przy powiększeniu 400x. Nicienie identyfikowano zarówno do gatunku, jak i grupy troficznej. Liczba nicieni przynależących do poszczególnych grup troficznych w każdej analizowanej próbce została przeliczona na jednostkę powierzchni [m²]. Różnice w liczbie nicieni reprezentujących grupy troficzne (roślinożerne, grzybożerne, bakteriożerne, drapieżne oraz wszystkożerne) między naturalnym lasem mieszanym a gospodarczymi monokulturami świerka analizowano za pomocą testu U Manna-Whitneya.

Analiza zebranych próbek ściółki leśnej wykazała występowanie 104 gatunków należących do 5 grup troficznych nicieni (tab. 1). Różnorodność gatunków nicieni była dwukrotnie wyższa w naturalnym lesie mieszanym (91 gatunków) w porównaniu do użytkowanych gospodarczo monokultur świerkowych (odpowiednio 47 i 51 gatunki w świerczynie w wieku 60-70 lat i 70-80 lat), a wykazane różnice były istotne statystycznie. Znacznie wyższa różnorodność gatunków w naturalnym lesie mieszanym dotyczyła gatunków drapieżnych, bakteriożernych i wszystkożernych, podczas gdy różnorodność gatunków grzybożernych i pasożytniczych na roślinach była podobna w naturalnym lesie mieszanym i monokulturach świerkowych (ryc. 1).

Liczebność nicieni należących do wszystkich grup troficznych różniła się istotnie między naturalnym lasem mieszanym a monokulturami świerkowymi (tab. 2-6). W przeciwieństwie do tego, obie badane monokultury świerkowe były podobne do siebie pod tym względem (tab. 2-6). Liczebność roślinożernej i grzybożernej nicieni na 1 m² ściółki leśnej była istotnie niższa w naturalnym lesie mieszanym niż w monokulturach świerkowych (ryc. 2 i 3), a różnice pomiędzy lasami były istotne statystycznie dla wszystkich pór roku i warstw ściółki (tab. 2 i 3). Z kolei liczebność nicieni bakteriożernej, drapieżnej i wszystkożernej wykazywała odwrotny wzorzec i była istotnie wyższa w naturalnym lesie mieszanym niż w użytkowanych gospodarczo monokulturach świerkowych (ryc. 4-6; tab. 4-6). Podsumowując: proporcje pomiędzy grupami troficznymi nicieni w ściółce pobranej z naturalnego lasu mieszanego i monokultur świerkowych wyraźnie się różniły (ryc. 7).

Przeprowadzone badania wykazały, że stosunek grup troficznych nicieni w naturalnym lesie mieszanym był korzystniejszy dla zdrowotności ekosystemu niż w nasadzonych przez człowieka monokulturach świerkowych. Dwudziestokrotny wzrost liczby nicieni roślinożernej (pasożytniczych na korzeniach drzew) w gospodarczych lasach świerkowych w porównaniu do naturalnych lasów mieszanych (ryc. 7) może tłumaczyć zamieranie monokultur świerkowych w Karpatach. Zwiększenie udziału nicieni pasożytniczych na korzeniach w lasach świerkowych jest konsekwencją istotnego zmniejszenia liczby nicieni drapieżnych, które utrzymują w równowadze liczebność pozostałych grup troficznych nicieni. Nicienie drapieżne są szczególnie wrażliwe na zmiany w ekosystemach spowodowane antropopresją. Jest zatem prawdopodobne, że zastępując naturalny las mieszany monokulturami świerkowymi, człowiek wpłynął na zmianę stosunków grup troficznych w sposób, który z czasem doprowadził do niesprzyjających warunków bytowych dla drzew.