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The effect of soil type and ecosystems on the soil nematode and microbial communities

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Summary

Integrated studies are required to better understand the relationships between groups of soil microfauna under the influence of various biotic and abiotic factors that drive and characterise ecosystems. We analysed soil nematode communities and microbial diversity and the properties of three soil types to assess the effect of these environmental variables on biological diversity in natural (forest), semi-natural (meadow), and managed (agriculture) habitats of the Slovak Republic. The type of ecosystem and soil and the interaction of both factors had considerable effects on most monitored abiotic and biotic soil properties. The forest with a Chernozem soil had the most nematode species, highest nematode diversity, highest abundance of nematode within functional guilds, best values of ecological and functional indices, highest microbial biomass, highest microbial richness and diversity, and the highest values of various soil properties, followed by meadows with a Cambisol soil. The agricultural ecosystem with a Stagnosol soil had the lowest biological diversity and values of the soil properties. Several nematode species were new for Slovak nematode fauna. Sampling date and the interaction of all three factors (ecosystem × soil × date) had minor or no effect on most of the parameters, except soil moisture content, microbial richness, nematode channel ratio, nematode maturity index, and plant parasitic index. Both the biological indicators and basic soil properties indicated that the natural forest with a Chernozem soil was the best habitat from an ecological point of view. This ecosystem is thus the most appropriate for ecological studies.

Keywords: soil trophic web; indicators; soil properties; nematodes; microbes; multivariate analysis

Introduction

Soil is an extremely heterogeneous environment in all aspects: biological, physical, chemical, and structural. Biological diversity is substantially higher in soil than above it, numbers are much larger for populations of soil organisms than aboveground communities (Young & Ritz, 1998). Microbes (fungi, bacteria, and algae), microfauna (protozoa), and mesofauna (arthropods and nematodes) belong to the most diverse soil organisms (Neher, 2001), affected mainly by vegetation and edaphic factors (Nielsen *et al.,* 2014). Nematodes inhabit nearly every environment and as biotic indicators are one of the most studied groups of soil organisms (Bhusal *et al.,* 2014). Since nematodes have diverse feeding behaviour and life strategies and play a key role in soil food web, they function as important indicator for ecosystems processes (Ferris 2010). As nematodes show different degrees of sensitivity to the environmental stimuli, alterations or disturbances because they have different long life cycles and reproduction capacity (Bongers, 1990),

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species diversity and structure of community what is important indicator of soil health and conditions (Neher, 2001). In addition, nematode indices allow the evaluation of ecosystem nutrient status (enriched vs. depleted), structure of soil food web (complexity vs. simplicity) and the prevailing decomposition of organic matter (slower fungal vs. faster bacterial) (Ferris *et al.*, 2001).

In contrast to nematode community's structure, however, potential microbial community structure for use as indicators of soil quality and functioning are hampered by a lack of standardised assays of microbial ecological diversity (Schutter *et al.,* 2001). Culturing techniques have been used to identify the number of specific taxonomic or functional groups, but only a small fraction of a microbial community (1 – 10 %) can be identified with these methods (Olembo & Hawksworth, 1991; Nannipieri *et al.,* 2003). Analyses of microbial DNA (Martin-Laurent *et al.,* 2001, Zhang *et al.*, 2014) can identify taxonomic groups at different levels, but developing specific primers, for example, is problematic. PLFA analyses cannot identify organisms to the species level but can be used to estimate gross changes in community structure (Kaur *et al.,* 2005). BIOLOG® EcoPlates are now commonly used for measuring microbial functional diversity based on the use of sources of available carbon (C) (Garland & Mills, 1991), and the method proposed by Degens and Harris (1997) for measuring the catabolic potential of microbial communities is often used in measurements of the impacts of soil management due to the easy use of both methods. Nevertheless, several microbial and biochemical attributes such as respiration, N mineralisation, or enzymatic activities can be reliably measured and are also frequently used as indicators of soil quality (Blagodatskii *et al.,* 2008; Gömöryová *et al.,* 2013, Bobuľská *et al.,* 2015, Zhang *et al.,* 2014).

Worldwide, several particular studies have revealed that environmental conditions determines the degree of species diversity of soil nematodes or nematode abundance e.g. ecosystem type and its properties (Neher *et al.,* 2005; Nielsen *et al.,* 2014), soil type and its properties (Lišková *et al.,* 2008, Hu *et al.,* 2018; Lima da Silva *et al.,* 2019); vegetation and its species diversity (Cesarz *et al.,* 2013; Renčo & Baležentienė, 2015). Similar, microbial activity and biomass have been evaluated in arable soils due to crop production as affected by tillage (Mangalassery *et al,* 2015); fertilizers (Kautz *et al.,* 2004; Zakarauskaitė, *et al.,* 2008) or management system (Bloem *et al.,* 1992); in forest soil as affected by forest type (Fang *et al.,* 2016) or in grasslands affected by plant diversity (Lange *et al.,* 2015). The structure of soil nematode communities and microbial diversity, however, have not been investigated or compared amongst various land use (ecosystems) and main soil types in the territory of Slovak Republic in collaborative study. We studied the soil properties and nematode-microbial assemblages in three soil types and three ecosystems to evaluate 1) nematode and microbial diversity in ecosystems with different soil types, 2) the fundamental variability in soil properties amongst and within the ecosystems and soil types, and 3) the effects of soil properties and sampling date on the nematodes and microbes in the ecosystems and soil types. We hypothesised that biological diversity would be lower in agroecosystems, that soil trophic webs would be more coherent in natural habitats, but that the differences between ecosystems would vary with the physicochemical properties of the soil type.

Materials and Methods

Site selection

We examined the physical and chemical properties, nematode communities, and microbial attributes in soil samples collected from a Stagnosol (SS), a Cambisol (CS), and a Chernozem (CM) in each of a forest (FOR), a meadow (MEA), and an agricultural field (AGR) ecosystems. The soil types, ecosystems, locations, and vegetation characteristics are shown in Table 1.

Soil samples and properties

Soil samples from each soil type and ecosystem were collected from five randomly established 1 × 1 m quadrats in selected plots of 20 × 20 m in May (M), July (J), and September (S) 2016. Five randomised subsamples were collected from the quadrats, one from each corner and one from the centre of the plots, for analysing the soil nematode communities, microbial activities, and physicochemical properties. The subsamples were bulked to produce a representative sample for the plot (1 kg). Samples were collected from a depth of 10 cm, excluding the surface humus layer. A total of 135 representative samples were collected; 5 from each ecosystem (FOR, MEA, and AGR, 5x3=15), from three soil type (SS, CS, and CM; 15x3=45), in three sampling date (M, J, and S; 45x3=135). The samples were transferred to the laboratory in sealed plastic bags and stored at 5 °C until processing for the nematode analysis or at -20 °C for the microbial analysis.

Total soil C and nitrogen (N) contents, soil moisture (SM) contents, and pH were measured in all samples. The organic C and total N contents were determined using a Vario MACRO Elemental Analyzer (CNS Version; Elementar, Hanau, Germany). Organic C content was determined based on the difference between total C and C bound in carbonates. SM content was estimated gravimetrically by oven-drying fresh soil at 105 °C overnight, and pH was measured potentiometrically in 1M KCl suspension by a digital pH meter separately for each representative sample.

Analysis of nematode communities

Each sample was homogenised by gentle hand mixing, and stones were manually removed. The nematodes were extracted from 100 g of fresh soil by a combination of Cobb sieving and decanting (Cobb 1918) and a modified Baermann technique (van Benzoijen, 2006). One hundred grams of soil from each representative sample were soaked in l L of tap water for 60 min to disrupt soil aggregates and promote nematode movement. The soaked sample was carefully passed through a 1-mm sieve (16 mesh) to remove plant parts and debris, and this suspension was passed

Table 1. Soil type, location, ecosystem type, and vegetation characteristics of the study plots.

Soil type	Location/characteristics	Ecosystem	Vegetation
Stagnosol	Hanušovce nad Topľou Altitude 258 – 308 m a.s.l., slope 3 – 7° Soil with strong mottling of the soil profile due to redox processes caused by stagnating surface water, The topsoil can also be completely bleached (albic horizon). A common name in many national classification systems for most Stagnosols is pseudogley.	Forest 49°00.339'N, 21°31.248'E	*Carpinus betulus* (90 %), *Pinus sylvestris* (5 %), sporadically *Prunus avium*, *Fagus sylvatica*, and *Betula pendula.* Understory vegetation dominated by grasses *Carex pilosa*, *Festuca drymej*a, and *Poa memoralis* and herbs *Dentaria bulbifera* and *Fragaria vesca*
		Meadow 49°00.658'N, 21°30.058'E	*Carex* sp., *Lolium perenne, Fragaria vesca, Trifolium pratense, Plantago* sp. *Leucanthemum* sp.
		Agricultural field 49°00.727'N, 21°30.344'E	*Zea mays* monoculture
Cambisol	Tŕnie Altitude 550 – 554 m a.s.l., slope 3 – 7° Soil with a beginning of soil formation. The horizon differentiation is weak. This is evident from weak, mostly brownish discolouration and/ or structure formation in the soil profile. Cambisols are developed in medium and fine-textured materials derived from a wide range of rocks, mostly in alluvial, colluvial and aeolian deposits.	Forest 48°36.712'N, 19°01.462'E	*Carpinus betulus* (75 %), *Quercus robur* (10 %), *Tilia cordata* (10 %), and sporadically *Prunus avium* Understory herbaceous vegetation dominated by *Viola reichenbachiana*, *Geranium robertianum*, *Asarum europaeum*, *Luzula sylvatica*, *Galium odoratum*, and *Hedera helix.*
		Meadow 48°36.683'N, 19°01.494'E	*Trifolium pratense*, *Agrimonia eupatoria*, and grasses such as *Carex* sp., *Poa* sp., *Dactylis glomerata, Trifolium pratense, Rumex acetosa*
		Agricultural field N 48°36.660'N, E 19°01.503'E	*Zea mays* monoculture
Chernozem	Močenok Altitude 135 – 180 m a.s.l., slope 0 – 3° Black-colored soil containing a high percentage of humus (4 % to 16 %) and high percentages of phosphoric cids, phosphorus, and ammonia. Chernozem is very fertile and can produce high agricultural yields with its high moisture storage capacity. Chernozems are also a reference soil group of the World reference base for soil resources	Forest 48°12.960'N, 17°57.854'E	*Fraxinus excelsior* (80 %), *Quercus petraea* (20 %), and sporadically *Robinia pseudoacacia.* Understory vegetation dominated by grasses *Poa nemoralis*, *Brachypodium sylvaticum*, *Melica uniflora*, and *Dactylis polygama*
		Meadow 49°00.339'N, 21°30.344'E	*Carex* sp*., Phleum pratense, Arrhenatherum elatius, Trifolium pratense, Vicia* sp., *Rumex acetosa, Achillea millefolium*
		Agricultural field 49°00.339'N, 21°30.344'E	*Zea mays* monoculture

through a 50-µm sieve (300 mesh) 2 min later to remove water and very fine soil particles. The nematodes were then extracted from the soil/water suspension by a set of two cotton-propylene filters in the Baermann funnels. Two filter trays were used per sample to limit material thickness to <0.5 cm. Suspensions containing the nematodes were collected after extraction for 24 h at room temperature. The nematodes were killed and fixed in a hot 99:1 solution of 4 % formaldehyde and pure glycerol (Seinhorst, 1962). The all nematodes were microscopically (100, 200, 400, 600, and 1000× magnification) identified to the species level (juveniles to the genus level) from temporary slides using an Eclipse 90*i* light microscope (Nikon Instruments Europe BV, Netherlands). Nematode abundance was expressed as the number of individuals per 100 g of dry soil.

The nematodes were assigned to fifteen functional guilds integrating nematode feeding strategies (trophic groups) and the nematode coloniser-persister (c-p) scale (Bongers & Bongers, 1998). The five nematode trophic groups were: bacterivores (Ba), fungivores (Fu), carnivores (Ca), omnivores (Om), and plant parasites (Pp) (Wasilewska, 1997). The Pp group included both obligatory plant parasites and facultative plant parasites that may attack plants or fungi. Colonisers-persisters characterising nematode life strategies are classified on a scale of 1 to 5 (Bongers, 1990). C-p1 represents "r-strategists" (colonisers) with short life cycles, small eggs, high fecundity, high colonisation ability, and high tolerance to disturbance, eutrophication, and anoxybiosis. Colonisers generally live in ephemeral habitats. At the other end of the scale, c-p5 nematodes represent "k-strategists" (persisters) with the longest generation times, largest bodies, lowest fecundities, and the highest sensitivity to disturbance. Persisters are never dominant in a sample and generally live in stable habitats where they become very abundant (Bongers, 1990). C-p scaling allows the calculation of the basal maturity index (MI) for non-parasitic nematodes, the plant parasitic index (PPI) for plant parasites only (Bongers, 1990), and the summ maturity index (ΣMI) (Yeates, 1994) for all nematode taxa. Functional guilds allow the calculation of the enrichment index (EI), the structure index (SI), and the channel index (CI) proposed by Ferris *et al.,* (2001). The species-diversity index (H´) defined by Shannon and Weaver (1949), the nematode channel ratio (NCR) defined by Yeates (2003), and trophic diversity (TD) defined by Heip *et al.,* (1998) were also calculated.

Nematode species were characterised as dominant at D >5 % (the species represents more than 5 % of the total nematode abundance in the ecosystem or soil type) and subdominant at D >2 % (the species represents more than 2 % of the total nematode abundance in the ecosystem or soil type) (Losos *et al.,* 1984).

Microbial biomass

Microbial biomass C (Cmic) content was determined following the procedure described by Islam and Weil (1998). Ten grams of oven-dried equivalent (ODE) of field moist soil adjusted to 80 % water-filled porosity was irradiated twice by microwaves (MW) at 400 J g^{-1} ODE soil to kill the microorganisms. The cooled samples were extracted with 0.5 M K_2SO_4, and the C content of the extract was quantified by oxidation with $K_2Cr_2O_7/H_2SO_4$. The same procedure was performed with a non-irradiated sample. Cmic content was determined as (Cirradiated content - Cnon-irradiated content)/KME, where KME represents the extraction efficiency (0.213) recommended by Islam and Weil (1998).

Functional diversity of microbial communities

The functional diversity of the soil microbiota was determined using the methods described by Insam (1997). Each well in a BIOLOG EcoPlate received 150 µl of an extract prepared by resuspending of fresh soil in 0.85 % NaCl and diluted 1:10000. The plates with the extracts were then incubated at 27 °C for 6 d, and absorbance at 590 nm was recorded every 24 h using a Sunrise Microplate reader (Tecan, Salzburg, Austria). The data were corrected against the initial readings at time zero and were expressed as optical densities of individual wells. The richness of the soil microbial community (Richn) was determined as the number of substrates used by the microbial community, i.e. the number of wells with a positive response after background correction. Hill's diversity index (Diver) (Hill, 1973) based on Eq. 1 was calculated for estimating the diversities of the microbial functional groups:

$$\text{Diver} = 1/\sum p_i^2 \quad (1)$$

in which p_i is the ratio of the activity on a substrate to the sum of activities on all substrates.

Data analysis

Data were log-transformed before analysis to improve normality. Soil and ecosystem types were included as fixed factors. The effects of soil type (SS, CS, and CM), type of ecosystem (FOR, MEA, and AGR), and sampling date (M, J, and S) on nematode trophic-web descriptors and functional guilds, soil properties, and microbial biomass, diversity, and richness were analysed by factorial analyses of variance (ANOVAs). Nonparametric Spearman's correlation coefficient (rs) was calculated to test the relationships between nematode functional guilds, microbial parameters, and soil parameters for each sample using STATISTICA v9.0. Correlations obtained at $P<0.05$ were considered significant.

We then used multivariate analyses to evaluate the effects of soil and ecosystem types on nematode-community composition and the microbial characteristics. The composition of the nematode functional guilds and the microbial parameters were thus used as response variables, and the soil and ecosystem types were used as explanatory variables in a multivariate framework of a redundancy analysis (RDA). The soil physicochemical parameters were used as supplementary variables. Canoco 5 for Windows was used for the multivariate analyses (vers. 5.04; Ter Braak & Šmilauer, 2012).

Ethical Approval and/or Informed Consent

This article does not contain any studies with human participants or animals by any of the authors, so formal consent is not required. Authors have no potential conflict of interest pertaining to this submission to Helminthologia.

Results

Soil properties

The factorial ANOVA found that ecosystem type (FOR, MEA, and AGR) and soil type (SS, CS, and CM) significantly affected all soil properties (except SM content vs. soil type) and that sampling date (M, J, and S) affected only SM content (P<0.01, Table 2). The bi-factorial interaction ecosystem × soil significantly affected all soil properties, ecosystem × date affected half of the properties, and soil × date and the interaction of all three factors (ecosystem × soil × date) had minor or no effects on the soil properties. The values of the soil properties were generally higher in the FOR soils (except pH) than the MEA and AGR soils and higher in CM (including pH) than CS and SS. pH and the C/N ratio were correlated negatively in FOR but positively in AGR and MEA (Fig. 1).

Nematode and microbial trophic webs

The three ecosystems and soil types contained 133 nematode species (32 bacterivores, 26 fungivores, 9 carnivores, 24 om-

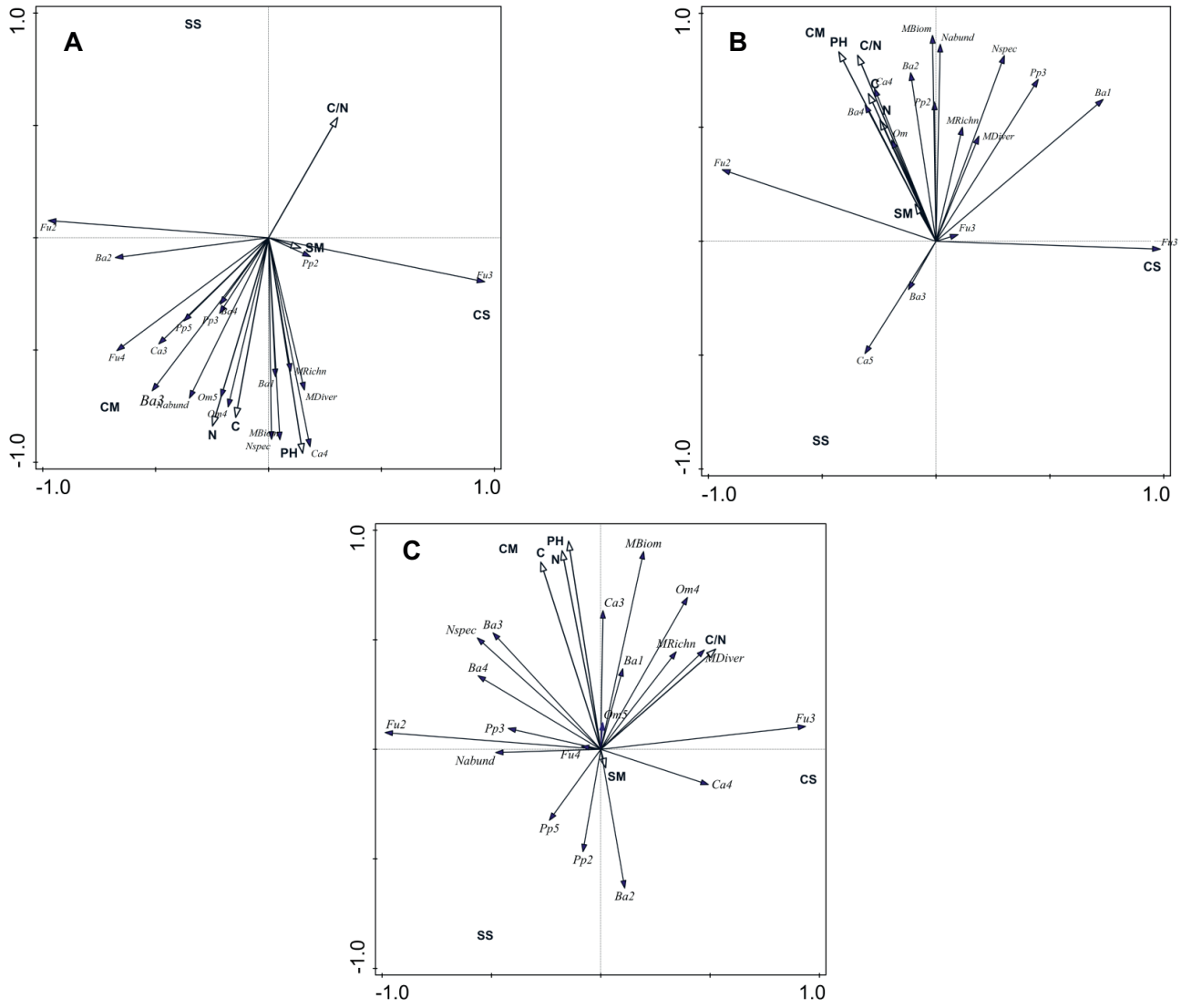

Fig. 1. RDA triplots of the relationships of abundance of nematode functional guilds, microbial parameters, and soil properties in the forest (A), agricultural field (B), and meadow (C) ecosystems and the Stagnosol (SS), Cambisol (CC), and Chernozem (CM) soil types.

Table 2. Effects of ecosystem type (E), type of soil (S), sampling date (D), and their interactions on basic soil physical and chemical characteristics.

	Ecosystem		Soil		Date		E × S		E × D		S × D		Ecosystem			Soil			Date			E × S × D	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	Meadow	Agricultural field	Forest	Stagnosol	Cambisol	Chernozem	May	July	Sept	*F*	*P*
pH/H_2O	28.91	< 0.01	598.43	< 0.01	2.95	ns	80.12	< 0.01	2.63	< 0.05	2.05	ns	5.88±0.78	5.79±0.75	5.54±1.08	4.82±0.61	5.71±0.41	6.68±0.32	5.68±0.88	5.71±0.87	5.81±0.92	1.08	ns
SM	60.14	< 0.01	0.99	ns	131.43	< 0.01	2.72	< 0.05	5.39	< 0.01	33.88	ns	26.33±7.28	22.14±5.14	30.78±8.64	26.15±8.96	26.93±8.85	26.15±5.75	26.68±8.04	20.52±5.47	32.10±5.3	2.53	< 0.05
N	156.52	< 0.01	122.56	< 0.01	0.15	ns	11.22	< 0.01	0.29	ns	2.60	ns	0.377±0.10	0.205±0.07	0.395±0.13	0.244±0.06	0.300±0.09	0.434±0.15	0.326±0.12	0.321±0.12	0.331±0.16	1.36	ns
C	275.46	< 0.01	140.58	< 0.01	0.08	ns	6.33	< 0.01	0.41	ns	1.89	ns	3.588±1.05	1.955±0.85	4.395±1.28	2.429±0.84	3.127±1.321	4.382±1.48	3.298±1.38	3.271±1.40	3.369±1.64	1.87	ns
S	32.62	< 0.01	51.84	< 0.01	2.11	ns	10.39	< 0.01	4.79	< 0.01	3.75	ns	0.071±0.02	0.048±0.01	0.070±0.02	0.049±0.02	0.060±0.01	0.082±0.02	0.067±0.03	0.060±0.18	0.063±0.02	2.71	< 0.01
C/N	171.64	< 0.01	7.51	< 0.01	1.81	ns	49.09	< 0.01	1.86	ns	1.21	ns	9.49±0.54	9.35±0.98	11.28±1.06	9.86±1.70	10.08±1.21	10.18±0.56	9.95±1.32	10.04±1.24	10.14±1.16	1.80	ns

E: meadow, agriculture and forest; S: Stagnosol, Cambisol and Chernozem; D: May, July, and September

pH/H_2O, acidity; SM, soil moisture content; N, total nitrogen content; C, organic carbon content; S, total sulphur content; C/N, carbon to nitrogen ratio. The means ±SEs of nematode abundance for the three ecosystems, soil types, and sampling dates are shown.

Table 3. Effects of ecosystem type (E), type of soil (S), sampling date (D), and their interactions on nematode abundance, functional guilds and microbial communities.

	Ecosystem		Soil		Date		E × S		E × D		S × D		Ecosystem			Soil			Date			E × S × D	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	F	*P*	*F*	*P*	Meadow	Agricultural field	Forest	Stagnosol	Cambisol	Chernozem	May	July	Sept	*F*	*P*
Nabund	2.36	ns	92.49	< 0.01	15.04	< 0.01	37.97	< 0.01	5.57	< 0.01	1.63	ns	479.8±119.8	540.1±322.5	451.8±169.5	351.6±150.1	435.8±104.9	671.3±260.3	549.2±276.3	418.1±165.9	504.1±201.8	1.59	ns
Nspec	5.69	< 0.01	4.87	< 0.01	0.88	ns	12.45	< 0.01	1.98	ns	2.98	ns	33.2±5.7	25.2±6.2	37.1±4.1	24.1±5.8	32.5±6.3	38.5±7.5	33.0±7.7	29.0±11	31.7±8.4	1.12	ns
Ba1	6.19	< 0.01	85.42	< 0.01	1.24	ns	21.63	< 0.01	1.78	ns	1.76	ns	10.9±11.1	38.6±43.9	22.18±21.8	4.2±5.8	41.9±41.6	25.6±20.7	22.6±30.4	21.1±25.6	28.1±36.3	0.97	ns
Ba2	5.49	< 0.01	12.36	< 0.01	11.48	< 0.01	35.72	< 0.01	6.11	< 0.01	2.44	ns	159.4±80.3	181.8±118.6	190.8±84.5	145.8±87.3	150.3±52.0	214.6±122.0	207.8±117.8	147.2±75.4	165.8±81.2	1.70	ns
Ba3	39.96	< 0.01	117.06	< 0.01	2.9	ns	29.93	< 0.01	1.24	ns	3.98	ns	2.3±5.0	0.0±0.0	3.1±5.5	0.0±0.0	0.2±0.7	5.11±6.5	1.0±2.6	2.9±6.4	1.4±3.3	2.12	ns
Ba4	5.82	< 0.01	28.8	< 0.01	0.07	ns	1.9	ns	0.69	ns	0.77	ns	3.7±7.2	1.5±3.6	2.9±4.0	0.9±1.6	0.6±1.3	6.6±7.5	2.9±6.3	2.5±4.8	2.7±4.7	0.83	ns
Ca3	15.89	< 0.01	24.98	< 0.01	0.67	ns	7.47	< 0.01	0.47	ns	0.27	ns	1.0±1.7	0.0±0.0	0.6±1.2	0.0 ±0.0	0.3±0.9	1.3±1.8	0.4±1.2	0.6±1.4	0.5±1.3	0.22	ns
Ca4	45.67	< 0.01	63.63	< 0.01	0.08	ns	31.3	< 0.01	0.23	ns	0.14	ns	3.9±3.9	1.8±3.5	10.4±9.7	1.0±2.2	7.0±7.6	8.1±8.4	5.1±6.8	5.8±8.3	5.2±6.9	0.80	ns
Ca5	11.63	< 0.01	11.63	< 0.01	1.22	ns	11.63	< 0.01	1.22	ns	1.22	ns	0.0±0.0	0.6±1.6	0.0±0.0	0.6±1.6	0.0±0.0	0.0±0.0	0.2±0.9	0.3±1.3	0.1±0.4	1.22	ns
Fu2	7.03	< 0.01	50.64	< 0.01	3.42	< 0.05	30.43	< 0.01	6.69	< 0.01	1.42	ns	97.8±34.7	155.6±156.7	87.5±52.6	68.1±38.5	90.1±40.4	182.7±143.5	122.4±127.5	92.2±126.2	126.2±104.5	1.42	ns
Fu3	4.06	< 0.05	4.06	< 0.05	0.79	ns	7.88	< 0.01	0.57	ns	0.57	ns	1.4±4.5	0.0±0.0	0.3±1.2	0.3±1.2	0.0±0.0	1.4±4.5	0.5±0.3	0.5±1.2	0.8±2.7	0.68	ns
Fu4	29.26	< 0.01	18.65	< 0.01	0.18	ns	14.74	< 0.01	1.20	ns	0.90	ns	3.7±4.9	0.0±0.0	5.3±9.3	1.9±4.4	0.9±2.2	6.2±9.2	3.6±8.3	2.8±5.4	2.5±5.3	0.89	ns
Om4	4.24	< 0.05	43.16	< 0.01	2.41	ns	10.80	< 0.01	0.62	ns	1.13	ns	31.2±29.8	21.7±19.0	41.0±37.0	16.0±16.8	35.8±22.2	52.1±35.1	41.5±37.2	33.2±25.2	29.3±24.0	0.55	ns
Om5	5.32	< 0.05	22.74	< 0.01	0.94	ns	4.84	< 0.01	0.65	ns	2.36	ns	19.8±7.4	8.7±12.1	15.4±13.2	8.2±9.1	8.6±5.3	20.1±13.7	12.8±10.3	12.5±14.2	11.7±9.1	1.87	ns
Pp2	19.66	< 0.01	1.02	ns	6.47	< 0.01	9.28	< 0.01	1.03	ns	2.55	ns	62.4±42.9	54.8±47.0	25.3±20.1	46.7±46.9	43.3±29.1	52.4±46.3	49.4±33.9	33.0±27.5	59.9±54.4	2.55	ns
Pp3	27.71	< 0.01	24.21	< 0.01	0.11	ns	14.19	< 0.01	0.75	ns	5.04	< 0.01	74.9±43.3	57.8±39.2	28.1±24.5	36.6±36.2	49.2±30.5	74.7±46.3	58.4±46.8	49.1±34.6	52.9±41.5	2.38	ns
Pp5	3.46	< 0.05	3.78	< 0.05	0.59	ns	7.78	< 0.01	0.37	ns	0.37	ns	0.27±0.95	0.0±0.0	0.5±1.3	0.3±0.9	0.0±0.0	0.5±1.3	0.4±1.2	0.2±0.8	0.2±0.8	0.48	ns
Cmic	175.55	< 0.01	295.91	< 0.01	2.84	ns	5.02	< 0.01	0.69	ns	2.64	< 0.05	335.2±118.3	207.9±91.5	400.1±145.5	183.0±65.9	325.9±119.4	434.4±109.2	316.0±129.1	300.4±143.4	326.8±157.8	19.0	ns
Richn	3.60	< 0.05	50.90	< 0.01	11.28	< 0.01	1.88	ns	0.68	ns	14.01	< 0.01	26.2±2.39	25.5±1.86	26.5±2.93	24.2±2.3	26.8±1.96	27.2±1.9	25.8±1.8	26.9±1.9	25.5±3.2	3.19	< 0.01
Diver	3.15	< 0.05	53.52	< 0.01	0.69	ns	1.96	ns	2.24	ns	4.69	< 0.01	14.51±2.6	13.85±2.4	14.9±3.0	12.1±2.9	15.6±2.3	15.6±2.4	14.2±2.1	14.7±2.7	14.5±3.2	34.2	< 0.01

E: meadow, agriculture and forest; S: Stagnosol, Cambisol and Chernozem; D: May, July, and September

$Ba_{1,2,3,4}$, bacterivores; $Fu_{2,3,4}$, fungivores; $Ca_{3,4,5}$, carnivores; $Om_{4,5}$, omnivores; $Pp_{2,3,5}$, plant parasites; Nabund, mean nematode abundance/100 g dry soil, Nspec, mean nematode species number/100 g dry soil; Cmic, microbial biomass carbon content; Richn, richness of microbial functional groups; Diver, diversity of microbial functional groups. The means ±SEs of nematode abundance for the three ecosystems, soil types, and sampling dates are shown.

Table 4. Effects of ecosystem type (E), type of soil (S), sampling date (D), and their interactions on nematode trophic-web descriptors.

	Ecosystem		Soil		Date		E × S		E × D		S × D		Ecosystem			Soil			Date			E × S × D	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	Meadow	Agricultural field	Forest	Stagnosol	Cambisol	Chernozem	May	July	Sept	*F*	*P*
MI	18.86	< 0.01	21.28	< 0.01	5.56	< 0.01	44.11	< 0.01	4.22	< 0.01	2.04	< 0.05	2.32±0.19	2.21±0.23	2.37±0.23	2.25±0.20	2.24±0.23	2.41±0.23	2.33±0.25	2.32±0.24	2.24±0.19	1.83	< 0.05
ΣMI	11.34	< 0.01	25.74	< 0.01	3.89	< 0.05	28.66	< 0.01	2.27	ns	0.95	ns	2.38±0.17	2.28±0.16	2.39±0.21	2.28±0.15	2.30±0.15	2.45±0.20	2.35±0.22	2.38±0.18	2.31±0.16	1.46	ns
PPI	0.70	ns	16.05	< 0.01	7.03	< 0.01	8.30	< 0.01	2.24	ns	6.25	< 0.01	2.5±0.20	2.53±0.22	2.51±0.26	2.43±0.24	2.53±0.20	2.62±0.20	2.59±0.23	2.60±0.21	2.38±0.22	6.41	< 0.01
H´	125.08	< 0.01	87.76	< 0.01	0.73	ns	22.99	< 0.01	0.99	ns	2.50	< 0.05	2.91±0.22	2.60±0.15	3.02±0.29	2.64±0.18	2.88±0.25	3.01±0.30	2.82±0.26	2.85±0.28	2.86±0.33	2.67	< 0.05
EI	4.52	< 0.05	9.05	< 0.01	1.46	ns	14.80	< 0.01	0.76	ns	2.32	ns	41.3±9.9	46.7±12.4	46.2±11.3	38.9±5.6	47.8±14.8	47.1±10.5	42.3±9.4	46.3±13.2	45.3±11.8	4.70	< 0.01
SI	4.53	< 0.05	61.88	< 0.01	1.78	ns	25.55	< 0.01	6.20	< 0.01	3.60	< 0.01	44.3±18.4	41.0±13.3	49.2±18.4	30.7±12.1	50.5±10.8	53.2±18.2	44.5±19.4	47.1±16.5	42.9±15.7	2.06	< 0.05
CI	53.82	< 0.01	61.48	< 0.01	0.11	ns	182.05	< 0.01	13.74	< 0.01	3.14	< 0.05	68.5±16.8	57.9±30.1	52.7±16.3	64.4±18.9	52.7±28.8	61.9±18.4	60.1±23.8	61.6±24.9	57.5±20.3	15.57	< 0.01
NCR	7.77	< 0.01	34.25	< 0.01	5.17	< 0.01	42.19	< 0.01	6.01	< 0.01	1.88	ns	0.65±0.12	0.63±0.16	0.69±0.13	0.69±0.14	0.70±0.12	0.57±0.12	0.69±0.12	0.65±0.13	0.64±0.16	4.02	< 0.01
TD	19.17	< 0.01	15.09	< 0.01	0.009	ns	16.81	< 0.01	1.75	ns	1.15	ns	12.2±2.4	10.5±4.2	14.7±2.1	10.5±3.2	13.2±1.9	13.7±2.4	12.3±0.8	12.5±0.7	12.9±0.7	1.34	ns

E: meadow, agriculture and forest; S: Stagnosol, Cambisol and Chernozem; D: May, July, and September

MI, maturity index; ΣMI, sigma maturity index; PPI, plant parasitic index; H´, Shannon diversity index; EI, enrichment index; SI, structure index; CI, channel index; NCR, nematode channel ratio; TD, trophic diversity. The means ±SEs of the nematode-community descriptors for the three ecosystems, soil types, and sampling dates are shown

Table 5. Spearman´s rank correlation coefficients between nematode abundance, species number, functional guild, microbial parameters and soil properties.

	pH/H_2O	SM	N	C	S	C/N
Nabund	0.35**	0.68***	0.42***	0.29**	ns	ns
Nspec	0.22*	ns	0.31*	0.37***	ns	ns
Ba_1	0.44**	ns	0.25***	0.22*	0.31***	ns
Ba_2	ns	-0.23***	ns	ns	ns	ns
Ba_3	0.54***	0.26*	0.44***	0.41***	0.42***	0.21*
Ba_4	0.43***	ns	0.30***	0.29***	0.30***	ns
Ca_3	0.44***	0.46***	0.39***	0.40***	0.39***	0.33***
Ca_4	0.41***	ns	0.21*	0.22*	0.22**	0.21**
Ca_5	ns	0.41***	0.35*	ns	0.36*	0.26*
Fu_2	0.55***	ns	0.35***	0.29**	0.37***	ns
Fu_3	ns	ns	ns	ns	ns	ns
Fu_4	0.39***	0.37***	0.29***	0.26**	0.27**	ns
Om_4	0.42***	ns	ns	ns	0.33**	ns
Om_5	0.38***	ns	0.21*	ns	0.23**	ns
Pp_2	ns	ns	ns	ns	ns	-0.27***
Pp_3	0.47***	0.24***	ns	ns	ns	ns
Pp_5	0.39***	0.37***	0.28***	0.28***	0.29**	0.38***
Cmic	0.70***	0.39***	0.90***	0.91***	0.83***	0.51***
Richn	0.46***	ns	0.47***	0.45***	0.53***	ns
Diver	0.47***	ns	0.40***	0.38***	0.50***	ns

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$; ns, not significant

$Ba_{1,2,3,4}$, bacteriovores; $Fu_{2,3,4}$, fungivores; $Ca_{3,4,5}$, carnivores; $Om_{4,5}$, omnivores; $Pp_{2,3,5}$, plant parasites; Cmic, microbial biomass carbon content; Richn, richness of microbial functional groups; Diver, diversity of microbial functional groups; pH/H_2O, acidity; SM, soil moisture content; N, total nitrogen content; C, organic carbon content; S, total sulphur content; C/N, carbon to nitrogen ratio

nivores, and 42 plant parasites) (Table S1). *Heterocephalobus eurystoma*, *Stegetellina leopolitensis*, *Ditylenchus parvus*, *Ditylenchus tenuides*, *Paraphelenchus obscurus*, *Boleodorus volutus*, *Cephalenchus intermedius*, and *Ecphyadophora tenusissima* were new to the list of Slovak nematode fauna, increasing the total number of soil nematode species to 732. The number of species (99) and diversity were highest in the FOR soils, followed by the MEA (90) and AGR (53) soils. Nematode species number and diversity were higher in CM than CS and SS (102, 81, and 60, respectively) (Tables S1, 4). The most abundant nematode species by trophic group were *Acrobeloides nanus* and *Chiloplacus propinquus* (bacterivores), *Aphelenchus avenae* and *Filenchus vulgaris* (fungivores), *Clarkus papillatus* and *Mylonchulus brachyuris* (carnivores), *Eudorylaimus carteri* (omnivores), and *Aglenchus agricola*, *Boleodorus thylactus*, and *Bitylenchus dubius* (facultative and obligate plant parasites) (Table S1).

Soil type and sampling date had significant effects on overall nematode abundance ($P<0.01$), but ecosystem type did not (Table 3). Ecosystem and soil types significantly influenced the abundances of all nematode functional guilds (except Om_5 and Pp_2, respectively), but the nematode-community compositions were similar.

The mean abundance of Ba_2 nematodes was significantly higher in FOR than MEA and AGR ($P<0.01$) and in CM than SS and CS ($P<0.01$). The amount of microbial biomass and microbial richness and diversity had tendencies similar to those of the Ba_2 nematodes; all were higher in FOR and CM (Table 3). Ba_4, Fu_3, and $Pp_{2,3}$ nematodes were most abundant in MEA, Ba_1 and Fu_2 were most abundant in AGR, and Ba_3, $Ca_{3,4}$, Fu_4, $Om_{4,5}$, and Pp_5 were most abundant in FOR. The majority of the nematode functional guilds were more abundant in CM than SS and CS. Only Ba_1 was significantly more abundant in CS ($P<0.01$). Sampling date only significantly affected the abundance of c-p2 nematode (Ba, Fu, and Pp) trophic groups, with higher values in M and S than J. Microbial richness was also affected by sampling date and was highest in J ($P<0.01$).

Nematode abundance, species number, and functional guilds and the microbial parameters were positively correlated with all soil properties. Only the Ba_2 nematode parameters were negatively correlated with SM content, and the Pp_2 nematode parameters were negatively correlated with the C/N ratio (Table 5). The RDA analysis, however, indicated that the abundance of most of the nematode guilds, total nematode abundance, nematode species

number, and the microbial parameters tended to be higher in environments with higher pHs and that N and C contents tended to be higher in FOR and CM soil (Figure 1A), except for Fu_2 and Fu_3 nematodes. The presence and distribution of nematodes within functional guilds, number of species, nematode abundance, and the microbial parameters in MEA were more affected by soil type than soil properties.

Nematode trophic-web descriptors

The ANOVA found that ecosystem and soil types significantly affected all descriptors (except PP vs. ecosystem type). Sampling date had a significant effect on MI, ΣMI, PPI, and NCR (P<0.01, 0.05, Table 4). The interaction ecosystem × soil significantly affected all descriptors (P<0.01), ecosystem × date and soil × date significantly affected half of the descriptors, and the interaction of all three factors (ecosystem × soil × date) affected the majority of the descriptors. MI, ΣMI, PPI, H´, SI, and TD were generally higher in FOR than MEA and AGR soils and in CM than CS and SS. EI was highest in AGR and CS, CI was highest in MEA and SS, and NCR was highest in FOR and CS.

Discussion

Nematode and microbial communities have been evaluated for their ability to detect changes in response to environmental impacts (e.g. wildfire, windstorms, and plant invasion) or human activities (e.g. pollution, land management, and ecosystem conversions) in many studies (Schutter *et al.,* 2001; Gömöryová *et al.,* 2011; Jangid *et al.,* 2011; Whitford *et al.,* 2014; Čerevková *et al.,* 2013; Renčo *et al.,* 2015; Renčo & Baležentienė, 2015; Sánchez-Moreno *et al.,* 2018). In present comprehensive study we evaluated their differences amongst ecosystems (natural, semi-natural, and managed) and soil types (CM, CS, and SS) measured by various community parameters. Such works where nematodes and microbes are surveyed together are rare (Ekschmitt *et al.,* 2001; Briar *et al.,* 2007). We also analysed the basal soil physicochemical properties and interactions with both nematode and microbial communities.

Relationships of ecosystem type with soil properties and nematode and microbial communities

Ecosystem type was an important factor shaping soil nematode and microbial communities and affecting soil properties. The abiotic and biotic soil properties and interactions amongst them were best for the FOR ecosystem. FOR had the highest SM, C, and N contents and C/N ratio but the lowest pH. C and N contents were twice as high in FOR than AGR but were similar to those in MEA. The supposed benefits of management of agricultural land (e.g. tillage, fertilisation, and crop rotation) include increased soil C and N contents, fertility, water retention, and overall provision of ecosystem services (Garbach *et al.,* 2017; Sánchez-Moreno *et al.,* 2018). The low C and N contents in our AGR soils, however, suggested differences in the quantity and quality of inputs to the soil, nutrient inputs and losses, low plant diversity and stimulation of decomposition by soil disturbance compared to the semi-natural (MEA) and natural (FOR) ecosystems. These results are in agreement with many studies of differences in soil C and N contents and changes following conversion of forest to managed agricultural land, well summarised in a review by Murty *et al.,* (2002). This review revealed that large amounts of C and N could be lost when forest is converted into cultivated land but that no changes in soil C and N contents were recorded when forests were converted to uncultivated pasture (similar to our meadow). In contrast, the abandonment and reforestation of agricultural land can substantially increase C and N storage (Compton and Boone 2000), due to increase in plant diversity (Lange *et al.,* 2015). Additionally, cultivated soils usually have lower C/N ratios than forest soils (Murty *et al.,* 2002), consistent with our and other results (Fernandes *et al.,* 1997; Smil, 1999; Compton & Boone, 2000). Our C/N ratio was negatively correlated with pH in FOR, consistent with the results reported by Högberg *et al.,* (2007).

Food, water, and temperature are the three primary factors that determine the habitats occupied by nematodes and microbes, the degree of species diversity, and the composition and structure of their communities. The availability of food, water, and temperature, however, are determined by ecosystem type, soil characteristics (e.g. structure, pH, and chemistry), plant composition, and microclimatic (Neher, 2010) or seasonal (Gaugler & Bilgrami, 2004) variations. More diverse nematode and microbial assemblages contribute to more resilient ecosystem services (Yeates, 2007; Fuhrman, 2009; Háněl, 2017). Forest soils, for example, contain more species than agricultural soils (Domsch *et al.,* 1983; Neher *et al.,* 2005), some with >400 nematode species (Yeates, 2007). This finding is consistent with our results; nematode species numbers and diversity (H´) were highest for FOR, even though FOR had the lowest overall nematode abundance, suggesting that established forests represent relatively stable environments providing suitable conditions for maintaining balanced and rich nematode trophic webs (Yeates, 2007). This was supported also by values of ecological and functional indices (Bongers, 1990; Ferris *et al.,* 2001). All maturity indices (MI, ΣMI, PPI) as well as Structure index and Trophic diversity were generally higher in forests than in grasslands and/or cultivated soils. These results partially agree with those by Neher *et al.,* (2005), who reported that MI, PPI and SI were higher in forests than in wetlands and agricultural soils. Ecosystem type has significant effect on values of CI, which was the highest in meadow soils in our study, indicates a higher proportion of fungal decomposition (fungal decomposition channels) and low abundance of c-p1 bacterial feeders (e.g. Rhabditidae and Panagrolaimidae) (Ferris *et al.,* 2001). In contrast, Neher *et al.*, (2005) revealed the highest CI value in forest soils.

We found several nematode species exclusively in one ecosystem e.g. *Paraphelenchus obscurus* in AGR, *Paratylenchus microdorus* in MEA, and *Filenchus polyhypnus* in FOR. Extreme disturbanc-

Table S1. Mean abundance of nematode species (100 g of dry soil) in the three ecosystems (forest (FOR), meadow (MEA), and agricultural field (AGR)) and types of soil (Stagnosol (SS), Cambisol (CS), and Chernozem (CM)) (n=45). Bold figures indicate dominance >2 but <5%, and bold and underlined figures indicate dominance >5%.

		Ecosystem			Soil		
Taxon	TG/FG	FOR	MEA	AGR	SS	CS	CM
Mesorhabditis spp. juvs	Ba1	**13.5**	0.6	**13.4**		**17.4**	10.1
Panagrolaimus rigidus	Ba1	2.0	6.1	7.2	1.3	5.8	8.2
Rhabditis spp. juvs	Ba1	6.7	4.3	**18.1**	2.9	**18.7**	7.4
Acrobeles ciliatus	Ba2	**20.3**	2.8	0.4			**23.4**
Acrobeloides buetschlii	Ba2		0.4		0.4		
Acrobeloides nanus	Ba2	**43.0**	**40.9**	**30.1**	**30.2**	**45.1**	**38.2**
Acrobelophis minimus	Ba2	0.6				0.6	
Acrolobus emarginatus	Ba2			0.1	0.1		
Anaplectus granulosus	Ba2	2.5	5.1	2.7	2.4	1.9	7.2
Cervidellus cervus	Ba2	0.1				0.1	
Cervidellus vexiliger	Ba2	5.8	2.7			0.6	8.4
Cephalobus persegnis	Ba2	**17.7**	**14.3**	**22.7**	**24.4**	**27.6**	11.5
Ereptonema arcticum	Ba2	1.9					1.9
Eucephalobus mucronatus	Ba2		2.9		1.3		1.6
Eucephalobus oxyuroides	Ba2	12.6	**13.5**	**17.5**	**22.1**	7.7	13.9
Eucephalobus striatus	Ba2	7.2	3.3	**44.8**	13.5	5.1	**39.4**
Eumonhystera dispar	Ba2	1.0					1.0
Eumonystera filiformis	Ba2	1.7				2.4	
Geomonhystera villosa	Ba2	1.0			1.0		
Heterocephalobus elongatus	Ba2	8.6	4.0	9.7	**10.2**	**9.9**	2.2
Heterocephalobus eurystoma (N)	Ba2		0.7				0.7
Chiloplacus demani	Ba2	7.4			5.8		1.6
Chiloplacus propinquus	Ba2	**18.2**	**22.6**	**23.8**	**21.6**	**12.2**	**30.8**
Chiloplacus symmetricus	Ba2		1.0			1.0	
Plectus acuminatus	Ba2	1.1		8.1	0.9	5.6	2.6
Plectus cirratus	Ba2	7.3	3.1		3.9	4.3	2.1
Plectus communis	Ba2	3.1			3.1		
Plectus longicaudatus	Ba2	3.8				2.0	1.8
Plectus parietinus	Ba2	6.3	**9.9**	7.6	7.0	4.4	12.4
Plectus parvus	Ba2	**10.9**	**15.0**		**15.5**	4.6	5.8
Plectus rhizophilus	Ba2	0.9				0.9	
Plectus silvaticus	Ba2	1.3					1.3
Seleborca complexa	Ba2		0.7				0.7
Stegelletina leopolitensis (N)	Ba2		0.1	3.2	0.9		2.4
Wilsonema schuurmansstekhoveni	Ba2	6.5	1.7		1.8	3.6	2.9
Aulolaimus oxycephalus	Ba3		1.1				1.1
Bastiania gracilis	Ba3		0.2				
Prismatolaimus intermedius	Ba3	2.3	1.2				3.5
Teratocephalus lirellus	Ba3	0.1					0.1
Teratocephalus terrestris	Ba3	0.7				0.2	0.5
Alaimus parvus	Ba4	0.6			0.6		
Alaimus primitivus	Ba4	2.2	3.7	1.3	0.4	0.5	6.3
Amphidelus coronatus	Ba4			0.2			0.2
Amphidelus elegans	Ba4	0.2	0.1			0.2	0.1
Tripyla affinis	Ca3	0.6	0.8				1.4
Trischistoma monohystera	Ca3		0.3			0.3	
Clarkus papillatus	Ca4	2.6	1.8	0.8		2.3	3.0
Coomansus parvus	Ca4	1.3		0.1		1.3	0.1
Coomanus zschokkei	Ca4	0.7				0.7	
Ironus macramphis	Ca4	0.4				0.4	

Mylonchulus brachyuris	Ca4	3.2	1.7	0.9	1.0	2.4	2.5
Prionchulus muscorum	Ca4	2.5					2.5
Paravulus hartingii	Ca5			0.6	0.6		
Aphelenchoides bicaudatus	Fu2	0.3	0.1			0.1	0.3
Aphelenchoides composticola	Fu2	**9.7**	**11.0**	0.9	**7.4**	5.3	8.9
Aphelenchoides limberi	Fu2			1.4	0.2		1.2
Aphelenchoides parietinus	Fu2	5.5	7.4	**14.8**	3.2	3.0	**21.6**
Aphelenchoides saprophilus	Fu2	1.1	1.3		1.0	0.1	1.3
Aphelenchus avenae	Fu2	**22.8**	**39.5**	**82.4**	**21.2**	**35.6**	**88.0**
Ditylenchus dipsaci	Fu2	0.6		0.5			1.1
Ditylenchus intermedius	Fu2	3.6		**15.7***	**8.3**	4.7	6.3
Ditylenchus longicauda	Fu2		1.1			0.7	0.4
Ditylenchus longimetricalis	Fu2	2.7				1.0	1.7
Ditylenchus myceliophagus	Fu2	1.7	0.7		0.6		1.7
Ditylenchus parvus (N)	Fu2		1.2		1.2		
Ditylenchus tenuidens (N)	Fu2	0.8			0.8		
Ditylenchus sp.	Fu2		1.7		1.7		
Filenchus discrepans	Fu2	2.6				2.6	
Filenchus misellus	Fu2	1.0				1.0	
Filenchus polyhypnus	Fu2	7.2					7.2
Filenchus thornei	Fu2	3.3	2.1		2.1	3.3	
Filenchus vulgaris	Fu2	8.1	**19.1**	**32.2**	**17.6**	**13.7**	**35.2**
Hexatylus viviparus	Fu2	0.5				0.5	
Nothotylenchus acris	Fu2			0.7			0.7
Paraphelenchus obscurus (N)	Fu2			4.6			4.6
Paraphelenchus pseudoparietinus	Fu2	1.5	1.8	0.8		2.1	2.1
Diphtherophora communis	Fu3	0.3	1.4		0.3		1.4
Tylencholaimus mirablis	Fu4	0.7	0.9				1.6
Tylencholaimus stecki	Fu4	4.3	2.8		1.9	0.9	
Tylencholaimus teres	Fu4	0.3					0.3
Aporcelaimus superbus	Om4	0.4					0.4
Campydora demonstrans	Om4		0.2				0.2
Crassolabium ettersbergense	Om4	2.4	1.0			1.4	2.0
Dorydorella bryophila	Om4	3.7	6.7				10.4
Dorylaimoides micoletzkyi	Om4	1.4	2.4		1.7	1.3	0.8
Ecumenicus monohystera	Om4	0.2	0.4	2.4		0.2	2.8
Eudorylaimus carteri	Om4	3.9	**19.5**	**9.2**	**10.8**	**10.5**	11.3
Eudorylaimus leuckarti	Om4	**9.9**	2.3	2.5	1.5	2.7	10.5
Eudorylaimus iners	Om4	3.4				3.4	
Eudorylaimus opistohystera	Om4	2.9	2.1	1.4		2.3	4.1
Eudorylaimus spp. juvs	Om4	7.5	3.1	3.3	2.1	6.5	5.3
Mesodorylaimus meyli	Om4	2.0				2.0	
Microdorylaimus parvus	Om4	2.8	0.2	2.4		5.6	0.2
Pungentus silvestris	Om4	0.7	3.5				4.2
Aporcelaimellus obtusicaudatus	Om5	7.8	2.2	6.8	2.3	4.7	11.6
Axonchium propinquum	Om5		0.1		0.1		
Discolaimus major	Om5	0.9					0.9
Discolaimus texanus	Om5			0.5			0.5
Epidorylaimus agilis	Om5	0.4				0.4	
Mesodorylaimus bastiani	Om5	2.6	2.9	2.1	4.8	0.6	2.1
Metaxonchium coronatum	Om5		0.6				0.6
Nygolaimus brachyuris	Om5		1.1			0.3	0.8
Oxydirus oxycephalus	Om5	2.5	2.1	1.7	0.6	2.0	2.6
Paraxonchium laetificans	Om5	0.6	0.1	0.5			1.2
Prodorylaimus acris	Om5	0.6	0.4		0.4	0.6	

Aglenchus agricola	Pp2	1.9	6.4	**32.9**	**10.3**	4.8	**28.7**
Basiria gracilis	Pp2	0.7				0.7	
Basiria similis	Pp2		0.6		0.3		0.3
Basiria tumida	Pp2	2.0			1.8		0.2
Boleodorus thylactus	Pp2	0.5	**24.8**	6.8	**21.3**	6.6	4.0
Boleodorus volutus (N)	Pp2	0.4	0.4				0.8
Cephalenchus intermedius (N)	Pp2		0.2		0.2		
Coslenchus andrássyi (N)	Pp2		0.7			0.7	
Coslenchus costatus	Pp2	1.8	1.9				3.7
Ecphyadophora tenuissima (N)	Pp2	0.4					0.4
Malenchus acarayensis	Pp2	**9.1**			**7.6**	4.4	
Malenchus bryophilus	Pp2	12.4	2.2			**14.6**	
Malenchus exiguus	Pp2	2.6	**10.1**	2.7		1.0	6.8
Malenchus gratiosus	Pp2	0.9					0.9
Neopsilenchus magnidens	Pp2		0.5		0.5		
Tylenchus davainei	Pp2	4.6	5.4	1.6	2.7	2.9	5.9
Paratylenchus bukowinensis	Pp2			**15.8**		**11.5**	4.3
Paratylenchus microdorus	Pp2		**10.9**		3.5	6.4	1.0
Paratylenchus projectus	Pp2	3.4				3.4	
Psilenchus hilarulus	Pp2		2.0	0.9		2.6	0.2
Amplimerlinius macrurus	Pp3	0.7	**14.8**		**14.3**		0.7
Bitylenchus dubius	Pp3		**10.8**	**12.8**	4.1	**19.5**	
Bitylenchus maximus	Pp3		2.2			1.7	0.5
Geocenamus brevidens	Pp3	7.1	5.2		6.5		1.7
Geocenamus microdorus	Pp3		**21.0**				**21.0**
Geocenamus nanus	Po3			8.8		**8.8**	5.0
Helicotylenchus canadensis	Pp3	3.8	1.3			5.1	
Helicotylenhus digonicus	Pp3	**11.0**	0.6			3.3	8.4
Helicotylencus dihystera	Pp3			10.2			10.2
Heterodera mani juvs	Pp3		1.2		1.2		
Heterodera avenae juvs	Pp3		0.3	0.6		0.9	
Meloidogyne hapla	Pp3		1.1			1.1	
Nagelus obscurus	Pp3		1.1				1.1
Pratylenchoides crenicauda	Pp3	0.8	0.5				1.3
Pratylenchus crenatus	Pp3			1.3		0.7	0.6
Pratylenchus penetrans	Pp3	4.6		9.7		7.5	9.7
Pratylenchus pratensis	Pp3		**9.1**	7.4	6.3	0.6	6.8
Tylenchorhynchus bicaudatus	Pp3	0.1					0.1
Tylenchorhynchus cylindricus	Pp3			2.3			2.3
Longidorus elongatus	Pp5		0.3		0.3		
Longidorus intermedius	Pp5	0.5					0.5
Total number of species		**99**	**90**	**53**	**60**	**81**	**102**

juvs, juveniles; (N), species new for Slovak fauna

es, such as bulldozing, slash-and-burn management, windstorms, and wildfires in forests, however, can substantially reduce nematode diversity (Yeates, 2007; Čerevková *et al.,* 2013). The species richness of the nematode fauna in FOR in our study was higher than in the soils of a protected forest in the Slovak Tatra National Park nine years after a windstorm and wildfire, likely due to the persistent influence of changes in the plant community and basal soil physicochemical properties (Renčo & Čerevková, 2015; Renčo *et al.,* 2015).

The FOR soils also had the highest microbial biomass, richness, and diversity, what positively correlated with C and N contents, and was consistent with the observations of Yergeau *et al.,* (2006)). Microbial biomass is involved in the control of the synthesis and decomposition of soil organic matter and acts as an accessible storage system for nutrients in ecosystems. Sites with high microbial biomass can therefore stock and recycle more nutrients for plant nutrition and thus improve the sustainability of an ecosystem (Kaschuk *et al*., 2010). In contrast, the number and diversity

of nematode species and diversity of microbial functional groups in our study were lowest in AGR. Additionally, AGR had half the amount of microbial biomass than FOR and MEA, and microbial biomass was negatively correlated with C and N contents. These findings support our hypothesis that biological diversity would be lowest in the agricultural soils due to periodic perturbation, land management, and crop monoculturing, consistent with the results by Neher *et al.,* (2005); even though AGR had the highest overall nematode abundance, likely due the periodic organic manure inputs (Hu *et al.,* 2018).

Bacterivorous nematodes are often the most dominant feeding group in forest (Neher *et al.,* 2005; Yeates, 2007; Renčo & Čerevková, 2017) and agricultural (Neher *et al.,* 2005, Renčo *et al.,* 2010) soils. The preponderance of Ba_2 bacterivores (*A. nanus*, *C. persegnis*, and *C. propinquus*) in all ecosystems in our study was likely due to the high microbial biomasses in FOR and MEA and to the management (tillage and fertilisation) in the corn monoculture in AGR. Microbial biomass was nevertheless significantly lower in AGR than FOR and MEA. Microbial diversity is often lower after a natural habitat has been cultivated (Buckley & Schmidt, 2001). These results are in agreement with Wasilewska (1997), who stated that a higher abundance of microflora would support larger numbers of bacterivorous nematodes. An increase in the abundance of this group is indicative of enhanced microbiological activity e.g. after the addition of cow and chicken manure or slurry (Wasilewska, 1997; Neher & Olson, 1999). Our study thus demonstrated the synchronisation between bacterivorous nematodes and their food resources, which has not been frequently reported (Wardle *et al.,* 2001, Papatheodorou *et al.,* 2004). Fungivorous nematodes (Fu_2) were the second most abundant trophic group in all ecosystems. AGR had the highest abundance of fungivores, mainly *A. avenae*, *F. vulgaris*, *Ditylenchus intermedius*, and *Aphelenchoides parietinus*, likely due to the high density of fungal hyphae and spores under *Z. mays* monoculture from the association of corn with arbuscular mycorrhizal fungi (Bai *et al.,* 2008).

Plants and their root systems serve as food for plant parasitic nematodes (Flis *et al.,* 2018; Le *et al.,* 2019) before they serve as a food source for microbivorous nematodes during decomposition. Root systems are more diverse in natural ecosystems with rich communities of plant species than for monocultured crops. Root growth is also more extensive and less ephemeral in perennial plants than annual crops and supports a soil community with many species of plant parasites, omnivores, and predators (Neher, 2010). Plant parasites are common in natural grasslands (Popovici & Ciobanu, 2000; Čerevková, 2006). The abundance of plant parasites, such as *Boleodorus thylactus*, *Malenchus exiguus*, and *Paratylenchus microdorus* (Pp_2) or *Amplimerlinius macrurus*, *Geocenamus microdorus*, and *Bitylenchus dubius* (Pp_3) was highest in MEA.

The importance and high population densities of plant parasitic nematodes in agriculture are mainly associated with specific crop pests, e.g. root-knot and cyst-forming endoparasites (e.g. *Meloidogyne*, *Heterodera*, and *Globodera*). The high overall abundance of Pp nematodes in AGR (*Aglenchus agricola* Pp_2, *Paratylenchus bukowinensis* Pp_2, *Bitylenchus dubius* Pp_3, and *Helicotylenchus dihystera* Pp_3 are all ectoparasites) suggests their close relationship with cultured crops. Omnivores and carnivores were significantly more abundant in MEA and FOR than AGR, consistent with previous findings by Neher *et al.,* (2005) and Renčo *et al.,* (2010).

Relationships of soil type with soil properties and nematode and microbial communities

Soil type was also an important factor affecting the nematode and microbial communities and soil properties. Soil properties were best in CM, with a neutral pH and the highest C and N contents and C/N ratio, followed by CS and SS. C and N contents were twice as high in CM than SS, in agreement with the general soil classification (www.vupop.sk).

Soil type was more important than ecosystem type for both the nematode and microbial communities. For example, nematode abundance, number of nematode species, and microbial biomass or diversity positively correlated in the CM soil type in two out of three ecosystems studied. Significant effects of soil type on the composition of nematode communities have been documented by Alphei (1998) and Lišková *et al.,* (2008) in forests, by Popovici and Ciobanu (2000) in grasslands, and by Neher *et al.,* (2005) in agricultural land. The populations of bacterivores (mainly *A. nanus*, *Eucephalobus striatus*, and *C. propinquus*) and fungivores (*A. avenae* and *F. vulgaris*) and microbial biomass in our study were highest in CM with aerobic conditions, a neutral pH, and a high humus content beneficial to microbial activities and associated nematodes (Wasilewska, 1997). In contrast, the abundances of bacterivores and fungivores were low in SS because of its oxygen deficiency and acidic conditions. These results partially agreed with those by Lišková *et al.,* (2008), who reported that Cephalobidae bacterivores (*Acrobeloides*, *Acrobeles* and *Cervidellus*) were more abundant in a light sandy Regosol with a high pH, but disagreed with those by Wasilewska (1997) and Lišková *et al.,* (2008), who reported that fungivores were more abundant in an acidic Cambisol.

The abundance of facultative plant parasites (Pp_2) did not differ amongst the soil types. *A. agricola* in CM, *Malenchus bryophilus* in CS, and *B. thylactus* in SS were nevertheless the most abundant, supporting the preference of various species of Pp_2 nematodes for different soil types, also reported by Lišková *et al.,* (2008). In contrast, obligate plant parasites (Pp_3) were most abundance in CM, followed by CS and SS, probably due to the different levels and distributions of food sources between these soil types, as also suggested by Popovici and Ciobanu (2000) and Lišková *et al.,* (2008). Natural ecosystems are characterised by high proportions of omnivores and predators (Wasilewska, 1997; Ferris *et al.,* 2001). Omnivores and predators were most abundant in CM, but only in FOR and MEA.

In our study soil type was also as important factor affecting values

of all ecological and functional indices, contradicting findings of Lišková *at al.,* (2008), who reported that only fungal to bacteria (F/B) ratio and channel index (CI) was significantly different among Cambisol, Regosol, Fluvisol and Rendzina soil types. Ruess (2003) studied CI and F/B at various sites and stated that soil and climate affect CI more strongly than does ecosystem type. In our study CI was significantly affected by both, ecosystem and soil type as well as their interactions, and sampling date has no impact on CI values.

In general, season (sampling date) in our study had relatively minor effects on both the abiotic and biotic characteristics. Only SM content fluctuated with the season (lowest in summer) what significantly affecting microbial biomass, confirming results of Buchanan and King (1992). Similar overall nematode abundance influences sampling date, which can partly be explained by changes in SM, in agreement with observation of Sohlenius and Boström (2001) from Swedish Scot pine forest soils. Out of functional guilds, Ba_2, Fu_2, and Pp_2 nematodes were influenced by sampling date, however only Ba_2 were negatively correlated with SM content.

Conclusion

The differences in soil properties, nematode communities, and microbial biomasses amongst the soil and ecosystem types suggest an obvious impact of environmental variables on biotic and abiotic soil characteristics. The differences were larger amongst the soil types than the ecosystems. CM had the best soil properties, with a neutral pH and the highest C and N contents and C/N ratio and thus the highest number of species and diversity of nematode communities, as well as the MI, ΣMI, PPI, SI, and TD nematode ecological indices, and microbial biomass, richness, and diversity. The majority of the abiotic and biotic characteristics varied the most between CM and SS. The abiotic and biotic soil properties and their interactions were best in FOR, where the number of species and diversity of nematode communities, as well as the MI, ΣMI, PPI, SI, and TD ecological indices, and microbial biomass, richness, and diversity were highest. SM, C, and N contents and the C/N ratio were also highest in FOR, but the pH was lowest. C and N contents were twice as high in FOR than AGR but were similar to those in MEA, suggesting that established forests and natural meadows represent relatively stable environments, providing suitable conditions for soil microbial and nematode communities. C/N ratios and biological diversity were lower in the cultivated soils than in the natural ecosystems soils, likely due to periodic perturbation. This resulted in a lower abundance and diversity of nematode communities and microbial diversity. FOR and AGR generally differed the most. The soil properties, nematode communities, and microbial biomass were more similar in FOR and MEA. A multivariate analysis indicated that the abundance of most of the nematode guilds, total nematode abundance, number of nematode species, and microbial characteristics tended to be higher in the environment with a higher pH, the N and C contents. Sampling dates had a minor or no effect on most of the parameters, except the SM content, abundance of c-p2 nematodes, microbial richness, and several of the nematode ecological indices.

Conflict of Interest

Authors have no potential conflict of interest pertaining to this submission to Helminthologia.

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