

# Nematode communities of forest ecosystems in association with various soil orders

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**Summary.** Soil nematodes were investigated at six sites in each of four different forest soil orders in Slovakia: Cambisol, Fluvisol, Regosol and Rendzina. The nematode fauna showed high diversity of genera (H'gen) and maturity (MI, PPI, SI) and those parameters were independent of soil order. The nematode communities were characterised by a high proportion of plant parasites (mainly *Trichodorus*, *Helicotylenchus*, *Paratrophurus*, and *Longidorus*) except for the Cambisol. The greatest proportions of bacterial feeders (*Acrobeloides* and *Alaimus*) were in Regosol and Rendzina. Fungal feeders (*Tylencholaimus*, *Diphtherophora*, *Aphelenchoides*) together with root fungal feeders (*Aglenchus*) were abundant in Cambisol with higher acidity and root-fungal feeders (*Malenchus*) in Fluvisol with a preponderance of anaerobic conditions. All soil orders were characterised by a high proportion of K-strategic omnivores (*Eudorylaimus*) and predators (*Mylonchulus* and *Clarkus*). The trophic structure of nematode communities suggested great activity of a fungal-based energy channel in Cambisol. Increasing activity of a bacterial-based energy channel was indicated through Fluvisol and Rendzina to Regosol. Cluster analysis and Principal component analysis showed that generic structure of nematode communities was strongly affected by soil orders, which were characterised by specific fauna. Nematode communities in the Rendzina sites showed greater variation than in other soil orders.

**Key words:** nematode communities, forest soil, Cambisol, Fluvisol, Regosol, Rendzina, Slovakia.

Forest ecosystems are major climax formations in Central Europe, which developed on different soil substrates and altitudes into various vegetation types. They are inhabited by heterogeneous soil nematode faunas, which can be influenced by many additional factors such as annual and long-term climatic changes (Sohlenius & Boström, 2001; Hoschitz & Kaufman, 2004; Bakonyi *et al.*, 2007), industrial emissions (Bassus, 1968; Háněl, 1993) and clearance cutting (Sohlenius, 1982; 2002; Háněl, 2004). Due to their abundance, diversity and interactions with other soil biota, nematodes are useful indicators of soil condition and soil processes in forests (Yeates, 2007).

The forests have immense importance in the ecology of Slovakia as they cover 40% of its territory. The country is represented by a great geological diversity that includes variable conditions of forest soil formation. Šály (1983) published data on nematode diversity in various Slovak forests mostly with respect to vegetation

and climatic conditions but he was less concerned with soil conditions. Findings on a very close association of *Longidorus* and *Xiphinema* spp. with specific soil conditions in Slovakian forests have been presented by Lišková & Planderová (1996), Lišková & Brown (1999) and Lišková & Sturhan (2000).

Site and related soil order have more important influence on composition of nematode fauna than season or year (Yeates, 1984; de Goede & Bongers, 1994; Popovici & Ciobanu, 2000; Háněl, 2003), and the effect of ecosystem type on different soil substrates affects interpretation of nematode community indices (Neher *et al.*, 2005). Disturbances (either by natural events or by anthropogeneous activities) to landscapes are increasing and management of landscape recovery implies knowledge of original status of biological communities in particular situations. Therefore, this paper surveys nematode faunas of (semi) natural forest ecosystems in four soil orders. The



main goal of the study is to find parameters of nematode communities that are common to forests in the Slovak Republic and those that are specifically related to the site pedology.

## MATERIAL AND METHODS

**Study sites.** Nematodes were studied in four forest soil orders – Cambisol, Fluvisol, Regosol and Rendzina. Each soil order was represented by six different localities. The forests were (semi) natural ecosystems more than 100 years old at different altitudes and located throughout the Slovak Republic. Characteristics of individual soil orders and plant cover were as follows.

Cambisol – soils derived from Carpathian flush. They are middle heavy, or heavy loamy, sandy-loamy or clay-loamy, rarely also light sandy gravelled soils with pH of 3.5 to 4.5 and are characteristic of northern and northern-east region of Slovakia (orographic units Oravská and Liptovská kotlina valley and Beskydské predhorie promontory) at altitudes of 300 to 1000 m. Mean annual air temperature is 5.9-7.5°C and an annual precipitation approximately 650-800 mm. Vegetation in an area of lower altitude is characterised by deciduous *Fageto – Carpinetum* with undergrowth of e.g. *Anemone nemorosa*, *Asarum europaeum*, and *Rubus caesius*. In areas of a higher altitude *Piceetum* forests prevail with undergrowth mostly of *Vaccinium myrtillus* and *Oxalis acetosella*.

Fluvisol – soils derived from river-born sediments of different kind (sand, gravel and clay). Floodplain forests are mostly concentrated in southern regions of Slovakia, in the warmest area of the country at an altitude of 90-150 m. Mean annual air temperature is 9.5 – 10.5°C and annual precipitation 500-600 mm. The landscape is a plain with a network of dead arms of the Moravia River in western areas, the Danube River in southern and south-western areas, and the Rivers Bodrog, Latorica and Tisa in eastern Slovakia. The soil texture varies from very light sandy soil to heavy clay soil. The soils are regularly flooded, mostly in spring. The soil pH varies from 3.1 to 7.3. The vegetation is generally characterised by *Saliceto-Alnetum*, *Querceto-Fraxinetum* and *Ulmeto-Fraxinetum* forests, sporadically in rarely flooded areas with *Populus* spp., undergrowth mostly with *Baldingera arundinacea*, *Carex* spp., *Rubus caesius* and *Urtica dioica*.

Regosol – soils derived from dune sand and characteristic drift sand landscape of Borská nížina lowland, Podunajská and Východoslovenská rovina plain. The areas with drift sand landscapes are at

an altitude of 100-150 m with a mean annual temperature of 9-10°C and an annual precipitation of approximately 500-550 mm. These soils consist of sand throughout the whole profile, with pH of 3.5-6.7. Forest vegetation is characterised by *Robinieto – Pineto – Quercetum* forest type with undergrowth mostly of *Sambucus nigra*, *Chelidonium majus*, *Aristolochia clematitis* and *Ornithogalum boucheanum*.

Rendzina – soils derived from calcareous parent rock. They are light sandy or middle heavy clay-loamy, mostly shallow gravelled or stony soils characteristic for areas such as Slovenský kras karst region, Súľovské skaly, Čergov and many others. These areas are locally distributed throughout Slovakia with different geographical and climatic conditions; the pH of soil is 5.8-7.4. Vegetation is characterised by *Pinetum*, or *Pineto – Piceetum*, undergrowth mostly of *Polygonatum latifolium*, *Primula auricula* and *Anemone* sp.

**Methods.** A total of 24 soil samples were collected during May in 2005 and 2006 from 6 localities of each soil order. At each locality a mixed soil sample consisted of five subsamples taken by using a hand spade. The depth of sampling depended on the depth of the soil profile on the parent rock. At deep soils of Regosol, Fluvisol and Cambisol the depth of sampling was 30 cm under the litter horizon. In shallow soils of Rendzina, samples were taken down to a depth of 10 cm under the organic layer of forest litter. Nematodes were extracted from 500 g of mixed soil by using the Cobb flotation-sieving method. Isolated nematodes were fixed in FAA and mounted on permanent glycerol slides and identified to genus level.

Parameters of nematode communities were studied as follows:

- Abundance of nematodes in 500 g of soil.
- Total number of nematode genera and abundance of individual genera.
- Trophic structure of nematode communities. The genera were allocated into six trophic groups according to the classification system of Yeates *et al.* (1993a): bacterial feeders, fungal feeders, plant feeders, omnivores, predators and insect parasites. Plant feeders were further divided into plant parasites (obligate plant feeders) and root-fungal feeders (facultative plant feeders, which include *Tylenchus* spp. and related species according to Yeates *et al.* (1993b), and fungivorous Tylenchidae in forest ecosystems according to Háněl (2004).
- Shannon index of diversity for genera ( $H'$ gen), proposed by Shannon & Weaver (1949).



– Maturity Index (MI) for non-parasitic nematodes.

– Plant Parasite Index (PPI) for plant-parasitic nematodes; both MI and PPI proposed by Bongers (1990).

– PPI/MI ratio: Proportion of Plant Parasite Index to Maturity Index, ratio introduced by Bongers & Korthals (1995).

– B/F ratio: Proportion of Bacterial Feeders to Fungal Feeders, ratio proposed by Wasilewska (1997). Root-fungal feeders were not included in the fungal feeders.

– Enrichment Index (EI), Structure Index (SI) and Channel Index (CI) were calculated according Ferris *et al.* (2001) with weightings of nematode taxa as suggested by the authors.

– Statistical calculations were performed using the STATISTICA (StatSoft, 2001) and CANOCO for Windows version 4.5 (Ter Braak & Šmilauer, 2002).

## RESULTS

**Generic composition of nematode faunas.** A total of 89 nematode genera were identified, 60 in Cambisol, 58 in Fluvisol, 62 in Regosol and 56 in Rendzina (Table 1). The greatest variety in generic composition was recorded in Rendzina soils, where the number of genera at individual localities fluctuated from 16 to 35. The lowest number was recorded in stony soils of calcareous canyons, or gravely soils derived from conglomerate. Different nematode fauna in localities of Rendzina soils were reflected in cluster analysis (Fig. 1) and also in ordination (Figs 2, 3). Forests in other localities had more similar nematode faunas that reflected the soil orders except for Cam1. The first cluster contained all localities of Fluvisol and two localities of Rendzina. The second cluster was composed of the majority of Cambisol and one locality of Rendzina. The third cluster contained all localities of Regosol (with two subclusters separating three locations in eastern Slovakia mostly with *Robiniatum* from three locations of western Slovakia with *Piceetum*), three of Rendzina and one of Cambisol. This result showed a close association of diversity of nematode communities with individual forest soil orders, including their specific vegetation.

In the fauna studied, 36 genera were common to all soil orders, for example *Alaimus*, *Amphidelus*, *Eucephalobus*, *Monhystera*, *Aphelenchoides*, *Diphtherophora*, *Steinernema*, *Eudorylaimus*, *Clarkus*, *Anatonchus*, *Tripyla*, *Longidorus*, *Paratylenchus*, *Aglenchus*, *Filenchus*, *Tylenchus*, and others (Table 1). On the other hand, some genera were recorded exclusively in individual soil orders.

*Pseudacrobeles*, *Teratocephalus*, *Ditylenchus*, *Aporcelaimus*, *Hoplotylus*, and *Lelenchus* occurred only in Cambisol, *Mesorhabditis*, *Cobbonchus*, *Paratrophurus*, *Pratylenchoides*, *Malenchus*, and *Psilenchus* in Fluvisol, *Acrobeles*, *Cervidellus*, *Eucephalobus*, *Pelodera*, *Carcharodiscus*, *Opailaimus*, *Paraxonchium*, *Seinura*, and *Paratrichodorus* in Regosol, *Chiloplacus*, *Iotonchus*, *Longidorella*, and *Paralongidorus* in Rendzina.

The most abundant genus was *Eudorylaimus* with dominance greater than 10.0% in Regosol, Fluvisol and Rendzina and with dominance of 8.7% in Cambisol sites. This genus tended slightly to prevail in Regosol (Figs 2, 3). Beside the genus *Eudorylaimus* the dominant (5–10%), or subdominant (2 – 5%) genera in individual soil orders were as follows:

In Cambisol, a typical forest soil of higher altitude of the Carpathian region characterised by heterogenic granulation and higher acidity, the dominating genera were *Acrobelloides*, *Alaimus*, *Plectus*, *Aphelenchoides*, *Tylencholaimus*, *Diphtherophora*, *Clarkus*, *Nygolaimus*, *Criconema*, *Longidorus*, *Trichodorus*, *Aglenchus* and *Tylenchus*.

In mostly heavy, very often wet, clay soils of Fluvisol the genera were *Alaimus*, *Mesorhabditis*, *Plectus*, *Tylencholaimus*, *Heterorhabditis*, *Aporcelaimellus*, *Prodorylaimus*, *Anatonchus*, *Mylonchulus*, *Helicotylenchus*, *Longidorus*, *Paratrophurus*, *Pratylenchoides*, *Malenchus* and *Tylenchus*.

In light sandy, permeable, very often dry Regosol of warm areas of the lowest altitude of the country, the prevailing genera were *Acrobeles*, *Acrobelloides*, *Alaimus*, *Cephalobus*, *Plectus*, *Rhabditis*, *Aphelenchoides*, *Geocenamus*, *Meloidogyne*, *Mesocriconema*, *Paratrichodorus*, *Pratylenchus*, *Rotylenchus*, *Trichodorus* and *Xiphinema*.

In shallow calcareous Rendzina distributed throughout the country the genera of greatest dominance were *Alaimus*, *Amphidelus*, *Eucephalobus*, *Prismatolaimus*, *Rhabditis*, *Tylencholaimus*, *Mylonchulus*, *Helicotylenchus*, *Longidorella*, *Longidorus*, *Rotylenchus*, *Trichodorus*, *Xiphinema* and *Tylenchus*.

From a total of 89 genera 21 were plant-parasitic nematodes, whose occurrence often varied with soil orders. Seven genera were found in all soil orders investigated whereas the others occurred mostly in one or two soil orders. Dominance of *Trichodorus* (11.1%) in Cambisol, *Longidorus* and *Paratrophurus* (7.1% and 8.2 %, respectively) in Fluvisol, and *Helicotylenchus* (8.5 %) in Rendzina was recorded. At Regosol, the most abundant, but subdominant genera (2 – 5%)



**Table 1.** Composition of nematode communities in four forest soil orders, their mean abundance per 500g soil  $\pm$  SD ( $n = 6$ ).

TG	Nematode genera	Code	c-p	Cambisol				Fluvisol				Regosol				Rendzina			
				mean	$\pm$	SD	D%	mean	$\pm$	SD	D%	mean	$\pm$	SD	D%	mean	$\pm$	SD	D%
B	<i>Acrobeles</i>	Acrobele	2	—				—				11.0	$\pm$	11.3	2.74	—			
B	<i>Acrobeloides</i>	Acrobdes	2	11.3	$\pm$	16.6	3.0	3.3	$\pm$	3.8	0.9	34.0	$\pm$	56.8	8.47	—			
B	<i>Alaimus</i>	Alaimus	4	12.3	$\pm$	15.1	3.3	8.7	$\pm$	11.9	2.3	27.8	$\pm$	47.4	6.93	26.0	$\pm$	20.5	6.85
B	<i>Amphidelus</i>	Amphidel	4	3.7	$\pm$	3.7	0.9	4.7	$\pm$	7.5	1.3	0.5	$\pm$	0.8	0.12	8.3	$\pm$	9.14	2.19
B	<i>Anaplectus</i>	Anaplect	2	0.7	$\pm$	1.5	0.2	1.3	$\pm$	2.6	0.4	1.0	$\pm$	1.2	0.25	3.7	$\pm$	4.11	0.97
B	<i>Aulolaimus</i>	Aulolaim	3	1	$\pm$	1.8	0.3	0.5	$\pm$	0.8	0.1	—				4.0	$\pm$	5.69	1.05
B	<i>Bastiania</i>	Bastiani	3	1.7	$\pm$	2.4	0.4	—				—				0.5	$\pm$	1.12	0.13
B	<i>Cephalobus</i>	Cephalob	2	4.5	$\pm$	4.7	1.2	4.3	$\pm$	6.2	1.2	9.2	$\pm$	8.6	2.28	6.5	$\pm$	5.94	1.71
B	<i>Cervidellus</i>	Cervidel	2	—				—				3.5	$\pm$	5.6	0.87	—			
B	<i>Diplogaster</i>	Diplogas	1	—				—				1.7	$\pm$	3.7	0.42	—			
B	<i>Eucephalobus</i>	Eucephal	2	2.3	$\pm$	3.5	0.6	6.5	$\pm$	5.0	1.8	6.8	$\pm$	6.5	1.7	11.3	$\pm$	10.62	2.98
B	<i>Heterocephalobus</i>	Heteroce	2	—				0.7	$\pm$	1.5	0.2	0.3	$\pm$	0.8	0.08	—			
B	<i>Chiloplacus</i>	Chilopla	2	—				—				—				0.5	$\pm$	1.12	0.13
B	<i>Mesorhabditis</i>	Mesorhab	1	—				14.5	$\pm$	32.4	3.9	—				—			
B	<i>Monhystera</i>	Monhyste	2	6.8	$\pm$	6.7	1.8	2.2	$\pm$	2.7	0.6	1.5	$\pm$	2.9	0.37	5.2	$\pm$	11.55	1.36
B	<i>Neodiplogaster</i>	Neodiplo	1	—				—				0.7	$\pm$	1.5	0.17	—			
B	<i>Pelodera</i>	Pelodera	1	—				0.7	$\pm$	1.5	0.2	—				0.7	$\pm$	1.49	0.18
B	<i>Plectus</i>	Plectus	2	14.8	$\pm$	9.9	3.9	8.7	$\pm$	9.0	2.3	8.5	$\pm$	8.9	2.12	17.2	$\pm$	24.07	4.52
B	<i>Prismatolaimus</i>	Prismato	3	1.7	$\pm$	2.4	0.4	1.2	$\pm$	2.2	0.3	0.7	$\pm$	0.9	0.17	0.5	$\pm$	1.12	0.13
B	<i>Pseudacrobeles</i>	Pseudacr	2	2.7	$\pm$	4.8	0.7	—				—				—			
B	<i>Rhabditis</i>	Rhabditi	1	3.2	$\pm$	1.9	0.8	5.2	$\pm$	4.3	1.4	12.8	$\pm$	15.0	3.2	12.0	$\pm$	6.24	3.16
B	<i>Teratocephalus</i>	Teratoce	3	1.2	$\pm$	1.7	0.3	—				—				—			
B	<i>Tylolaimophorus</i>	Tylolaim	3	4.8	$\pm$	6.9	1.3	—				7.8	$\pm$	13.2	1.95	5.3	$\pm$	10.18	1.4
B	<i>Wilsonema</i>	Wilsonem	2	2.2	$\pm$	3.4	0.6	0.3	$\pm$	0.5	0.1	5.0	$\pm$	4.4	1.25	—			
B	<i>Zeldia</i>	Zeldia	2	1.5	$\pm$	3.4	0.4	—				3.0	$\pm$	2.4	0.75	—			
F	<i>Aphelenchoides</i>	Apheldes	2	12.8	$\pm$	10.9	3.4	0.7	$\pm$	0.8	0.2	8.7	$\pm$	11.3	2.16	2.0	$\pm$	3.32	0.53
F	<i>Aphelenchus</i>	Aphelchu	2	0.7	$\pm$	1.5	0.2	2.0	$\pm$	1.8	0.5	3.5	$\pm$	3.6	0.87	1.8	$\pm$	2.48	0.48
F	<i>Diphtherophora</i>	Diphther	3	16.5	$\pm$	20.8	4.4	2.5	$\pm$	3.6	0.7	2.5	$\pm$	2.4	0.62	2.5	$\pm$	2.36	0.66
F	<i>Ditylenchus</i>	Ditylenc	2	1.0	$\pm$	2.3	0.3	—				—				—			
F	<i>Nothotylenchus</i>	Nothotyl	2	1.7	$\pm$	1.8	0.4	2.5	$\pm$	2.8	0.7	0.8	$\pm$	1.2	0.21	1.0	$\pm$	1.83	0.26
F	<i>Paraphelenchus</i>	Paraphel	2	0.5	$\pm$	1.1	0.1	0.2	$\pm$	0.4	0.1	0.7	$\pm$	1.1	0.17	—			
F	<i>Tylencholaimus</i>	Tylencho	4	20.3	$\pm$	23.1	5.4	15.7	$\pm$	25.6	4.2	5.0	$\pm$	4.4	1.25	8.5	$\pm$	8.8	2.2

Dominance (D %), trophic group (TG); B – bacterial feeders, F – fungal feeders, PP – plant parasites, RFF – root-fungal feeders, O – omnivores, P – predators, IN – insect parasites, Code of genera used for Principal component analysis.

**Table 1 (continued).** Composition of nematode communities in four forest soil orders, their mean abundance per 500g soil  $\pm$  SD ( $n = 6$ )/continuation

TG	Nematode genera	Code	c-p	Cambisol				Fluvisol				Regosol				Rendzina			
				mean	$\pm$	SD	D%	mean	$\pm$	SD	D%	mean	$\pm$	SD	D%	mean	$\pm$	SD	D%
PP	<i>Criconema</i>	Criconem	3	8.0	$\pm$	11.4	2.1	0.3	$\pm$	0.8	0.1	1.8	$\pm$	4.1	0.46	2.3	$\pm$	3.3	0.6
PP	<i>Criconemoides</i>	Cricodes	3	—				1.7	$\pm$	2.9	0.5	0.7	$\pm$	1.5	0.17	—			
PP	<i>Geocenamus</i>	Geocenam	3	—				—				9.0	$\pm$	10.3	2.24	0.5	$\pm$	1.1	0.1
PP	<i>Helicotylenchus</i>	Helicoty	3	0.5	$\pm$	1.1	0.1	10.8	$\pm$	16.4	2.9	4.8	$\pm$	10.8	1.2	32.3	$\pm$	43.8	8.5
PP	<i>Hemicycliophora</i>	Hemicycl	3	—				0.3	$\pm$	0.5	0.1	—				0.5	$\pm$	1.1	0.1
PP	<i>Hoplotylus</i>	Hoplotyl	2	4.3	$\pm$	9.7	1.2	—				—				—			
PP	<i>Longidorella</i>	Longilla	4	—				—				—				16.7	$\pm$	36.8	4.4
PP	<i>Longidorus</i>	Longidor	5	8.3	$\pm$	6.9	2.2	26.5	$\pm$	25.8	7.1	2.3	$\pm$	3.2	0.58	12.3	$\pm$	14.2	3.3
PP	<i>Meloidogyne</i>	Moloidog	3	—				0.3	$\pm$	0.8	0.1	12.8	$\pm$	26.1	3.2	—			
PP	<i>Mesocriconema</i>	Mesocric	3	1.2	$\pm$	2.6	0.3	2.5	$\pm$	3.6	0.7	12.0	$\pm$	16.7	2.99	3.2	$\pm$	6.6	0.8
PP	<i>Paralongidorus</i>	Paralong	5	—				—				—				4.5	$\pm$	8.8	1.2
PP	<i>Paratrichodorius</i>	Paratric	4	—				—				18.2	$\pm$	13.9	4.52	—			
PP	<i>Paratrophurus</i>	Paratrop	3	—				30.7	$\pm$	47.3	8.2	—				—			
PP	<i>Paratylenchus</i>	Paratyle	2	0.3	$\pm$	0.8	0.1	5.5	$\pm$	10.1	1.5	1.5	$\pm$	2.1	0.37	0.5	$\pm$	1.1	0.1
PP	<i>Pratylenchoides</i>	Pratydes	2	—				8.2	$\pm$	18.3	2.2	—				—			
PP	<i>Pratylenchus</i>	Pratylen	3	0.3	$\pm$	0.8	0.1	—				18.0	$\pm$	9.2	4.48	—			
PP	<i>Rotylenchus</i>	Rotylenc	3	1.8	$\pm$	3.7	0.5	1.3	$\pm$	1.9	0.4	14.33	$\pm$	18.2	3.57	9.5	$\pm$	19.5	2.5
PP	<i>Trichodorus</i>	Trichodo	4	41.7	$\pm$	51.4	11.1	—				14.5	$\pm$	19.8	3.61	14.7	$\pm$	25.4	3.9
PP	<i>Tylenchorhynchus</i>	Tylenrhy	3	0.7	$\pm$	1.5	0.2	0.3	$\pm$	0.8	0.1	6.5	$\pm$	9.9	1.62	3.0	$\pm$	5.9	0.8
PP	<i>Xenocriconemella</i>	Xenocric	3	1.7	$\pm$	3.7	0.4	—				2.7	$\pm$	5.9	0.66	—			
PP	<i>Xiphinema</i>	Xiphinem	5	—				5.7	$\pm$	9.7	1.5	9.0	$\pm$	17.9	2.24	7.7	$\pm$	7.4	2.0
RFF	<i>Aglenchus</i>	Aglenchu	2	27.7	$\pm$	45.1	7.3	4.2	$\pm$	5.0	1.1	1.2	$\pm$	2.6	0.29	2.5	$\pm$	5.6	0.7
RFF	<i>Basiria</i>	Basiria	2	1.7	$\pm$	3.7	0.4	2.5	$\pm$	4.3	0.7	2.0	$\pm$	3.7	0.5	7.2	$\pm$	9.7	1.9
RFF	<i>Coslenchus</i>	Coslench	2	0.5	$\pm$	1.1	0.1	0.2	$\pm$	0.4	0.1	—				0.7	$\pm$	1.5	0.2
RFF	<i>Filenchus</i>	Filenchu	2	3.3	$\pm$	3.1	0.9	0.17	$\pm$	0.4	0.1	0.3	$\pm$	0.8	0.08	3.2	$\pm$	7.1	0.8
RFF	<i>Lelenchus</i>	Lelenchu	2	5.2	$\pm$	9.9	1.4	—				—				—			
RFF	<i>Malenchus</i>	Malenchu	2	—				38.0	$\pm$	32.9	10.2	—				—			

Dominance (D %), trophic group (TG); B – bacterial feeders, F – fungal feeders, PP – plant parasites, RFF – root-fungal feeders, O – omnivores, P – predators, IN – insect parasites, Code of genera used for Principal component analysis.



**Table 1 (continued).** Composition of nematode communities in four forest soil orders, their mean abundance per 500g soil  $\pm$  SD ( $n = 6$ )/continuation

TG	Nematode genera	Code	c-p	Cambisol				Fluvisol				Regosol				Rendzina			
				mean	$\pm$	SD	D%	mean	$\pm$	SD	D%	mean	$\pm$	SD	D%	mean	$\pm$	SD	D%
RFF	<i>Psilenchus</i>	Psilenchu	2	—				0.5	$\pm$	0.8	0.1	—			—				
RFF	<i>Tylenchus</i>	Tilenchu	2	10.0	$\pm$	11.6	2.7	9.5	$\pm$	9.3	2.6	5.8	$\pm$	4.8	1.45	15.5	$\pm$	20.8	4.1
O	<i>Aporcelaimellus</i>	Aporcllu	5	2.0	$\pm$	2.5	0.5	10.8	$\pm$	9.7	2.9	3.2	$\pm$	2.8	0.79	1.8	$\pm$	4.1	0.5
O	<i>Aporcelaimus</i>	Aporcela	5	0.5	$\pm$	1.1	0.1	—			—				—				
O	<i>Metaxonchium</i>	Metaxonc	5	—				3.7	$\pm$	4.78	1.0	—			—	2.0	$\pm$	4.5	0.5
O	<i>Carcharodiscus</i>	Carcharo	5	—				—			—	0.7	$\pm$	1.1	0.2	—			
O	<i>Dorylaimoides</i>	Dorylaim	4	1.0	$\pm$	2.2	0.3	1.2	$\pm$	1.5	0.3	—			—	0.7	$\pm$	1.5	0.2
O	<i>Enchodelus</i>	Enchodel	4	2.2	$\pm$	4.0	0.6	—			—	0.3	$\pm$	0.8	0.1	2.3	$\pm$	4.0	0.6
O	<i>Eudorylaimus</i>	Eudoryla	4	32.7	$\pm$	15.9	8.7	38.8	$\pm$	25.6	10.4	63.5	$\pm$	33.9	15.8	38.7	$\pm$	28.3	10.2
O	<i>Mesodorylaimus</i>	Mesodory	5	—				6.3	$\pm$	6.9	1.7	0.8	$\pm$	1.1	0.2	6.7	$\pm$	9.5	1.8
O	<i>Microdorylaimus</i>	Microdor	4	0.5	$\pm$	1.1	0.1	—			—	0.5	$\pm$	1.1	0.1	—			
O	<i>Opailaimus</i>	Opailaim	5	—				—			—	0.5	$\pm$	1.1	0.1	—			
O	<i>Oxydirus</i>	Oxydirus	5	2.5	$\pm$	4.4	0.7	1.3	$\pm$	2.6	0.4	0.2	$\pm$	0.4	0.1	2.8	$\pm$	5.5	0.8
O	<i>Paraxonchium</i>	Paraxonc	5	—				—			—	1.8	$\pm$	3.3	0.5	—			
O	<i>Prodorylaimus</i>	Prodoryl	5	—				8.8	$\pm$	7.2	2.4	—			—	0.7	$\pm$	1.1	0.2
O	<i>Pungentus</i>	Pungentu	4	4.7	$\pm$	4.4	1.2	—			—	1.2	$\pm$	1.5	0.3	0.5	$\pm$	1.1	0.1
P	<i>Anatonchus</i>	Anatonch	4	2.2	$\pm$	4.8	0.6	10.3	$\pm$	16.1	2.8	0.2	$\pm$	0.4	0.1	3.7	$\pm$	3.8	0.9
P	<i>Clarkus</i>	Clarkus	4	20.2	$\pm$	25.5	5.4	6.5	$\pm$	5.3	1.8	7.3	$\pm$	6.1	1.8	3.3	$\pm$	5.1	0.9
P	<i>Cobbonchus</i>	Cobbonch	4	—				2.7	$\pm$	4.2	0.7	—			—	—			
P	<i>Coomansus</i>	Coomansu	4	1.7	$\pm$	3.7	0.4	—			—	0.7	$\pm$	1.5	0.2	—			
P	<i>Iotonchus</i>	Iotonchu	4	—				—			—	—			—	0.2	$\pm$	0.4	0.1
P	<i>Miconchus</i>	Miconchu	4	6.8	$\pm$	9.8	1.8	0.7	$\pm$	1.1	0.2	—			—	5.7	$\pm$	6.1	1.5
P	<i>Mylonchulus</i>	Mylonchu	4	1.8	$\pm$	2.9	0.5	22.0	$\pm$	18.2	5.9	2.0	$\pm$	3.7	0.5	20.2	$\pm$	15.2	5.3
P	<i>Nygolaimus</i>	Nygolaim	5	11.8	$\pm$	10.7	3.1	1.7	$\pm$	3.3	0.5	0.2	$\pm$	0.4	0.1	0.8	$\pm$	1.2	0.2
P	<i>Prionchulus</i>	Prionchu	4	1.0	$\pm$	2.2	0.3	—			—	0.3	$\pm$	0.8	0.1	—			
P	<i>Seinura</i>	Seinura	2	—				—			—	2.5	$\pm$	4.4	0.6	—			
P	<i>Tripyla</i>	Tripyla	3	3.3	$\pm$	3.4	0.9	7.2	$\pm$	8.0	1.9	1.7	$\pm$	2.4	0.4	4.3	$\pm$	4.8	1.1
IN	<i>Heterorhabditis</i>	Heterorh	1	2.0	$\pm$	4.5	0.5	7.5	$\pm$	7.4	2.0	1.8	$\pm$	1.4	0.5	4.8	$\pm$	10.8	1.3
IN	<i>Steinernema</i>	Steinern	1	32.5	$\pm$	37.1	8.6	6.7	$\pm$	5.0	1.8	17.3	$\pm$	21.3	4.3	24.5	$\pm$	30.4	6.5

Dominance (D %), trophic group (TG); B – bacterial feeders, F – fungal feeders, PP – plant parasites, RFF – root-fungal feeders, O – omnivores, P – predators, IN – insect parasites, Code of genera used for Principal component analysis.

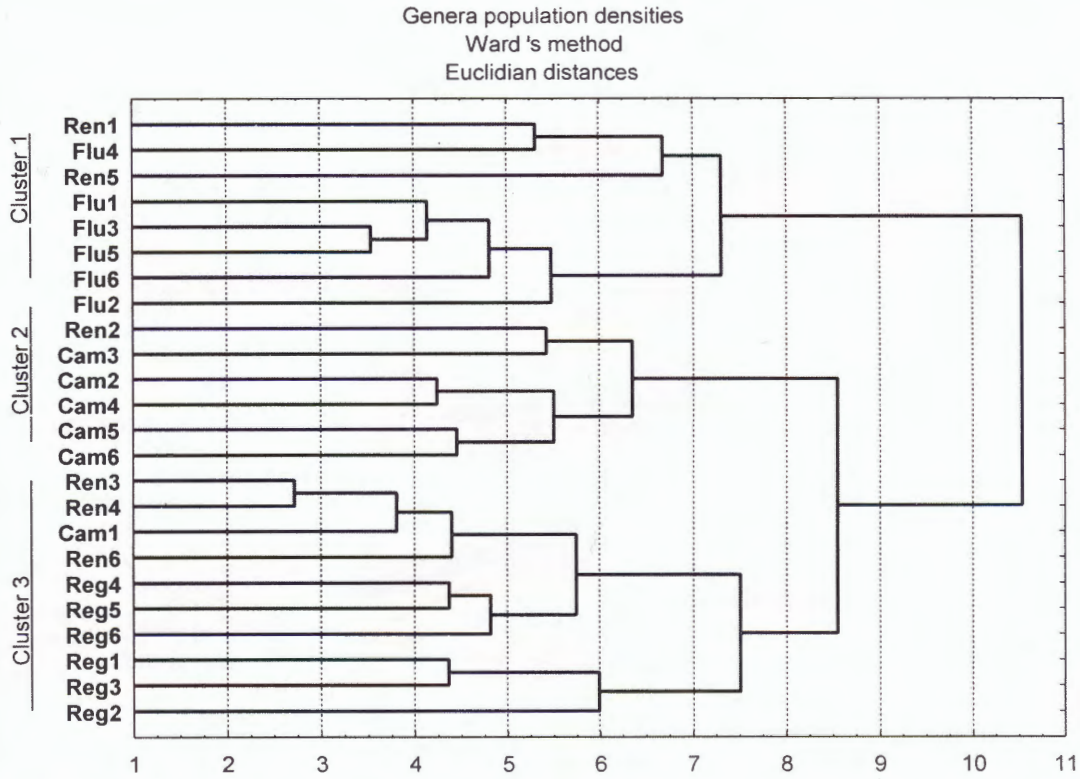


Fig. 1. Cluster analysis of abundance of nematode genera  $\log(x+1)$  in individual localities and different soil orders (Cambisol – Cam; Fluvisol – Flu; Regosol – Reg; Rendzina – Ren).

Table 2. Community indices of soil nematodes in four forest soil orders in the Slovak Republic, mean value  $\pm$  SD ( $n = 6$ ).

Index	Cambisol		Fluvisol		Regosol		Rendzina	
Abundance ind./500g	376.8	$\pm$ 122.8	372.0	$\pm$ 105.4	401.5	$\pm$ 180.4	379.8	$\pm$ 249.8
Bacterial feeders %	21.5	$\pm$ 4.7 <sup>ab</sup>	16.8	$\pm$ 9.3 <sup>a</sup>	29.9	$\pm$ 12.3 <sup>b</sup>	25.1	$\pm$ 5.4 <sup>ab</sup>
Fungal feeders %	13.6	$\pm$ 6.1	6.6	$\pm$ 5.5	5.2	$\pm$ 3.3	5.3	$\pm$ 3.0
Root-fungal feeders %	11.5	$\pm$ 10.7	14.3	$\pm$ 5.6	2.6	$\pm$ 2.2	6.2	$\pm$ 3.7
Plant parasites %	16.3	$\pm$ 11.4	25.2	$\pm$ 6.2	32.7	$\pm$ 6.5	28.5	$\pm$ 8.0
Omnivores %	13.4	$\pm$ 5.0	19.6	$\pm$ 7.8	20.5	$\pm$ 10.0	15.5	$\pm$ 6.4
Predators %	15.1	$\pm$ 10.3	13.3	$\pm$ 5.8	4.7	$\pm$ 2.8	10.8	$\pm$ 5.1
Insect parasites %	8.4	$\pm$ 8.6	4.4	$\pm$ 3.0	4.5	$\pm$ 3.7	8.7	$\pm$ 10.1
Number of genera	60		58		62		56	
H'gen	2.7	$\pm$ 0.1	2.8	$\pm$ 0.2	2.7	$\pm$ 0.3	2.8	$\pm$ 0.3
MI	3.3	$\pm$ 0.2	3.5	$\pm$ 0.5	3.0	$\pm$ 0.6	3.4	$\pm$ 0.2
PPI	3.0	$\pm$ 0.5	3.1	$\pm$ 0.6	3.2	$\pm$ 0.2	3.5	$\pm$ 0.4
PPI/MI	0.9	$\pm$ 0.2	0.9	$\pm$ 0.2	1.1	$\pm$ 0.3	1.0	$\pm$ 0.1
B/F	1.8	$\pm$ 0.6 <sup>a</sup>	4.6	$\pm$ 3.3 <sup>ab</sup>	9.1	$\pm$ 6.9 <sup>b</sup>	7.3	$\pm$ 6.5 <sup>ab</sup>
CI	53.0	$\pm$ 23.6 <sup>a</sup>	12.5	$\pm$ 9.0 <sup>b</sup>	35.7	$\pm$ 39.0 <sup>ab</sup>	9.4	$\pm$ 6.2 <sup>b</sup>
EI	62.8	$\pm$ 16.7	71.3	$\pm$ 18.2	58.4	$\pm$ 16.0	75.4	$\pm$ 11.1
SI	91.1	$\pm$ 4.2	94.5	$\pm$ 4.1	86.2	$\pm$ 12.4	93.9	$\pm$ 2.7

Significant differences (ANOVA, Fischer LSD post-hoc test at  $\alpha = 0.05$ ) between soil orders indicated by different letters.



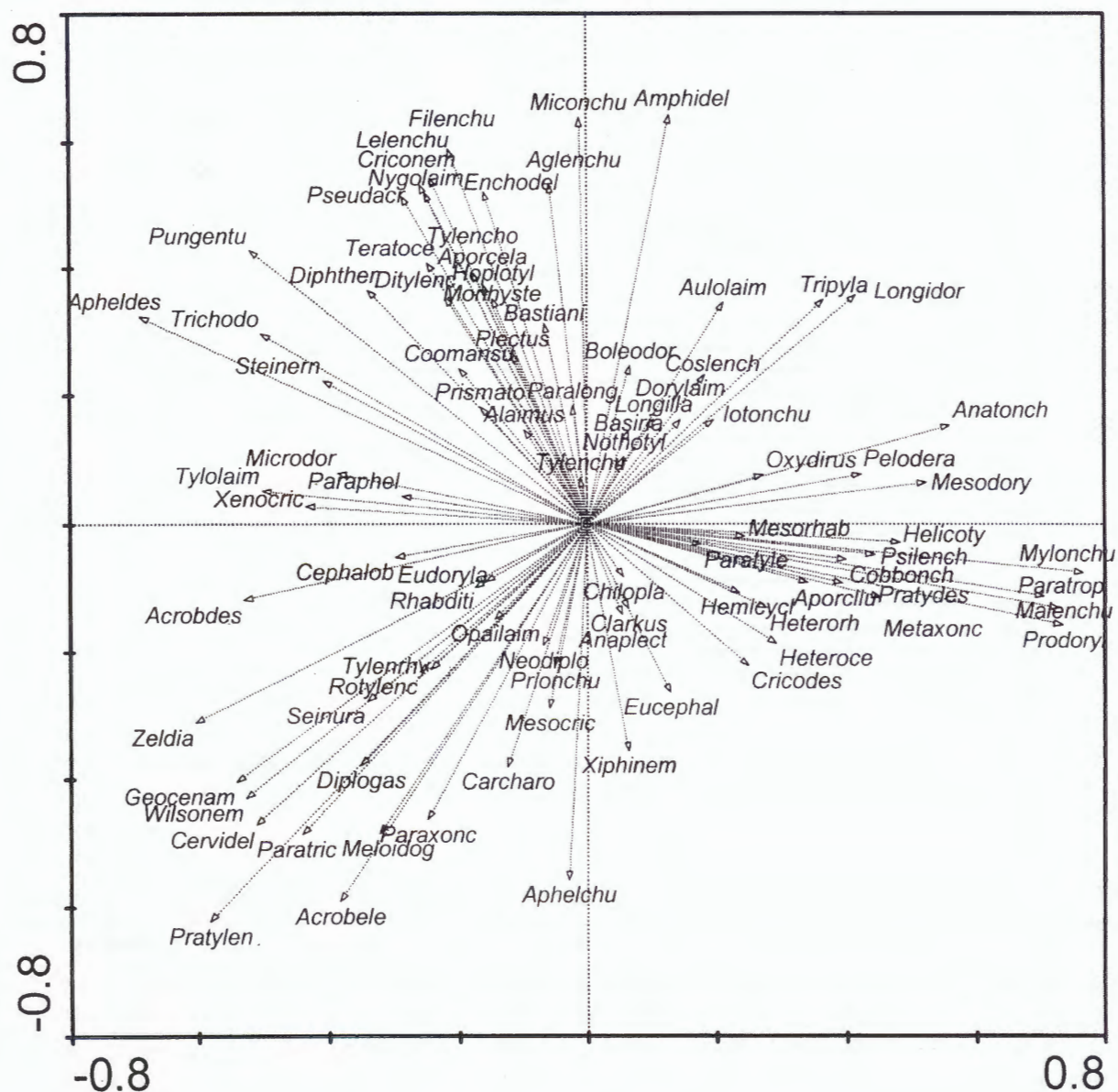


Fig. 2. Genus scatter plot of Principal component analysis, 1<sup>st</sup> and 2<sup>nd</sup> axis, log(y+1) transformed genera abundance and correlation matrix applied in the analysis. Eigenvalues for 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> ordination axes were 0.155, 0.103, 0.087, and 0.079, respectively. Codes of genera are given in Table 1.

were *Geocenamus*, *Meloidogyne*, *Mesocriconema*, *Paratrichodorus*, *Pratylenchus*, *Rotylenchus*, *Trichodorus* and *Xiphinema*.

**Trophic structure and community indices.** The total abundance of nematodes in 500 g of soil varied from 109 to 737 specimens at individual sites. The mean abundance in soil orders did not differ statistically (Table 2). Plant parasites (PP) were the dominant trophic group in Regosol, Rendzina and Fluvisol representing 33, 28, and

25% of the total nematode abundance, respectively. An exception was the Cambisol with 16% of plant parasites (Table 2). In Regosol a high proportion of PP comprised numerous taxa with lower dominance (2–5%) such as *Geocenamus*, *Meloidogyne*, *Mesocriconema*, *Paratrichodorus*, *Pratylenchus*, *Rotylenchus*, *Trichodorus* and *Xiphinema*. In other soil orders, PP were represented by a few genera with a very high dominance, e.g. in Cambisol by *Trichodorus*



(11%), in Fluvisol by *Longidorus* and *Paratrophurus* (7 and 8%, respectively), and in Rendzina by *Helicotylenchus* (9%) followed by *Longidorella* and *Trichodorus* (both with 4%).

The proportion of bacterial feeders varied from 17 to 30% and was significantly greater in sandy Regosol than in heavy Fluvisol,  $P < 0.05$  (Table 2). The fungal feeders represented 14% of all nematodes in Cambisol, whereas in the other three soil orders they represented only 5–7%. All soil orders studied were characterised by a higher proportion of omnivores (13–21%). A high proportion of root-fungal feeders was recorded in Fluvisol (14%) and Cambisol (11%) in comparison with Rendzina (6%) and Regosol (3%). A high and relatively balanced proportion of predators was

in Cambisol, Fluvisol and Rendzina (15, 13 and 11%, respectively), but in Regosol they contributed only 5%. The proportion of insect parasites (mostly dauerlarvae of *Steinernema*) was somewhat greater in Rendzina and Cambisol (9 and 8%, respectively) than in Fluvisol and Regosol (4%).

The values of Shannon diversity index of genera ( $H'_{gen}$ ) varied from 2.15 to 3.09 in individual localities but the mean values of  $H'_{gen}$  in soil orders were not significantly different. The B/F ratio showed a great variability within soil orders as a significantly greater value was found in Regosol (9.1) than in Cambisol (1.8). The Channel Index differed significantly between soil orders and was greater in Cambisol than in Fluvisol and Rendzina (Table 2).

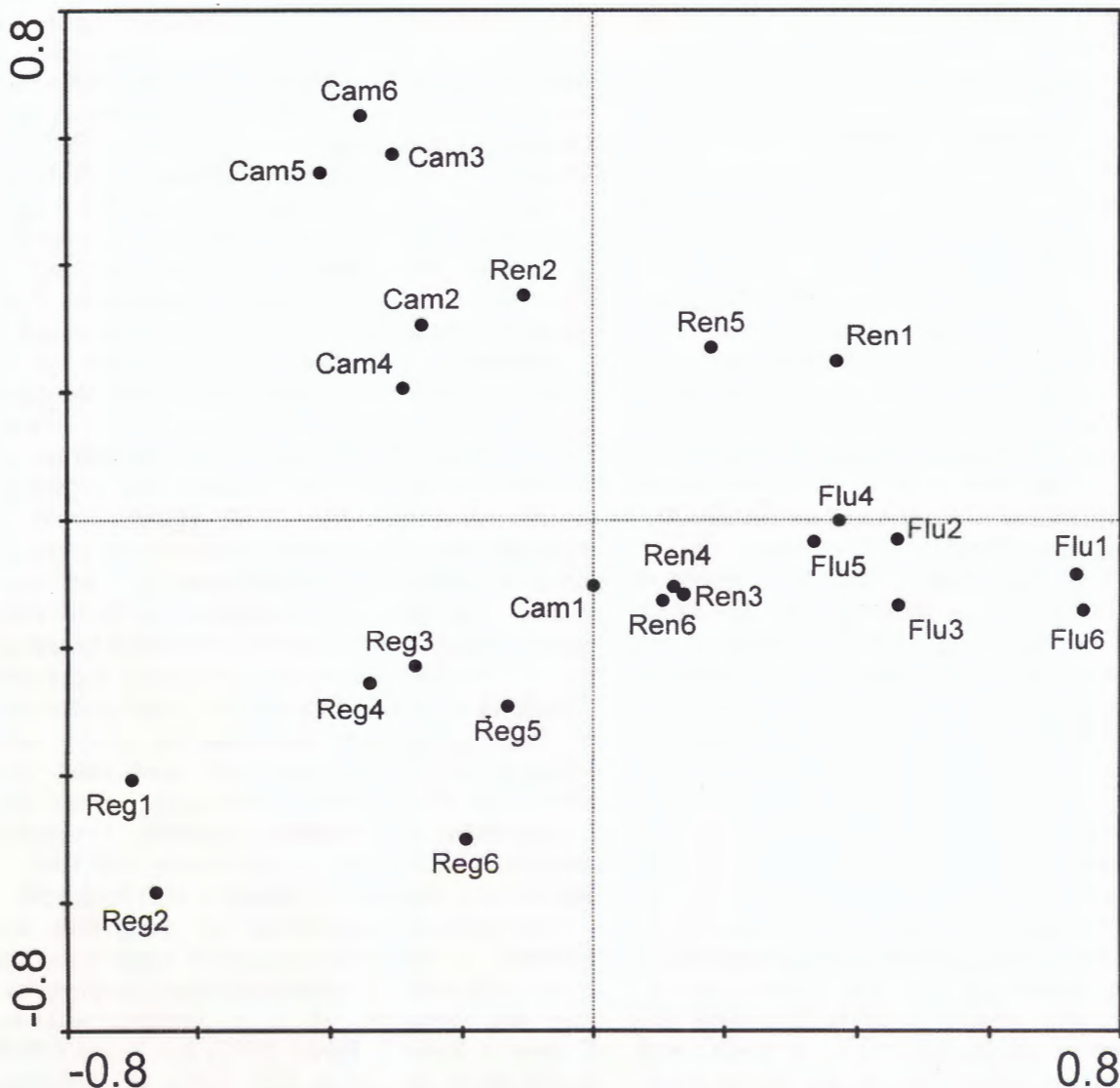


Fig. 3. Sample scatter plot of Principal component analysis, 1<sup>st</sup> and 2<sup>nd</sup> axis, (Cambisol – Cam; Fluvisol – Flu; Regosol – Reg; Rendzina – Ren; 1, 2, 3, 4, 5, and 6 – individual localities).



The mean values of Maturity Index (MI) in soil orders were fairly uniform – from 3.0 in Regosol to 3.5 in Fluvisol, although the index varied among localities of individual soil orders. The greatest difference was recorded in Fluvisol with MI 2.5–4.0 where the lowest value of MI was associated with a very low proportion of omnivores (6.1%) and predators (9.8%) having greater c-p values and with a high proportion of bacterivores (29.9%) having low c-p values. In contrast, the locality with a highest value of MI=4.0 had a very low proportion of bacterivores (6.1%) and a high proportion of predators and omnivores (25.5 and 18.9%, respectively). Similarly to MI, the values of Plant Parasitic Index (PPI) in soil orders were fairly uniform – from 3.0 in Cambisol to 3.5 in Rendzina but varied among localities where a greater value of PPI was associated with a higher proportion of *Longidorus* and *Xiphinema* genera with c-p=5. there were no significant differences in those indexes between different soil orders ( $P > 0.05$ ).

## DISCUSSION

**Taxonomical evaluation.** Composition of nematode communities changes with soil order and vegetation type (*e.g.* Yeates, 1980, 1981; Bongers *et al.*, 1989; de Goede, 1993; Popovici, 1995). The present study showed a relatively greater importance of soil order than vegetation type on nematode fauna. An example is larger cluster of Regosol with two sub-clusters separating three locations in eastern Slovakia mostly with *Robiniatum* from three locations of western Slovakia with *Piceetum*. Most variable faunae were at Rendzina sites (Figs 1, 2, 3), which was in agreement with Šály (1985) who also recorded variations in faunal composition at Rendzina localities in the Protected Landscape Area of the Slovak Paradise. Significant effect of soil order on composition of nematode communities in beech forests in Germany was also documented by Alpeh (1998).

Some nematode genera occurred exclusively in one locality or in one soil order only. According to previous results from numerous ecosystems in Slovakia (Lišková & Planderová, 1996; Lišková & Brown, 1999; Lišková & Sturhan, 2000; Lišková & Čerevková, 2005) some genera in a given soil can often be represented by only one or two species. Similarly, in the present study in Cambisol the genus *Hoplotylus* was represented by *H. femina* and the genus *Xenocriconemella* by *X. macrodora*. From the genera *Longidorus* and *Xiphinema* in Fluvisol, *L. poessneckensis* and *L. intermedius* were present

in clay or clay-loamy soils, and *X. diversicaudatum* was present in loamy and sand-loamy soils. In light Regosol the genus *Acrobeloides* was represented by *A. nanus* and *Paratrichodoros* by *P. pachydermus*, whereas in Rendzina the genus *Longidorella* was represented by *L. parva* and the genus *Xiphinema* by *X. taylori* and *X. dentatum*.

Increasing importance of nematode genera in the various soil orders is shown in Fig. 2 and 3. Nevertheless, the most abundant genus in all soil orders studied was *Eudorylaimus* (except for *Trichodoros* in Cambisol and *Malenchus* in Fluvisol) and its dominance was greater than in forest sites studied by Šály (1983). Greater abundance of *Tylencholaimus* (about 10×) was recorded in soils of deciduous forests than from coniferous forest studied, and similar results are known from Czech Republic (Háněl, 1996; 1997; 2004). On the other hand, *Filenchus* belongs to the most dominant nematodes and *Malenchus* is common in various forests of the Czech Republic, whereas in the soils studied in the present work *Filenchus* dominance was less than 1% and *Malenchus* occurred only in Fluvisol (Table 1). Evidently, forest nematode fauna in close Bohemian Massif and Western Carpathian orogenic units show similarities as well as dissimilarities that are hardly predictable from recent knowledge but must be ascertained *in situ*.

**Ecological evaluation.** Bacterivorous nematodes are often most dominant trophic groups in forests (Wasilewska, 1979; Šály, 1983; Háněl, 1997; Yeates, 2007) and their proportion in nematode community can increase after ecosystem disturbance (Sohlenius, 2002; Háněl, 2004). A relatively low proportion of bacterivores can thus indicate undisturbed conditions of the soils studied. The greatest populations of bacterivores were in Regosol with aerobic conditions beneficial to microbial activities and associated nematodes (Wasilewska, 1997). In contrast, a low proportion of bacterivores was recorded in heavy clay Fluvisol, where they had lower proportion than plant parasites and omnivores. Generally, Cephalobidae (*Acrobeloides*, *Acrobeles*, *Cervidellus*) were more abundant in light sandy soil such as Regosol and *Rhabditis* in Rendzina with higher pH.

The greatest proportion of fungivores was recorded in Cambisol with acidic conditions, and in this soil order *Aphelenchoides* and *Diphtherophora* were also prevalent, which is consistent with the findings of Ruess & Funke (1992) and Yeates (1994). In the other soil orders with higher pH fungivores decreased and this observation agrees with the findings of Wasilewska (1997).



The proportion of root fungal feeders was greater in Fluvisol (heavy) and Cambisol (mid-heavy soils) than in light Regosol and Rendzina. In Cambisol *Aglenchus*, in Fluvisol *Malenchus* and in Rendzina *Tylenchus* were dominant. The sporadic occurrence *Filenchus* in Fluvisol confirmed their scarcity in wet soils (Wasilewska, 1996; Háněl, 2002). Some authors (Sohlenius & Boström, 2001; Sohlenius, 2002; Háněl, 2004) consider high *Filenchus* abundance characteristic of vital forests, what is in contrast to our results. Root-fungal feeding can be a sensitive bioindicator of processes in soils. However, nematode variation associated with local conditions needs to be determined at least to the genus level.

The prevalence of plant-parasitic nematodes in Fluvisol, Regosol and Rendzina was mostly associated with a high abundance of only one or two nematode genera. *Trichodorus* prevailed in Cambisol, *Longidorus* and *Paratrophurus* in Fluvisol, *Paratrichodorus* and *Pratylenchus* in Regosol, and *Helicotylenchus* in Rendzina. The results also confirmed preferences of *Meloidogyne*, *Mesocriconema* and *Paratrichodorus* for light sandy soils, (Lišková & Sturhan, 1998, 1999, 2000; Lišková *et al.*, 2004), and *Paratrophurus* and *Paratylenchus* (*P. straeleni*) for heavy wet soils (Sturhan & Lišková, 2004; Brzeski, 1998). The feeding behaviour of tylenchid, dorylaimid and triplonchid plant parasites differs (Bird and Bird, 1991) as well as their life-history traits (Bongers, 1990) and phylogenies (De Ley & Blaxter, 2002). Our results showed that those nematodes also differ in their preference for naturally formed forest soil orders, and classification of nematode communities should be based on genus and species levels; considering only the proportion of plant parasites as a trophic group is insufficient.

A high proportion of omnivores and predators characterise natural ecosystems (Wasilewska, 1975, 1997). The greatest percentage of omnivores was in Fluvisol and Regosol with completely different structures and vegetation. This indicated a large variability of this group in environments with closer association to 'natural' ecosystems than to a special forest vegetation type. Of the predators, *Clarkus* showed a preference for Cambisol and *Mylonchulus* for Fluvisol and Rendzina. This phenomenon could be associated with different humus orders – acid *versus* calcic mull (Arpin, 1991).

The high values of H', MI, PPI and SI together with relatively low values of PPI/MI ratios pointed at undisturbed conditions of the ecosystems studied (Bongers & Bongers, 1998; Ferris *et al.*,

2001). Ruess (2003) studied the fungal to bacteria feeder ratio and channel index (CI) in various sites and stated that soil and climate affect those indices more strongly than does ecosystem type and that the CI indicated a fungal-based energy channel in coniferous forest sites. In our study CI was significantly greater in Cambisol than in Fluvisol and Rendzina while B/F ratio was significantly greater in Regosol than in Cambisol. Therefore, the two indices suggested the prevalence of a fungal-based energy channel in Cambisol, whereas in other soil orders (especially in Regosol) an increasing importance of bacterial-based energy channel occurred.

**Conclusion.** Communities of soil nematodes in forest ecosystems in Slovakia showed high diversity and maturity and those parameters were independent of soil order. Trophic structure of nematode communities suggested a great activity of fungal-based energy channel in Cambisol. Increasing activity of bacterial-based energy channel was indicated through Fluvisol and Rendzina to Regosol. Generic structure of nematode communities was strongly affected by soil orders, which were characterised by specific fauna.

## ACKNOWLEDGEMENT

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**Lišková, M., Čerevková, A. & Háněl, L.** Ассоциация сообществ нематод из лесных экосистем с различными типами почв.

**Резюме.** Почвенных нематод исследовали на 6 различных участках, относящихся к 4 основным типам лесных почв Словакии: камбисолям, флювисолям, регосолям и рендзинам. Фауна нематод демонстрирует высокий уровень разнообразия родов (H'gen) и показателей зрелости (MI, PPI, SI), причем эти параметры независимы от типа почв. Все сообщества нематод, за исключением присущих камбисолям, характеризовались значительной долей паразитов растений (в основном *Trichodorus*, *Helicotylenchus*, *Paratrophurus* и *Longidorus*). Наибольшее число нематод, питающихся бактериями (*Acrobeloides* и *Alaimus*), были отмечены в рендзинах и регосолях. Микофаги (*Tylencholaimus*, *Diphtherophora*, *Aphelenchoides*) вместе с формами, питающимися прикорневыми грибами (*Aglenchus*), были многочисленны в камбисолях высокой кислотности. Питающиеся прикорневыми грибами формы (*Malenchus*) были обычны и во флювисолях, где наблюдалась склонность к образованию анаэробных условий. Все типы почв характеризовались высокой долей всеядных форм с К-стратегией (*Eudorylaimus*) и хищных нематод (*Mylonchulus* и *Clarkus*). Трофическая структура указывает на существенное значение канала передачи энергии, связанного с грибами в камбисолях. Существенное повышение значения бактериального канала передачи энергии отмечено в ряду от флювисолей и рендзин к регосолям. Кластерный анализ и анализ основных компонент показывают, что такой таксономический параметр, как число родов, находится под сильным воздействием типов почв, поскольку каждый из последних характеризуется специфичной фауной. Нематодные сообщества в рендзинах показали значительно большие пределы вариации, чем в других почвах.

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