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Soil nematodes (Nematoda) in the Voděradské bučiny National Nature Reserve (Czech Republic) – an overall characterization of the fauna

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Abstract. Soil nematodes were studied in ten forest habitats in the Voděradské bučiny National Nature Reserve in the Czech Republic. A total of 108 species of nematodes were found. The total mean abundance of nematodes was 1665 x 10^3 ind.m^{-2} and the abundance recorded on different dates varied from 339 to 4282×10^3 ind.m^{-2}. Most of the nematodes belonged to the trophic groups: root-fungal feeders (44%, mainly *Filenchus* accompanied by *Malenchus*), bacterivores (25%, mainly *Plectus* and *Acrobeloides*) and fungivores (19%, *Aphelenchoides*). The mean biomass of nematode assemblages was 229 mg.m^{-2} and on the different dates varied from 31 to 813 mg.m^{-2}. The most diverse and mature nematode fauna was recorded in an herbaceous plant-rich alder-beech forest near a small stream where the soil was well supplied with water and soil pH and carbon content were the highest of all the localities studied.

Key words. Soil zoology, ecology, Nematoda, diversity, maturity, forest, Voděradské bučiny National Nature Reserve, Czech Republic.

INTRODUCTION

Forests are one of the first ecosystems to develop and persist after the glacial period before the intensive land-use by humans in most areas of the Czech Republic. In open areas left to natural primary or secondary succession forests regenerate and this process proceeds along with changes in soil nematode faunas (Háněl 2008, 2010a). How and to what extent the nematodes can directly affect the formation of woodland is little known but they do reflect the successive regeneration of woodland soil as documented in the papers mentioned above. However, when using nematodes as bioindicators of forest soil restoration we need to know the original composition of the nematode communities. I faced this problem when investigating forest restoration on coal mining spoil heaps and industrial wastes (Háněl 2002a, 2003, 2004a, 2008, 2009a). Samples were collected at various localities but only a part of the data on forest soil nematodes in the Czech Republic is published (Háněl 1992a, b, c, d, 1993, 1994a, b, c, 1995, 1996a, b, c, 1997, 1998a, b, 1999a, b, 2000a, b, c, 2002b, 2004b, 2009b, 2010b, 2011, Bartošová & Háněl 1994, Renčo et al. 2012). This paper presents the first part of a study on soil nematodes in the woodland complex of the Voděradské bučiny NNR in Central Bohemia. The aim of this study was to determine the overall characteristics of the nematode fauna in this area and to contribute to the knowledge of nematode assemblages in natural forest ecosystems in the Czech Republic and Europe.

MATERIALS AND METHODS

Description of the sites

The Voděradské bučiny National Nature Reserve is a large forest complex on the north-east slope of Kobyla (501.3 m a. s. l.) in the Jevany highlands between Louňovice, Vyžlovka, Jevany and Černé Voděrady municipalities in Central Bohemia in the Czech Republic. The area of the Reserve (established in 1955) is 658 ha and its altitude varies between 345 and 501 m a. s. l.; GPS 49° 57' 53.1" N, 14° 46' 27.2" E. The climate is temperate with long-term mean annual air temperatures of 7–8 °C and precipitation of about 550–650 mm. The predominant parent rocks are granites of the Říčany type. Main soil types are acid oligotrophic and eutrophic cambisols. Locally there are pseudogley cambisols along water bodies and rankers at the higher altitudes. Prevailing humus form is moder. Soil pH (H_2O) was determined potentiometrically, ratio soil: distilled water was 1:2.5 (Kalčík 1994) for localities 1–6. Soil organic carbon was determined by oxidization using chromic acid (Kalousková 1995) for localities 1–5. To determine gravimetric water content the soil was dried for 48 hours at 25 °C and then for 4 hours at 105 °C. Soil moisture was expressed as the percentage of water in wet soil.

Vegetation is mostly beech forest (*Luzulo-Fagetum*) with some spruce-silver fir forest (*Luzulo pilosae-Abietetum*) and forests of the alliances *Alnion incanae* along streams and *Tilio-Acerion* in ravines. Norway spruce originally occurred in the valleys. Because this area was used for silviculture spruce was planted and now covers and is the dominant species at many sites of former silver fir woods of *Luzolo pilosae-Abietetum*. This area is a refuge for some sub-mountain to mountain species of plants, fungi and animals (Ložek et al. 2005). Čvančara & Samek (1957) distinguish 24 types of forest and the soil fauna of some of these were investigated at the following localities (L).

L1: Spruce forest, *Luzulo pilosae-Abietetum*, 50–100-year-old *Picea abies* (L.) Karst. accompanied by some larch *Larix decidua* Mill. of about 100-years-old and silver fir *Abies alba* Mill., sparse shrubby *Fagus sylvatica* L. with understorey of *Luzula pilosa* (L.) Willd., *Luzula sylvatica* (Huds.) Gaud., *Avenella flexuosa* (L.) Parl., *Calamagrostis* sp., *Oxalis acetosella* L. and others, some patches of moss, about 50% of bare litter with spruce seedlings. C_{ox} 20.0%, pH (H_2O) 3.71, soil moisture 34.0(27.7–51.2)%.

L2: Beech-hornbeam forest, *Carpino-Fagetum***,** 80–120-year-old, dominant *Carpinus betulus* L. accompanied by some beech *Fagus sylvatica* and oak *Quercus robur* L., without shrubs, understorey of *Luzula pilosa*, *Luzula nemorosa* (Poll.) E. Meyer, *Avenella flexuosa*, *Milium effusum* L., *Calamagrostis* sp., *Carex* sp. *Polytrichum* spp., scarce patches of bare litter. C_{ox} 14.8%, pH (H_2O) 3.94, soil moisture 24.8(23.1–26.6)%.

L3: Submontane species-poor acidophilous beech forest, *Luzulo-Fagetum* with *Cladonia* and *Dicranum scoparium* Hedw., 60–100-year-old beech trees, without shrubs except for some saplings of spruce. Understorey 50–70% of bare litter with patches of the mosses *Dicranum scoparium* and *Polytrichum* spp., and lichens *Cladonia* spp., almost without grass and herbaceous plants except for some *Luzula albida* (Hoffm.) DC. in Lam. et DC. – a "windblown beech forest". C_{ox} 16.7%, pH (H_2O) 3.57, soil moisture 34.1(29.2–38.7)%.

L4: Submontane species-poor acidophilous beech forest, *Luzulo-Fagetum typicum*, 50–60-year-old without shrubs, sparse *Luzula pilosa*, *Luzula nemorosa*, *Poa nemoralis* L., *Oxalis acetosella*, *Polytrichum formosum* Hedw., *Dicranum scoparium* and patches of bare litter. C_{ox} 7.6%, pH (H_2O) 3.79, soil moisture 28.4(22.0–33.0)%.

L5: Wet alder-beech forest, *Impatiento-Fagetum* (submontane herbaceous plant rich beech forest), ca. 50–year-old with dominant alder *Alnus glutinosa* (L.) Gaertn. and some beech and spruce trees and shrubs, on a wet bank of a small stream (Lesní potok), understorey of *Impatiens noli-tangere* L., *Urtica dioica* L., *Oxalis acetosella*, ferns *Athyrium filix-femina* (L.) Roth, *Dryopteris filix-mas* (L.) Schott, horsetails *Equisetum palustre* L., *Equisetum sylvaticum* L. and others; a richer species understorey than at Locality 6. C_{ox} 29.8%, pH (H_2O) 5.35, soil moisture 51.3(39.8–56.3)%.

L6: Beech forest, *Impatiento-Fagetum* (submontane herbaceous plant rich beech forest), 40–60-year-old, a stand of beech on the drier side of the Lesní potok stream, a part of forest opposite to L5, with very scarce *Impatiens noli-tangere*, *Oxalis acetosella*, *Poa nemoralis* and some others. pH (H_2O) 3.44, soil moisture 32.7(30.5–36.6)%.

L7: Dry acidophilous oak forest with some beech trees, *Luzulo albidae-Quercetum* with *Dicranum scoparium*, 40–60--year-old, stand on dry granite rock, understorey of *Dicranum scoparium*, *Luzula* spp., *Cladonia* spp., patches of bare litter. Soil moisture 35.3%.

L8: Spruce forest, *Luzulo pilosae-Abietetum*, mostly ca. 100–120-year-old spruce and some beech trees, understorey of *Luzula pillosa*, *Luzula nemorosa* (Poll.) E. Mey., *Oxalis acetosella*, *Carex* sp., *Agrostis* sp., *Maianthemum bifolium* (L.) F.W. Schmidt, spruce seedlings. Soil moisture 35.4%.

L9: Wet spruce forest, *Equiseto-Abietetum*, ca. 40–60-year-old, a stand growing in wet conditions along the Jevanský potok stream with *Equisetum sylvaticum*, *Oxalis acetosella*, *Luzula* spp., *Carex* sp., *Athyrium filix-femina*, *Dryopteris filix-mas*, spruce seedlings and patches of bare litter in understorey. Soil moisture 34.0%.

L10: Maple-hornbeam ravine forest, *Aceri-Carpinetum,* ca. 40–50-year-old maple *Acer pseudoplatanus* L., hornbeam *Carpinus betulus*, ash *Fraxinus excelsior* L., and some beech trees with *Dentaria bulbifera* L. in understorey. Soil moisture 36.0%.

Sampling, processing and identification of nematodes

At localities 1–6, soil samples were collected on 2 November 1993, 25 October 1994, 17 May 1995 and 12 October 1995. At localities 7–10, samples were collected on 17 May 1995. At each locality and on each date sampled ten soil samples were collected using a cylindrical soil corer of cross-sectional area 10 cm^2 inserted down to a depth of 10 cm. The soil in the ten samples was weighed, carefully mixed and four 10-g sub-samples were used for the study of nematodes and some other groups of soil fauna (enchytraeids, rotifers, tardigrades). Animals in each sub-sample were counted and nematodes were counted and determined. The counts were then adjusted to give the total number of animals per composite sample and converted to a per m^2 basis. The rest of the soil was used for the study of testate amoebae (Balík 2001) and to determine the water content.

Nematodes, together with enchytraeids, rotifers and tardigrades, were extracted from soil by means of a modified Baermann funnel, preserved in 3% formaldehyde and mounted on slides in glycerol. In total 11,864 nematodes were determined to species/genus level, and 164 enchytraeids, 459 rotifers and 253 tardigrades were counted. For the determination of nematode species I used books of Andrássy (2005, 2007, 2009) and Brzeski (1998). The biomass (wet mass) of adult nematodes was estimated using the method described by Andrássy (1956). The biomass of juveniles was assumed to be one half of that of the adults (Šály 1975), except for the dauer-stage juveniles of the families Rhabditidae and Steinernematidae for which biomass was calculated separately, for details see Háněl (2010a).

Statistical analyses and nematode community indices

Statistical analyses were done using STATISTICA (StatSoft Inc., Tulsa, OK, USA, 2001) and CANOCO for Windows version 4.5 (Ter Braak & Šmilauer 2002). Abundance and biomass of the different trophic groups of nematodes and the abundance of Rotifera, Tardigrada and Enchytraeidae were $ln(x+1)$ transformed prior to calculation of Pearson correlation coefficient r and one-way ANOVA. If the Levene's test detected heterogeneity of variances a Kruskal-Wallis ANOVA was also calculated. According to Detrended Correspondence Analysis (DCA) by segments (performed on the abundance of nematode genera as primary data) the first ordination axis had a length of 2.009 S.D., which indicated a linear (monotonous) response model along the data gradient. Therefore, nematode data were further analyzed using Principal Component Analysis (Ter Braak & Šmilauer 2002).

To compare diversity and maturity of the nematode assemblages recorded in this study with those simultaneously studied at the Křivoklátsko Biosphere Reserve (Háněl 1996b) the community indices were calculated as follows:
– number of species and number of genera.
– Shannon index (Shannon & Weaver 1949) of diversity calculated for genera H'gen = $-\sum p_i * \ln(p_i)$, where p_i is the proportion of individuals of taxon i in the total nematode population in a sample.
– maturity index MI=$\sum v(i)*f(i)$, (Bongers 1990), where $v(i)$ is the *cp*-value of taxon i (Bongers & Bongers 1998) and $f(i)$ is the frequency of that taxon (free-living nematodes) in the total free-living nematode population in a sample.
– plant parasite index PPI=$\sum v(j)*f(j)$, (Bongers 1990), where $v(j)$ is the *cp*-value of taxon j (Bongers & Bongers 1998) and $f(j)$ is the frequency of that taxon (plant-feeding nematodes) in the total plant-feeding nematode population in a sample.
– sum maturity index ∑MI=$\sum v(k)*f(k)$, (Yeates 1994), where $v(k)$ is the *cp*-value of taxon k (Bongers & Bongers 1998) and $f(k)$ is the frequency of that taxon (free-living, plant-feeding nematodes) in the total free-living + plant-feeding nematode populations in a sample.
– heterogeneity maturity index calculated for genera HMI = $-\sum v(k)*f(k)*\ln f(k)$, (Háněl 1996b), where $v(k)$ is the *cp*-value of taxon k (Bongers & Bongers 1998) and $f(k)$ is the frequency of that taxon (free-living, plant-feeding nematodes) in the total free-living + plant-feeding nematode populations in a sample.

Greater values of these indices indicate more diverse (species, genera, H'gen), more mature (MI, PPI and ∑MI) and more structured nematode assemblages in terms of a greater variety of nematode genera with different and *K*-selected life-history strategies (HMI).

To evaluate the role of nematodes in the detritus food web in the soil of the forests studied nematodes were allocated to trophic groups (Tabs 1–2). The nematode channel ratio 1 [NCR1=B/(B+F)] according to Yeates (2003) and the nematode channel ratio 2 [NCR2=B/(B+F+RFF)] according to Háněl (2010a) were calculated from the abundance of the microbivorous trophic groups. NCR2 takes the mycetophagous habits of Tylenchidae (Okada et al. 2002) into account. Greater the values of these ratios the greater the role of bacteria in the detritus food web (1 – totally determined by bacteria, 0 – totally determined by fungi).

RESULTS

Species composition of the nematode fauna

A total of 108 species and 56 genera were recorded (Tables 1, 2). Most of the species belonged to the orders Tylenchida (34), Dorylaimida (17), Rhabditida (16) and Araeolaimida (16) and most of the species and genera were recorded at L5 of localities 1–6 (Table 3). Nevertheless, one-way ANOVA indicated that the mean number of species and genera recorded per sample on each of the dates did not differ significantly ($F_{(5,18)}=1.964$, $p=0.133$ and $F_{(5,18)}=1.176$, $p=0.359$, respectively). Kruskal-Wallis ANOVA ($H(5, N=24)=10.571$, $p=0.061$) indicated a lower number of species at L3 than L2. Neither the numbers of species or genera recorded on the different dates were correlated with soil moisture ($n=28$).

Table 1. Check-list of nematode species recorded in forest habitats in the Voděradské bučiny State Natural Reserve, L1–L10 = localities, see Material and methods. Classes: Torquentia (TO), Secernentia (SE) and Penetrantia (PE). Trophic groups (TG): bacterivores (B), fungivores (F), root-fungal feeders (RFF), plant parasites (PP), omnivores (O), predators (P), and insect parasites (IP)

	nematodes and localities	TG	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
TO	Monohystrida											
1	*Eumonhystera longicaudatula* (Gerlach et Riemann, 1973)	B					+					
2	*Eumonhystera vulgaris* (de Man, 1880)	B		+								+
TO	Araeolaimida											
3	*Aphanolaimus deconincki* Coomans et de Waele, 1983	B					+					
4	*Rhabdolaimus* cf. *minor* Cobb, 1914	B					+					
5	*Plectus acuminatus* Bastian, 1865	B	+	+	+	+	+	+	+	+	+	+
6	*Plectus amorphotelus* Ebsary, 1985	B		+		+	+				+	
7	*Plectus communis* Bütschli, 1873	B	+	+	+	+	+	+	+	+	+	+
8	*Plectus exinocaudatus* Truskova, 1976	B					+					
9	*Plectus geophilus* de Man, 1880	B	+	+		+	+					
10	*Plectus longicaudatus* Bütschli, 1873	B	+	+	+	+	+	+	+	+	+	+
11	*Plectus parietinus* Bastian, 1865	B		+			+	+				+
12	*Plectus parvus* Bastian, 1865	B	+	+	+	+				+	+	
13	*Ceratoplectus armatus* (Bütschli, 1873)	B		+			+	+				
14	*Tylocephalus auriculatus* (Bütschli, 1873)	B						+				
15	*Wilsonema otophorum* (de Man, 1880)	B	+	+			+	+			+	+
16	*Wilsonema schuurmansstekhoveni* (De Coninck, 1931)	B	+	+	+	+		+	+	+		
17	*Metateratocephalus crassidens* (de Man, 1880)	B	+	+	+	+	+	+	+	+	+	+
18	*Metateratocephalis gracilicaudatus* (Andrássy, 1985)	B					+					
TO	Chromadorida											
19	*Prodesmodora* Micoletzky, 1923 sp.	B		+								
SE	Rhabditida											
20	*Teratocephalus costatus* Andrássy, 1958	B					+	+				
21	*Teratocephalus lirellus* Anderson, 1969	B	+			+						
22	*Teratocephalus paratenuis* Eroshenko, 1973	B	+	+		+	+	+		+		
23	*Teratocephalus stratumus* Eroshenko, 1973	B		+	+		+	+				
24	*Teratocephalus terrestris* (Bütschli, 1873)	B					+	+				
25	*Cephalobus persegnis* Bastian, 1865	B	+									
26	*Heterocephalobus elongatus* (de Man, 1880)	B	+	+		+	+			+		
27	*Bunobus loofi* (Andrássy, 1968)	B	+	+			+	+				
28	*Eucephalobus oxyuroides* (de Man, 1876)	B		+								
29	*Acrobeloides nanus* (de Man, 1880)	B	+	+	+	+	+	+	+	+	+	+
30	*Panagrolaimus rigidus* (Steiner, 1866)	B	+	+	+		+			+		
31	*Panagrolaimus* cf. *spondyli* Körner, 1954	B			+			+				
32	*Rhabditis terricola* Dujardin, 1845	B	+	+	+	+	+	+				+
33	*Bursilla monhystera* (Bütschli, 1873)	B		+	+	+		+				
34	*Bunonema reticulatum* Richters, 1905	B	+									
35	*Steinernema* Travassos, 1927 dauer larvae	IP	+	+	+	+	+	+				
SE	Aphelenchida											
36	*Aphelenchus avenae* Bastian, 1865	F				+	+					
37	*Aphelenchoides conimucronatus* Bessarabova, 1966	F	+	+	+					+		
38	*Aphelenchoides curiolis* Gritsenko, 1971	F	+				+					
39	*Aphelenchoides dactylocercus* Hooper, 1958	F				+						
40	*Aphelenchoides editocaputis* Shavrov, 1967	F	+	+					+		+	
41	*Aphelenchoides ferrandini* Meyl, 1954	F	+	+	+	+	+	+	+	+	+	+
42	*Aphelenchoides lagenoferrus* Baranovskaya, 1963	F	+	+	+	+		+	+		+	
43	*Aphelenchoides macronucleatus* Baranovskaya, 1963	F	+	+	+	+		+		+	+	+
44	*Aphelenchoides parasubtenuis* Shavrov, 1967	F	+		+			+		+		

Table 1. (continued)

	nematodes and localities	TG	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
45	*Aphelenchoides parietinus* (Bastian, 1865)	F			+							
46	*Aphelenchoides* Fischer, 1894	F	+							+	+	
SE	Tylenchida											
47	*Aglenchus agricola* (de Man, 1884)	RFF	+				+					
48	*Filenchus* cf. *aquilonius* (Wu, 1961)	RFF					+	+				+
49	*Filenchus discrepans* (Andrássy, 1954)	RFF	+		+	+	+	+	+	+		+
50	*Filenchus facultativus* (Szczygieł, 1970)	RFF	+			+		+		+	+	+
51	*Filenchus istvani* Zell, 1988	RFF	+	+	+	+	+	+	+	+	+	+
52	*Filenchus longicaudatulus* Zell, 1988	RFF		+		+	+	+			+	
53	*Filenchus misellus* (Andrássy, 1958) s.l.	RFF	+	+	+	+	+	+	+	+	+	+
54	*Filenchus spicatus* (Brzeski, 1986)	RFF		+								
55	*Filenchus vulgaris* (Brzeski, 1963)	RFF	+	+	+	+	+	+			+	
56	*Filenchus* Andrássy, 1954 sp.	RFF	+		+					+	+	
57	*Tylenchus davainei* Bastian, 1865	RFF			+		+	+	+			+
58	*Basiria gracilis* (Thorne, 1949)	RFF	+			+	+	+		+		
59	*Malenchus acarayensis* Andrássy, 1968	RFF	+	+	+	+	+	+				
60	*Malenchus bryophilus* (Steiner, 1914)	RFF		+						+		
61	*Malenchus neosulcus* Geraert et Raski, 1986	RFF		+		+						
62	*Malenchus pachycephalus* Andrássy, 1981	RFF		+	+	+	+	+		+		
63	*Malenchus* Andrássy, 1968 sp.	RFF					+					
64	*Miculenchus salvus* Andrássy, 1959	RFF		+								+
65	*Cephalenchus hexalineatus* (Geraert, 1962)	RFF	+	+	+	+	+	+	+	+		+
66	*Lelenchus leptosoma* (de Man, 1880)	RFF		+	+	+	+	+				
67	*Ditylenchus longimatricalis* (Kazachenko, 1975)	F									+	+
68	*Ditylenchus parvus* Zell, 1988	F	+	+				+	+	+		+
69	*Ditylenchus silvaticus* Brzeski, 1991	F				+						
70	*Ditylenchus tenuidens* Gritzenko, 1971	F		+								
71	*Ditylenchus terricolus* Brzeski, 1991	F			+							
72	*Ditylenchus valveus* Thorne et Malek, 1968	F					+					
73	*Helicotylenchus pseudorobustus* (Steiner, 1914)	PP				+						
74	*Heterodera* Schmidt, 1871 juv.	PP					+					
75	*Paratylenchus projectus* Jenkins, 1956	PP		+								
76	*Gracilacus straeleni* (de Coninck, 1931)	PP	+	+	+	+	+	+	+			+
77	*Sphaeronema* cf. *alni* Turkina et Chizhov, 1986 juv.	PP					+					
78	*Xenocriconemella macrodora* (Taylor, 1936)	PP		+	+	+	+	+				
79	*Criconema annuliferum* (de Man, 1921)	PP										+
80	*Deladenus* Thorne, 1941 sp. juv.	F	+		+	+	+	+				
PE	Enoplida											
81	*Prismatolaimus intermedius* (Bütschli, 1873) s.l.	B	+				+	+				
82	*Prismatolaimus dolichurus* de Man, 1880	B			+	+	+					
83	*Tripyla glomerans* Bastian, 1865	P				+	+					
PE	Alaimida											
84	*Alaimus arcuatus* Thorne, 1939	B									+	
85	*Alaimus jaulasali* Siddiqi et Husain, 1967	B				+				+		
86	*Alaimus parvus* Thorne, 1936	B				+	+		+			
87	*Alaimus primitivus* de Man, 1880	B		+	+		+	+			+	
88	*Paramphidelus* Andrássy, 1977 sp. juv.	B					+					
PE	Diphtherophorida											
89	*Trichodorus sparsus* Szczygieł, 1968	PP	+									+
PE	Monochida											
90	*Clarkus papillatus* (Bastian, 1865)	P		+			+					
91	*Prionchulus punctatus* (Cobb, 1917)	P	+	+		+	+	+				+

Table 1. (continued)

	nematodes and localities	TG	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
PE	Dorylaimida											
92	*Prodorylaimus* Andrássy, 1959 sp. juv.	O					+					
93	*Dorylaimus stagnalis* Dujardin, 1845	O					+					
94	*Mesodorylaimus bastiani* (Bütschli, 1973)	O	+				+					
95	*Paractinolaimus macrolaimus* (de Man, 1880)	P					+					
96	*Eudorylaimus altherri* Tjepkema, Ferris et Ferris, 1971	O				+	+					
97	*Eudorylaimus brevis* (Altherr, 1952)	O		+	+	+	+		+			
98	*Eudorylaimus discolaimioideus* (Andrássy, 1958)	O		+	+	+		+	+			+
99	*Eudorylaimus paucipapillatus* Andrássy, 1986	O		+	+	+		+			+	
100	*Eudorylaimus silvaticus* Brzeski, 1960	O	+		+	+				+		
101	*Eudorylaimus* Andrássy, 1959 sp. juv.	O		+								
102	*Crassolabium* Yeates, 1967 sp. juv.	O						+				
103	*Aporcelaimellus obtusicaudatus* (Bastian, 1865)	O	+	+	+	+	+	+				+
104	*Pungentus silvestris* (de Man, 1912)	O	+									+
105	*Dorylaimellus monticolus* Clark, 1963	O										+
106	*Tylencholaimus mirabilis* (Bütschli, 1873)	F		+	+			+				
107	*Tylencholaimus* cf. *obscurus* Jairajpuri, 1965	F					+					
108	*Tylencholaimus stecki* Steiner, 1914	F	+			+		+				
total number of species			47	54	41	49	63	49	19	27	23	29
mean number of species per sampling date			26	32	21	30	31	28	19	27	23	29

Generic composition of the nematode assemblages

The most abundant and dominant genera (Table 2) were *Filenchus* (34.3% of all nematodes recorded at the localities studied), *Aphelenchoides* (16.4%), *Plectus* (8.9%), *Acrobeloides* (7.5%), *Malenchus* (6.0%) and *Eudorylaimus* (5%.). The dendrogram based on a cluster analysis of the generic composition of nematode faunas showed two main clusters, a large one in the upper part and small one in the lower part of the chart (Fig. 1). The smaller cluster consisted of the samples from L2, most of the samples from L4 and some samples from L6 and L5. These samples were on the right hand side of the biplot of the Principal Component Analysis in the direction of increasing abundance of the most representative genera of the nematode fauna in the Voděradské bučiny National Nature Reserve (Fig. 2).

The data indicated that the most optimum environments for the genera *Rhabditis*, *Metateratocephalus*, *Wilsonema*, *Teratocephalus*, *Malenchus*, *Basiria*, *Gracilacus* and *Xenocriconemella* were the soils in oak-hornbeam (*Carpino-Fagetum*, L2), submontane species-poor acidophilous beech (*Luzulo-Fagetum typicum*, L4) and submontane herbaceous plant rich beech (*Impatiento-Fagetum*, L5 and L6) forests. Infective juveniles of *Steinernena* were most abundant in *Carpino-Fagetum* (L2). *Cephalenchus hexalineatus* was recorded at all localities except L9 and was most abundant in *Aceri-Carpinetum* (L10). The genera *Plectus*, *Acrobeloides*, *Aphelenchoides*, *Filenchus*, *Eudorylaimus* and *Ditylenchus* were ubiquitous and abundant almost everywhere.

Abundance of nematode trophic groups

The mean total abundance of nematodes for all dates and localities was 1665.5×10^3 ind.m^{-2}. The total abundance of nematodes recorded on different dates at localities L1–L6 varied from 338.9 to 4281.8×10^3 ind.m^{-2} and did not differ significantly (p<0.05) between localities.

In terms of trophic groups and localities L1–L6 (Table 2) a one-way ANOVA and post-hoc LSD test with *alpha*=0.05, revealed a significantly greater abundance of plant parasites at L4 and L6 than L1 and L5 ($F_{(5,18)}$=3.275, p=0.028). The abundance of predators was significantly greater

Table 2. The mean abundance of nematode trophic groups and genera recorded at the different localities ($\times 10^3$ ind.m^{-2}). For the localities L1–L6 $F_{(5,18)}$ and *p* values for the one-way ANOVA of the trophic groups are also shown. The same letters indicate homogeneous groups of means detected using Fisher LSD post-hoc test, *alpha*=0.05 or *alpha*=0.10. Underlined figures denote that this particular nematode makes up more than 5% of the total nematode population at that locality

nematodes and localities	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
bacterivores	431	617	233	534	406	289	399	255	475	403
F=2.160, *p*=0.104, LSD *alpha*=0.10	abc	a	c	ab	abc	bc				
Plectus Bastian, 1865	132	194	96	158	190	99	167	115	200	185
Acrobeloides Cobb, 1924	197	130	95	141	51	103	216	77	240	100
Rhabditis Dujardin, 1845	17	172	7	149	26	20				76
Metateratocephalus Eroshenko, 1973	29	44	7	13	58	17	4	14	17	33
Wilsonema Cobb, 1913	32	38	1	40	13	15	4	5	6	5
Teratocephalus de Man, 1876	11	6	6	17	24	17		5		
Heterocephalobus Brzeski, 1960	6	8		4	3			29		
Prismatolaimus de Man, 1880	1		1	5	17	2				
Alaimus de Man, 1880		5	0.3	3	5	2	8	5	11	
Panagrolaimus Fuchs, 1930	3	7	18		2	6		5		
unidentified juveniles	0.4	2		1	4	2				
Eumonhystera Andrássy, 1981		3			4					5
Bursilla Andrássy, 1976		2	2	2		1				
Bunobus De Ley, Siddiqi et Boström, 1993	0.2	2			1	1				
Ceratoplectus Andrássy, 1985		0.4			2	2				
Prodesmodora Micoletzky, 1923		3								
Rhabdolaimus de Man, 1880					3					
Paramphidelus Andrássy, 1977 juv					3					
Tylocephalus Crossman, 1933						2				
Aphanolaimus de Man, 1880					2					
Cephalobus Bastian, 1865	1									
Bunonema Jägerskiöld, 1905	1									
Eucephalobus Steiner, 1936		0.4								
fungivores	303	441	349	288	139	385	460	187	235	185
F=1.995, *p*=0.128, LSD *alpha*=0.10	a	a	a	a	b	a				
Aphelenchoides Fischer, 1894	247	388	337	250	85	363	452	163	229	138
Ditylenchus Filipjev, 1936	54	48	10	33	21	17	8	24	6	47
Tylencholaimus de Man, 1876	1	5	0.3	2	30	5				
Deladenus Thorne, 1941	1		2	2	1	0.4				
Aphelenchus Bastian, 1865				2	1					
root-fungal feeders	741	1598	262	747	210	1301	200	216	475	413
F=1.953, *p*=0.135, LSD *alpha*=0.10	abc	a	bc	ab	c	ab				
Filenchus Andrássy, 1954	682	1279	240	478	146	964	114	187	475	90
Malenchus Andrássy, 1968	9	280	3	146	42	213		10		
Cephalenchus Goodey, 1962	47	20	1	43	4	5	81	10		304
Basiria Siddiqi, 1959	2			79	12	116		10		
Tylenchus Bastian, 1865			17		3	3	4			14
Miculenchus Andrássy, 1959		15								5
Lelenchus Andrássy, 1954		4	2	1	0.3	1				
Aglenchus Andrássy, 1954	2				3					
plant parasites	5	71	85	171	33	213	4			47
F=3.275, *p*=0.028, LSD *alpha*=0.05	b	ab	ab	a	b	a				
Gracilacus Raski, 1962	4	48	65	148	14	62	4			9
Xenocriconemella De Grisse et Loof, 1985		19	19	21	3	151				
Heterodera Schmidt, 1871 juv.					14					
Trichodorus Cobb, 1913	1									33
Paratylenchus Micoletzky, 1922		5								
Sphaeronema Raski et Sher, 1952 juv.					3					

Table 2. (continued)

nematodes and localities	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
Helicotylenchus Steiner, 1945				2						
Criconema Hofmänner et Menzel, 1914										5
omnivores	46	148	78	139	53	96	53	14	74	85
F=2.483, p=0.071, LSD *alpha*=0.10	b	a	ab	a	b	ab				
Eudorylaimus Andrássy, 1959	43	143	76	137	43	88	53	14	74	66
Aporcelaimellus Heyns, 1965	1	5	2	2	2	3				5
Crassolabium Yeates, 1967 juv.						5				
Dorylaimus Dujardin, 1845					5					
Mesodorylaimus Andrássy, 1959	2				2					
Prodorylaimus Andrássy, 1959 juv.					3					
Pungentus Thorne et Swanger, 1936	0.2									9
Dorylaimellus Cobb, 1913										5
predators	1	20	0	8	35	2	0	0	0	5
F=6.961, p<0.001, LSD *alpha*=0.05	c	ab	c	bc	a	c				
Prionchulus Cobb, 1916	1	17		7	26	2				5
Paractinolaimus Meyl, 1957					6					
Clarkus Jairajpuri, 1970		3			2					
Tripyla Bastian, 1865				1	2					
insect parasites	15	96	3	18	0.3	1	0	0	0	0
F=12.191, p<0.001, LSD *alpha*=0.05	bc	a	cd	b	d	d				
Steinernema Travassos, 1927 juv.	15	96	3	18	0.3	1				
sum of all nematode individuals	1542	2991	1011	1904	876	2288	1116	673	1259	1138
F=2.138, p=0.107, LSD *alpha*=0.10	bc	a	bc	ab	c	ab				

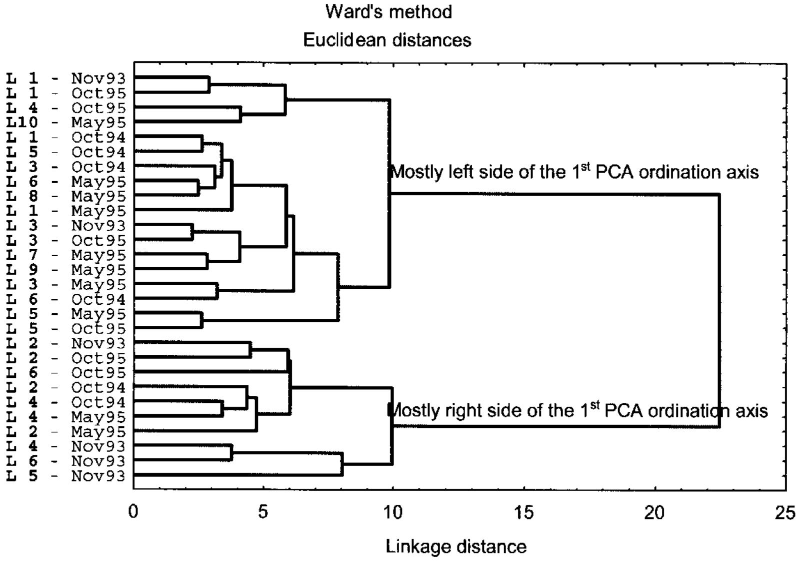

Fig. 1. Dendrogram based on Cluster analysis of the *ln*(x+1) transformed abundance of nematode genera, Euclidean distance and Ward's clustering method.

Table 3. Nematode community indices and the mean abundance ($\times 10^3$ ind.m^{-2}) of Rotifera, Tardigrada and Enchytraeidae. Mean values of the indices were calculated from values for each locality and four dates based on species presence and genus abundance recorded on particular dates (n=4 for L1–L6). Total values of the indices were calculated from the mean abundance of nematode genera recorded over the whole period at each locality and include the total numbers of species and genera recorded at each locality. Because the nematodes in the forests at L7–L10 were recorded only on 17 May 1995 the values of indices for these localities are in the mean value row

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
nematodes and localities										
species (mean)	25.5	31.8	20.5	30.0	31.0	28.0	19	27	23	29
species (total)	47	54	41	49	63	49				
genera (mean)	17.0	22.0	15.3	20.3	21.0	18.5	12	15	9	20
genera (total)	30	33	25	29	43	31				
H'gen (mean)	1.95	1.99	1.82	2.27	2.14	1.91	1.69	1.99	1.60	2.30
H'gen (total)	1.89	2.09	2.00	2.45	2.76	2.01				
∑MI (mean)	2.12	2.04	2.16	2.09	2.41	2.18	2.11	2.08	2.15	2.19
∑MI (total)	2.07	2.05	2.16	2.10	2.41	2.16				
HMI (mean)	4.24	4.25	4.04	4.86	5.38	4.35	3.76	4.30	3.69	5.34
HMI (total)	4.05	4.44	4.44	5.26	7.07	4.58				
MI (mean)	2.19	2.20	2.22	2.18	2.53	2.29	2.14	2.12	2.24	2.22
MI (total)	2.15	2.19	2.22	2.19	2.54	2.29				
PPI (mean)	2.00	2.03	2.04	2.02	2.04	2.07	2.00	2.00	2.00	2.15
PPI (total)	2.00	2.01	2.06	2.02	2.08	2.10				
PPI/MI (mean)	0.92	0.93	0.92	0.93	0.81	0.91	0.94	0.95	0.89	0.97
PPI/MI (total)	0.93	0.92	0.93	0.92	0.82	0.92				
NCR1 (mean)	0.63	0.60	0.42	0.63	0.74	0.43	0.46	0.58	0.67	0.69
NCR1 (total)	0.59	0.58	0.40	0.65	0.75	0.43				
NCR2 (mean)	0.39	0.28	0.31	0.34	0.57	0.21	0.38	0.39	0.40	0.40
NCR2 (total)	0.29	0.23	0.28	0.34	0.54	0.15				
other animals and localities										
Rotifera ($\times 10^3$ ind.m^{-2}; mean)	80.8	61.6	44.2	57.4	82.7	48.7	93.6	14.4	108.7	71.1
Tardigrada ($\times 10^3$ ind.m^{-2}; mean)	17.5	51.5	11.0	58.0	65.5	29.0	48.9	14.4	5.7	56.9
Enchytraeidae ($\times 10^3$ ind.m^{-2}; mean)	20.3	14.3	10.0	30.2	52.5	11.0	16.3	14.4	62.9	37.9

at L5 than L3, L1, L6 and L4 ($F_{(5,18)}=6.961$, $p<0.001$), but Levene's test detected heterogeneity of variances ($F_{(5,18)}=3.951$, $p=0.013$). The differences in the abundance of predators were partly confirmed by the Kruskal-Wallis ANOVA, $H(5, N=24)=15.083$, $p=0.010$, but post-host multiple comparison of mean ranks of all pairs of groups failed to confirm the differences between localities indicated by the LSD test. The abundance of insect parasites was significantly greater at L2 than L5, L6, L3, L1 and L4 ($F_{(5,18)}=12.191$, $p<0.001$), but Levene's test detected heterogeneity of variances ($F_{(5,18)}=3.798$, $p=0.016$), however, the result was supported by Kruskal-Wallis ANOVA and post-hoc tests, $H(5, N=24)=18.742$, $p=0.002$. The abundance of the other trophic groups did not differ significantly (for $p<0.05$).

To evaluate the relationships between the abundance of nematode trophic groups, soil moisture, and other groups of soil fauna Pearson correlation coefficients (r, $n=28$, $p<0.05$) were calculated. Bacterivores were significantly positively correlated with the abundance of Rotifera and Tardigrada ($r=+0.663$ and $r=+0.511$, respectively). Fungivores, root-fungal feeders, plant parasites, omnivores and insect parasites were significantly negatively correlated with soil moisture ($r=-0.697$, $r=-0.596$, $r=-0.383$, $r=-0.387$ and $r=-0.604$, respectively). Predators were significantly positively correlated with soil moisture ($r=+0.395$), Tardigrada ($r=+0.706$) and Enchytraeidae ($r=+0.460$).

Total nematode populations were significantly negatively correlated with soil moisture ($r = -0.577$) and significantly positively with Rotifera ($r = +0.411$).

In terms of mean abundance of the trophic groups, fungivores were significantly negatively correlated with soil moisture, pH (H_2O) and the mean abundance of Enchytraeidae ($n = 6$, $p < 0.05$; $r = -0.910$, $r = -0.884$ and $r = -0.908$, respectively) at L1–L6. Predators were significantly positively correlated with pH (H_2O) and Tardigrada ($r = +0.857$ and $r = +0.873$, respectively). The mean abundance of all nematodes was significantly negatively correlated with soil moisture ($r = -0.815$). Fungivores and omnivores were negatively but insignificantly correlated with C_{ox} ($n = 5$; $p = 0.174$, $r = -0.716$ and $p = 0.123$, $r = -0.776$, respectively).

Biomass of each of the nematode trophic groups

The mean total biomass of nematodes for all dates and localities was 229 $mg.m^{-2}$. The total biomass of nematodes on particular dates at localities L1–L6 varied from 31 to 813 $mg.m^{-2}$ and differed significantly between localities (one-way ANOVA, $F_{(5,18)} = 2.914$, $p = 0.042$).

The mean biomass of a nematode recorded during this study was 0.173 µg and on particular dates varied from 0.052 to 0.831 µg. At localities L1–L6 the mean biomass of a nematode was significantly greater at L5 than at the other localities (Table 4; $F_{(5,18)} = 6.201$, $p = 0.002$). Levene's

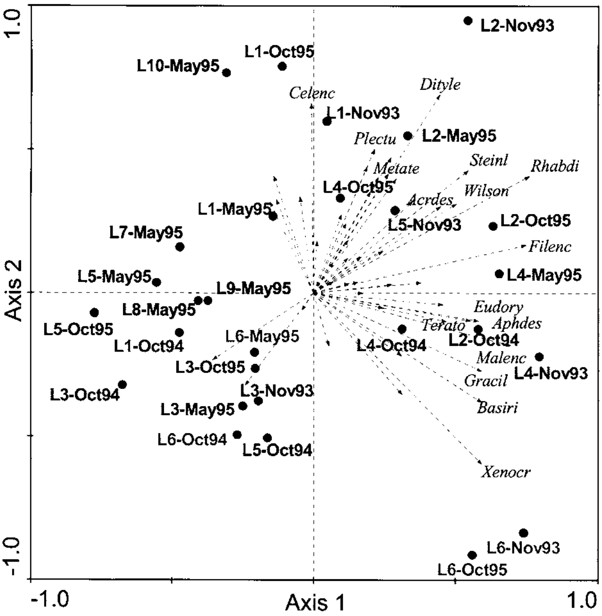

Fig. 2. Biplot of nematode genera and samples based on a Principal Component analysis (PCA) using *log*(x+1) transformed genera abundances. Eigenvalues for ordination axes 1, 2, 3 and 4 were 0.307, 0.127, 0.123 and 0.095. Cumulative percentage variance of genus data for ordination axes 1, 2, 3 and 4 were 30.7, 43.4, 55.7 and 65.2. All genera were included in this analysis but only the genera with an overall dominance in the area greater than 0.5% are shown in the biplot. Abbreviations for these genera are: *Acrdes – Acrobeloides*, *Aphdes – Aphelenchoides*, *Basiri – Basiria*, *Celenc – Cephalenchus*, *Dityle – Ditylenchus*, *Eudory – Eudorylaimus*, *Filenc – Filenchus*, *Gracil – Gracilacus*, *Malenc – Malenchus*, *Metate – Metateratocephalus*, *Plectu – Plectus*, *Rhabdi – Rhabditis*, *Steinl – Steinernema* larvae, *Terato – Teratocephalus*, *Wilson – Wilsonema*, *Xenocr – Xenocriconemella*.

Table 4. The mean biomass of nematode trophic groups and all nematode populations in mg.m^{-2} and mean individual biomass of a nematode in assemblages at individual localities in µg. For localities L1–L6 $F_{(5,18)}$ and p values for the one-way ANOVA are also shown. The same letters indicate homogeneous group of means detected using Fisher LSD post-hoc test, *alpha*=0.05 or * *alpha*=0.10

nematodes and localities	*F*	*p*	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10
bacterivores	3.186	0.031	51^{bc}	129^{a}	29^{c}	79^{ab}	91^{abc}	41^{bc}	46	27	72	99
fungivores	0.137	0.981	8	9	7	9	14	6	5	6	8	5
root-fungal feeders	1.436	0.259	26	63	17	29	8	49	10	8	18	28
plant parasites*	2.258	0.093	1^{c}	5^{bc}	6^{bc}	11^{ab}	2^{c}	23^{a}	0	0	0	23
omnivores	0.464	0.798	29	103	54	73	131	58	18	6	21	78
predators	6.367	0.001	4^{bc}	66^{a}	0^{c}	35^{ab}	164^{a}	7^{bc}	0	0	0	30
insect parasites	8.287	<0.001	4^{b}	26^{a}	1^{b}	5^{b}	0^{b}	0^{b}	0	0	0	0
all nematodes	2.914	0.042	123^{c}	401^{a}	114^{c}	241^{abc}	410^{ab}	183^{bc}	79	48	120	263
mean individual biomass	6.201	0.002	0.102^{b}	0.150^{b}	0.116^{b}	0.129^{b}	0.506^{a}	0.088^{b}	0.071	0.072	0.095	0.231

test indicated that the variances were heterogeneous ($F_{(5,18)}=3.074$, $p=0.035$). However, Kruskal-Wallis ANOVA, $H(5, N=24)=10.817$, $p=0.055$, also indicated a higher mean nematode individual biomass at L5.

The greatest biomass of bacterivorous nematodes was recorded at L2 (Table 4; $F_{(5,18)}=3.186$, $p=0.031$). The greatest biomass of predators was recorded at L5 ($F_{(5,18)}=6.367$, $p=0.001$) and although Levene's test indicated that the variances were heterogeneous ($F_{(5,18)}=3.777$, $p=0.016$) the Kruskal-Wallis ANOVA ($H(5, \mathrm{N}=24)=14.585$, $p=0.012$) supported this result. The greatest biomass of insect parasites was recorded at L2 ($F_{(5,18)}=8.287$, $p<0.001$) and Levene's test indicated the variances were heterogeneous ($F_{(5,18)}=4.771$, $p=0.006$) but this result was supported by the Kruskal-Wallis ANOVA, ($H(5, \mathrm{N}=24)=18.742$, $p=0.002$).

The greatest biomass of plant parasites (mainly due to the high population densities of *Xenocriconemella macrodora*) was recorded at L6. Nevertheless, the significance of the differences in plant parasite biomass was uncertain because the results of the one-way ANOVA ($F_{(5,18)}=2.258$, $p=0.093$) and Kruskal-Wallis ANOVA ($H(5, \mathrm{N}=24)=9.092$, $p=0.092$) and the Levene's test indicated that the variances were heterogeneous ($F_{(5,18)}=3.709$, $p=0.018$). The biomass of fungivores, root-fungal feeders and omnivores at L1–L6 did not differ significantly.

For all dates and localities, the biomass of predators and the mean nematode individual biomass were significantly positively correlated with soil moisture ($n=28$, $p<0.05$; $r=+0.387$ and $r=+0.725$, respectively). The biomass of root-fungal feeders and insect parasites were significantly negatively correlated with soil moisture ($n=28$, $p<0.05$; $r=-0.540$ and $r=-0.527$, respectively).

In terms of the mean biomass of trophic groups at L1–L6 fungivores and predators were significantly positively correlated with pH (H_2O) ($n=6$, $p<0.05$; $r=+0.959$ and $r=+0.841$, respectively). Root-fungal feeders were significantly negatively correlated with soil moisture ($n=6$, $p<0.05$; $r=-0.848$). The biomass of plant parasites was negatively but insignificantly correlated with C_{ox} ($n=5$, $p=0.067$, $r=-0.852$).

Mean individual biomass at L1–L6 was significantly positively correlated with pH (H_2O) and soil moisture ($n=6$, $p<0.05$; $r=+0.992$ and $r=+0.854$, respectively) and insignificantly positively correlated with C_{ox} ($n=5$, $p=0.113$, $r=0.789$).

Community indices

The community indices in Table 3 do not differ much for the different localities. For localities L1–L6 a one-way ANOVA only revealed a difference in $\sum$MI, the significantly greatest of which was recorded at L5 ($F_{(5,18)}$=5.096, p=0.004). Levene's test detected that the variances were heterogeneous ($F_{(5,18)}$=3.173, p=0.032). Nevertheless, the Kruskal-Wallis ANOVA confirmed that the highest ∑MI was recorded at L5 (H(5, N=24)=11.630, p=0.040).

In Table 3 are the mean values of the indices ∑MI, MI, PPI, PPI/MI, NCR1 and NCR2, which are very similar to the total values calculated using the mean abundances of the genera recorded at the localities. The total values of the indices based on all the taxa recorded during this investigation (numbers of species and genera, H'gen, HMI) were mostly greater than the mean values.

Most species and genera of nematodes and the greatest values of the indices H'gen, ∑MI, HMI, MI, NCR1 and NCR2 were recorded at locality L5, where the values of soil C_{ox}, pH (H_2O) and moisture were greatest. Total numbers of species, genera, total values of H'gen, ∑MI, HMI, MI and NCR2 at L1–L6 were significantly positively correlated with pH(H_2O) (n=6, p<0.05, r=+0.835–0.918) and insignificantly positively with C_{ox}. ∑MI and MI were significantly positively correlated with soil moisture (r=+0.944 and r=+0.894, respectively). The PPI/MI ratio was significantly negatively correlated with soil moisture (r=–0.883) and pH(H_2O) (r=–0.965), and negatively but insignificantly with C_{ox} (n=5, r=–0.795, p=0.108).

Rotifera, Tardigrada and Enchytraeidae

There were no significant differences in the abundance of Rotifera, Tardigrada and Enchytraeidae (Table 3). Nevertheless, Enchytraeidae tended to be most abundant at locality 5. Rotifera were significantly positively correlated (n=28, p<0.05) with the abundance of bactivorous nematodes (r=+0.663) and the total number of nematodes (r=+0.411). Tardigrada were significantly positively correlated with the abundance of bacterivores (r=+0.511) and predators (r=+0.706). Enchytraeidae were significantly positively correlated with the abundance of predators (r=+0.460) and with soil moisture (r=+0.374). At localities L1–L6 the mean abundance of Enchytraeidae was significantly positively correlated with pH (H_2O) (n=6, p<0.05, r=+0.857).

DISCUSSION

Taxonomic composition of nematode fauna

The nematode fauna in the area studied consisted of a set of relatively similar assemblages as indicated by the short gradient of 2.009 S.D. along the first ordination axis of the DCA. Genera with an overall dominance of 5% or more occurred at all localities except for *Malenchus*. Nevertheless, the cluster analysis indicated two main clusters of nematode assemblages and distinguished some the groups in the nematode faunas. The first group of nematode assemblages, which had a relatively low taxonomic richness and abundance, was recorded in *Luzulo pilosae-Abietetum* (L1) and *Luzulo-Fagetum* (L3) forests. The second group of nematode assemblages with a relatively greater taxonomic richness and abundance occurred in *Carpino-Fagetum* (L2) and *Luzulo-Fagetum typicum* (L4) forests. Nematode assemblages in *Impatiento-Fagetum* (L5 and L6) forests were in an intermediate position and the composition of nematode assemblages depended on the date sampled. The values for the taxonomic richness, diversity, maturity and biomass of the nematode assemblages recorded in the wetter parts along a stream (L5) were the highest, whereas those for abundance were relatively low.

Nevertheless, species and generic composition of nematode faunas in beech woodlands can be very different. Alphei (1998) reports that of the 112 species recorded in two beech forests only 28 species occurred in both. Nine species of predatory nematodes were recorded at a mull-type humus site on terra fusca soil on limestone but only one species at a moder-type humus site on acid brown earth soil on sandstone. Similarly, Popovici (1984) records ten predatory species in a mull-humus beech forest. In the Voděradské bučiny (where moder humus prevails) only four predatory species were recorded (Table 1). Armendáriz & Arpin (1996) report finding abundant populations of *Tylolaimophorus typicus* de Man, 1880 in beech forests in France but this species was absent from the localities surveyed in the present study. Šály (1989) reports that the most abundant omnivore is *Ecumenicus monohystera* (de Man, 1880) but this species did not occur at Voděradské bučiny where the most abundant omnivores were small species of the genus *Eudorylaimus*. Regional composition of nematode assemblages is associated with soils derived from different parent rocks and under different climates (Lišková et al. 2008, Renčo et al. 2012). These regional factors are important and should be taken into consideration when evaluating the effects of management and disturbance on forests using nematodes as bioindicators (Bjørnlund et al. 2002, Čerevková & Renčo 2009, Čerevková et al. 2013).

An important indicator of the development of a soil system and disturbance is the taxonomic richness of nematode faunas (Háněl 2010a). In large forest areas in the Czech Republic Háněl (1996b) records 138 species in three deciduous forests in the Křivoklátsko Biosphere Reserve and Háněl (1996c) 92 species in five spruce forests in the Beskydy Mts. Háněl (2010b) records finding 161 species in three gorges in the České Švýcarsko National Park during a single survey. Wasilewska (1970) records finding 107 species in the Kampinos Forest woodland in Poland and Háněl & Čerevková (2010) 198 species in the Vihorlat woodland in Slovakia. And in a man made landscape Háněl (2009a) records finding 174 species of nematodes in 20–30-year-old tree plantations and spontaneous successions on colliery spoils near Sokolov in the Czech Republic. The relatively low number of nematode species (108) recorded at Voděradské bučiny could be due to several factors.

Between 68 and 112 species of nematodes are recorded in six beech forests in Romania at altitudes ranging from 490 to 1250 m a. s. l. (Popovici 1989). There was no correlation between the number of species and altitude but it was significantly positively correlated with pH (H_2O). On the other hand, Háněl & Čerevková (2010) report that the numbers of species and genera of soil nematodes in forest ecosystems in Slovakia is significantly negatively correlated with altitude, soil moisture and C_{ox}, and significantly positively correlated with soil pH (H_2O). For Voděradské bučiny the correlation of the total number of species and genera with mean soil moisture and C_{ox} at L1–L6 were positive but insignificant and the correlation with soil pH (H_2O) positive and significant.

Alphei (1998) records 74 species at a beech site with mull humus and pH of 6.2–6.8 and 66 species at a beech site with moder humus and pH of 3.0–3.4. Soil with a high pH thus support a greater nematode species richness. Háněl (1996b) records 89 species at a beech forest in the Křivoklátsko Biosphere Reserve with soil pH (H_2O) of 4.31–4.87. At L1–L6 the total number of species varied from 41 to 63 and soil pH (H_2O) was lower than 4, except at L5 with 63 species, where soil pH (H_2O) was 5.35. In 20–33-year-old tree plantations and shrubby natural successions on clay colliery spoils in western Bohemia the mean pH(H_2O) values varied from 6.47 to 7.43 and the mean number of species of nematodes ranged from 28.5 to 41.9 (Háněl 2008). The mean number of species recorded at L1–L6 on each date ranged from 20.5 to 31.8 (Table 3). It is very likely that the low soil pH was one of the factors limiting the taxonomic richness of nematodes at Voděradské bučiny. Nevertheless, the number of species, genera, and values of H'gen, MI, ∑MI, and HMI tended to be greater at locality L5, where the soil pH was highest.

The second factor limiting taxonomic richness could be shortage of water in soil susceptible to desiccation. This is indicated, for example, by the absence of the large species of the genus *Eudorylaimus*, except for the occurrence of *E. altherri* at L5 and L4. Also the large *Plectus parietinus* was rare and occurred only at L5, L6 and L2, whereas smaller species of this genus prevailed throughout the area studied. This situation is similar to the distribution of nematodes in gorges in the České Švýcarsko National Park (Háněl 2010b). Few small species occurred on the tops and sides of the gorges exposed to sun and susceptible to desiccation and most of the large species occurred at bottoms where there are periodic or permanent streams. Relatively poor plant understorey (except at L5), when compared with the forests in the Křivoklátsko Biosphere Reserve studied by Háněl (1996b), could also negatively affect the diversity of nematodes recorded at Voděradské bučiny.

Temperate European soils are relatively young because they developed later due to glaciation. There is a greater taxonomic richness of nematodes in continental climax subtropical and tropical forest soils (with more dorylaimid species) than in temperate soils. There are however exceptions and some sites have low nematode richness, especially on islands (Boag & Yeates 1998). Nematode assemblages in the tropics may be less affected by moderate levels of forest management and disturbance than temperate climate soils, at least in some cases (Bloemers et al. 1997, Baniyamuddin et al. 2007). In managed subtropical forests nematodes are strongly affected by soil disturbance whereas above ground management practices have relatively little effect (Matlack 2001). Consequences of severe soil disturbance may last for at least 50 years (Thornton & Matlack 2002).

In coastal Douglas-fir forests in British Columbia, Canada, the taxonomic and trophic structure are only slightly altered by different harvesting systems, while abundance and biomass are lower in clear cut and shelter wood plots (Panesar et al. 2000). In Slovakia, the number of species, their abundance, H'spp and Maturity Index in storm-felled spruce forests from which salvaged timber was removed are not significantly different from those recorded at reference sites (Čerevková et al. 2013). In the Czech Republic, the most marked difference between nematode assemblages in spruce forests and clearings is in the proportion of the fauna made up of the root-fungal feeders *Filenchus* and *Aglenchus,* with other parameters little affected Háněl (2004b). There is little known about the long-term effects of repeated disturbance on nematodes in forest ecosystems but extreme disturbance of soil and understorey vegetation generally reduce nematode abundance and diversity (Yeates 2007). Based on Thornton & Matlack's (2002) findings we suggest that negative effects of repeated disturbances over periods shorter than 50 years may be cumulative.

The Voděradské bučiny forests have been moderately managed for several centuries and this may account for the current relatively low diversity of soil nematodes. Of the 2637 species and 263 genera in the order Dorylaimida only 702 species and 97 genera have been recorded from Europe (Andrássy 2009) and only the genus *Eudorylaimus* from continental Antarctica (Andrássy 1998). There are fewer dorylaimid nematodes in areas where the climate is harsh as the stressful environment there is unfavourable for them (Freckman & Virginia 1997, Ruess et al. 2002), which makes them good bioindicators of disturbance in ecosystems (Johnson et al. 1974, Wasilewska 1997). There is a similar number of species of Tylenchida, with a total of 2876 worldwide, 771 in Europe (Andrássy 2007) and 2 in continental Antarctica (Andrássy 1998). But at Voděradské bučiny 34 species of Tylenchida and only 17 species of Dorylaimida were recorded. This may be in accordance with Johnson's et al. (1974) conclusion that in forests Dorylaimida are more sensitive to disturbance than Tylenchida. On the other hand, in a natural woodland in India a total of 52 genera are reported of which 38% belong to the order Dorylaimida and 19% to Tylenchida (Tomar & Ahmad 2009).

There are 35 species of the order Tylenchida and 23 of the order Dorylaimida in undisturbed forest in the Křivoklátsko Biosphere Reserve (Háněl 1996b). There are 51 species of the order Tylenchida and 26 of the order Dorylaimida, and the species richness of Dorylaimida on the slopes of the gorges in the České Švýcarsko National Park is very likely limited by dry spells and acid soils (Háněl 2010b). Young forests on neutral-alkaline spoils harbour 50 species of Tylenchida and 42 of Dorylaimida (Háněl 2009a), which is a more balanced proportion of species richness composed of these two orders. This may indicate that Tylenchida and Dorylaimida are similarly able to colonize pristine pedogenetic substrates at least in some landscapes in Central Europe. As the development of an ecosystem progresses Tylenchida may become more diverse because many species of this order are plant feeders and probably more of these species are resistant to adverse stress factors than are the species of Dorylaimida.

Abundance, biomass and feeding habits

Nematode assemblages in the Voděradské bučiny National Nature Reserve were moderately abundant but of a low biomass because of the prevalence there of specimens with small bodies (see paragraphs below). Greater biomass was recorded along the stream at L5. This is similar to the situation in the Brtnický potok gorge in the České Švýcarsko National Park (Háněl 2010b). The wet soil adjacent to the stream is favourable for large and heavier species of nematodes whereas the shortage or intermittent supply of water on the sides of the gorge are favourable for small nematodes. Nematode fauna at Voděradské bučiny is probably well adapted to periods of soil water shortage because the mean individual nematode biomass recorded there was low (0.173 µg).

The abundance of nematodes, except that of predators with large bodies, was negatively correlated with soil moisture, whereas the mean nematode individual biomass was positively correlated with soil moisture. This "negative effect" of soil moisture upon nematode population abundance is also recorded in semiarid grassland and shrubland (Bakonyi & Nagy 2000, Bakonyi et al. 2007). However, thickness of water film on surface of soil particles appears to be of greater importance for nematodes than soil water content determined gravimetrically (Yeates et al. 2002). Nematode genera respond differently to the matric potential of soils and drier soils are more favourable for fungal than bacterial activity (Neher et al. 1999). The ratio of fungal to bacterial feeders is high in dry forest soils (Sohlenius & Boström 2001). Fungi are more acid-tolerant than bacteria (Mulder et al. 2005). These findings are in agreement with the predominance of small species of fungivorous *Filenchus* and *Aphelenchoides* recorded at Voděradské bučiny where the soils are acidic and humus form is moder. A negative correlation between the abundance of omnivores and soil moisture indicates that they also feed on fungi or upon bacteria adapted to drier soils such as actinomycetes (Zvyagintsev et al. 2007). Actinomycetes are also positively associated with diverse populations of nematodes in faecal pellets of millipedes, which are important in the formation of arthropod moder humus soils (Tajovský et al. 1992).

A low mean individual biomass is typical of high-mountain spruce forests (Háněl 1996ac, 2004b) and spruce forests at lower altitudes (Háněl 1992d, 2000b). In broad-leaved forest in the Czech Republic the mean individual biomass is usually greater than 0.5 µg (Háněl 1996b, 2000c, 2002a, 2003, 2010a). A mean individual biomass of 1.14 µg is reported for a mountain beech forest ecosystem in Romania (Popovici 1984) and 1.0 µg for a beech forest in Germany (Büttner 1989). A mean individual biomass of 0.512 µg is recorded for a beech forest (Šály 1989), of 0.650 µg for an alder stand (Šály 1980) and of 1.803 µg for a hornbeam-oak wood in Slovakia (Šály 1975).

As a consequence of the predominance of small species of nematodes the total biomass of nematode assemblages recorded in the Voděradské bučiny National Nature Reserve was relatively low, 229 mg.m^{-2} on average. Popovici (1984) reports the mean biomass of 470.4 mg.m^{-2} over six months in a beech forest and in other six beech forests in the Romanian Carpathians it ranges between 154.4 to 398.2 mg.m^{-2} (Popovici 1989). The nematode biomass recorded in two beech forests in Germany is 208 mg.m^{-2} (site with moder humus-type) and 461 mg.m^{-2} (in site with mull humus-type) (Alphei 1998). The average biomass of nematodes recorded in beech forests in Germany is 282 mg.m^{-2} (Zell 1989), 732 mg.m^{-2} (Büttner 1989) and in Czech Republic 920 mg.m^{-2} (Háněl 1996b).

These data indicate that the total biomass of soil nematodes in beech forests tends to decrease with increase in the altitude of the site. This phenomenon is connected with increasing proportion of small fungal & plant feeding (root-fungal feeding) individuals in nematode assemblages. The biomass of nematodes in spruce forest soil in the Voděradské bučiny region is low (Háněl 1992d) and the biota in the Voděradské bučiny National Nature Reserve have some sub-mountain to mountain elements (Ložek et al. 2005). The low biomass of soil nematode assemblages can also be interpreted as an azonal (sub)mountain phenomenon. At least, the biomass of nematodes at Voděradské bučiny was lower than expected from previously published data for lowland and highland forests and is rather similar to the values recorded in mountain forests.

Community indices, nature conservation and condition of the soil food-web

The overall characteristics of nematode assemblages at Voděradské bučiny, such as the number of species and genera, total biomass, mean individual biomass, H'gen, MI, PPI, ∑MI, and HMI are generally lower than those recorded in the Křivoklátsko Biosphere Reserve (Háněl 1996b). The levels of diversity and maturity of the two nematode faunas were thus different even within a relatively small region such as Central Bohemia. These indices indicate less diverse and less mature soil nematode assemblages at Voděradské bučiny than in the Křivoklátsko woodland.

Nevertheless, we can also consider conservation and preservation of species diversity from another point of view. The landscape at Voděradské bučiny is more affected by human activities than that in which Křivoklátsko woodland is located. The meadow and meadow–spruce forest ecotone studied at Voděradské bučiny by Háněl (1992d) had diverse nematode faunas. Meadows in process of succession from abandoned fields to forests in South Bohemia harboured most diverse nematode assemblages, with species and genera that do not occur in forests (Háněl 2010a). Meadows in the two Bohemian landscapes were azonal, man-established, systems with more diverse nematode faunas than in (semi) natural woodland areas. In these meadows the soil pH is higher, mull-humus is formed and dense herbaceous plant and grass roots provide an abundance of food for more species of nematodes. The results of nematode studies thus indicate that reasonable landscape management aimed at the formation of a mosaic of various types of ecosystems can increase the biological diversity of the landscape. Consequently, reduced diversity in one system can be compensated and improved by ecotonal effects between various systems.

The trophic composition of nematode faunas (very high abundance of root-fungal feeder + fungivores, low values of the index NCR2) indicate that fungi were the most important component of the detritus food web in the soils studied. NCR2 however significantly increased with pH (H_2O). Namely in a wet part of the *Impatiento-Fagetum* forest (L5) a greater participation of bacteria in the detritus food web was indicated by nematodes. The greater biomass of bacterivores at some localities (Table 4) could also indicate a greater abundance of bacteria. Nevertheless, the significance of differences in the abundance of bacterivores, fungivores, root-fungal feeders and omnivores at L1–L6 is ambiguous (Table 2). Such situations indicate that the soil detritus food web functioning in Voděradské bučiny ecosystems was similar and very likely, as discussed above, dominated by fungi.

Significant difference in the abundance of plant parasites, juvenile stages of insect parasites and predators reflected local differences in the composition of nematode assemblages. It is likely that there was top-down control of soil food webs by predacious nematodes at L5 as their biomass at this locality was greater than that of all the other trophic groups (Table 4). Monochid nematodes can feed on nematodes and bacteria (Yeates 1987), and other small soil animals (Small 1987), and in the present study their abundance were positively correlated with the abundance of Enchytraeidae and Tardigrada. Tardigrada are known to suppress nematode populations (Sánchez-Moreno et al. 2008). Their abundance was positively correlated with the abundance of predators and bacterivores and was greater than in the beech forest studied by Büttner (1989). The abundance of Rotifera was significantly positively correlated with the abundance of bacterivorous nematodes, which may indicate that both these groups of soil animals fed on bacteria. Their abundance was greater than the 4.9×10^3 ind.m^{-2} recorded by Büttner (1989) but lower than the 212–513×10^3 ind.m^{-2} in a wet climax beech forest in south Bohemia recorded by Devetter (2009).

CONCLUSIONS

The nematode assemblages in the Voděradské bučiny National Nature Reserve were moderately abundant, of low total biomass because of the dominance of small species, with relatively low species and generic richness, and low diversity and maturity indices. This could be due to the low pH of the soil with moder humus, which is susceptible to desiccation, and at least at some sites to the poor plant understorey. It cannot be excluded that the moderate long-term management of these forests also contributed to the relatively low nematode richness. Predominance of root-fungal feeding and fungivorous nematodes indicate a detritus soil food web governed mainly by fungi.

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