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A survey of assemblages of nematodes at different elevations in the Tatra Mountains (Slovakia) as a baseline for a soil transplantation experiment to simulate climate warming

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Abstract. Soil nematodes were studied in the alpine zone in the Tatra Mountains as a part of soil meso-cosmos transplant experiment. The aim of the experiment is to simulate the effects of elevated temperatures (by 1.5–3.0 °C) on soil chemistry, microbial communities and invertebrates by transplanting intact blocks of soil from higher to lower elevations. The study was done at three sites in the Furkotská dolina Valley of the Vyšné Wahlenbergovo Lake (VWL), which is a soil-poor catchment, and at two sites in the Veľká studená dolina Valley of the Starolesnianské Lake (SL) a soil-rich catchment, which are at between 2,200 and 1,760 m a. s. l. The first set of samples was collected in September 2013, when the soil meso-cosmoses were transplanted. The second set was collected in September 2014. Nematode assemblages were evaluated as reference data for comparing the assemblages in transplanted meso-cosmoses, which are to be analyzed in September 2015. A total of 105 species of nematodes were identified. On individual sampling dates the number of species varied from 29 to 58, number of genera from 19 to 33 and the total abundance of nematodes from 405 to $2,762 \times 10^3$ ind.m^{-2}. Bacterivorous genera *Plectus* and *Acrobeloides* and omnivorous *Eudorylaimus* dominated (D≥4.5%) at almost all sites. Epidermal root feeder *Aglenchus agricola* was most abundant at sites at higher elevations (VWL1, VWL2 and SL1) while plant parasitic *Helicotylenchus varicaudatus*, *Nagelus leptus* and partly *Paratylenchus microdorus* were most abundant at the lowest elevation site SL2. Despite the variations in the abundance of different genera Cluster and Principal Components Analyses showed that nematode assemblages at higher elevations differed from those at lower elevations in both years. Maturity Index varied from 2.27 to 3.18 independent of the altitude of the sites.

Key words. Soil zoology, ecology, Nematoda, trophic group, community composition, Enchytraeidae, Rotifera, Tardigrada, alpine habitat, meadow, Tatra Mountains, Slovak Republic, climate change.

INTRODUCTION

Climate change and its effects on nature and human society are among the most discussed topics nowadays. The current predictions of atmospheric warming during the 21st century are from 1 °C to 6 °C. Some parts of the biosphere, such as alpine or polar zones, are particularly sensitive to warming. Nevertheless, all ecosystems will experience climate change. Temperate regions are generally predicted to become warmer and wetter while arid and semi-arid lands may become more arid, with less or more marked effect upon their biota (Pauli et al. 2001, Darby et al. 2011, Nielsen et al. 2011, A'Bear et al. 2014). In the Tatra Mountains in Central Europe, there was a steep increase in air temperature from 1970 onwards, with the most rapid change of +1.5 °C during the last two decades. At the average lapse rate of –5.2 °C km^{-1} in this region the temperature increase represents a similar effect for water (as well as soil) biota of a 200–300 m difference in altitude (Kopáček et al. 2014).

Contributors to the Intergovernmental Panel on Climate Change generally agree that increases in the atmospheric concentrations of greenhouse trace gases (i.e., CO_2, CH_4, N_2O, O_3) attributed

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mainly to the use of fossil fuels and changes in land-use have led to changes in the earth's climate. Soil processes directly affect changes in climate through the production and consumption of CO_2, CH_4 and N_2O and, indirectly, through the production and consumption of NH_3, NO_x and CO (Mosier 1998). While the production of greenhouse gases by the fossil fuel industry is relatively easy to measure, calculating and predicting the effect of natural processes in balancing the composition of the atmosphere is a complicated task. The above ground changes are visible, the changes below ground are mostly hidden but both are closely linked (Verhoef & Brussaard 1990, Adams & Wall 2000, Bardgett et al. 2005, van der Putten et al. 2009). Nematodes, the most abundant and taxonomically and functionally diverse multicellular animals on Earth (Bongers & Ferris 1999) are an important component of soil systems (Boag & Yeates 1998, Bongers & Bongers 1998, Ettema 1998). They are also sensitive indicators of soil status and health (Gupta & Yeates 1997, Wilson & Kakouli-Duarte 2009). Studies of communities of soil nematodes in high mountain ecosystems (at altitudes of about 1000 m a. s. l. or more) in Central Europe are not rare (Franz 1950, Wasilewska 1974, 1996, Šály & Žuffa 1980, 1985, Šály 1983, 1985, Popovici 1984, 1997, 1998, Žuffa & Šály 1986, Vinciguerra 1988, Gerber 1991, Háněl 1994a, b, 1996a, b, 1999, 2004, 2013a, Ruess, 1995, Ruess & Funke 1995, Popovici & Ciobanu 2000, Hoschitz 2003, Čerevková 2006, Lišková et al. 2008, Čerevková & Renčo 2009, Háněl & Čerevková 2010, Čerevková et al. 2013) but only a few are relevant to climate change (Hoschitz & Kaufmann 2004a, b).

This study surveys nematode assemblages in samples collected at five alpine sites in the Tatra Mountains in September 2013 and September 2014. In addition to the samples analyzed in this report, in September 2013 blocks of intact soil were removed from the sites and placed in meso-cosmoses, which were transplanted back into the sites and from sites at higher elevations to those at lower elevations. The aim of the experiment is to simulate the effects of the elevated temperatures (by 1.5–3.0 °C) expected as a result of climate warming upon soil chemical parameters, microbial communities and invertebrates (Kopáček et al. 2014). Analysis of nematode faunas were carried out (i) to obtain reference data for comparison with the assemblages in transplanted meso-cosmoses that are to be analyzed in September 2015 and (ii) to find methods of nematode data analysis, which can best distinguish differences in the nematode assemblages in the area studied.

MATERIALS AND METHODS

Descriptions of the sites

This study was carried out above the timberline in alpine parts of the High Tatra Mountains (Tatra National Park), in the Slovak Republic. Generally, the climate in this area is of the cold alpine type, with an average annual temperature of 0 °C and average July temperature of 10 °C, and yearly precipitation of about 1700–1800 mm. The parent rocks in the area studied are mostly granite and soil types are rankers, podzols and cambic podzols. Soils are rich in accumulated dead organic matter, at some of the highest elevations there is almost no mineral layer and the organic layer lies directly on fragmented parent rock, and the pH(H_2O) values usually range from 4 to 5 (Rusek 1993). The detailed soil physico-chemical and botanical characteristics of the sites are currently being studied by other participants in project No. 14-09231S.

Samples were collected at five sites in two mountain valleys of two lake catchments:

(i) the Furkotská dolina Valley of the Vyšné Wahlenbergovo Lake (VWL), a soil-poor catchment.
VWL1: 49°09'46.8"N, 20°01'41.5"E; ca. 2200 m a. s. l.; poor alpine grassy site (dominant *Oreochloa disticha* (Wulf.) Link, *Luzula alpinopilosa* (Chaix) Breistr.)
VWL2: 49°09'22.3"N, 20°01'40.4"E; ca. 2003 m a. s. l.; grassy alpine meadow (dominant *Juncus trifidus* L.)
VWL3: 49°08'48.5"N, 20°01'40.8"E; ca. 1766 m a. s. l.; grass-herbaceous plant alpine meadow (dominant *Nardus stricta* L., *Agrostis rupestris* All.)

(ii) the Veľká studená dolina Valley of the Starolesnianské Lake (SL) soil-rich catchment
SL1: 49°10'56.5"N, 20°09'50.8"E; ca. 1994 m a. s. l.; grassy alpine meadow (dominant *Agrostis rupestris* All.; with *Senecio carniolicus* Willd. and *Salix retusa* L.)
SL2: 49°10'41.7"N, 20°10'33.3"E; ca. 1763 m a. s. l.; herbaceous plant rich alpine meadow (dominant *Calamagrostis villosa* (Chaix) J. F. Gmel., *Mulgedium alpinum* (L.) Less.)

The first set of samples was collected in September 2013 when the soil meso-cosmoses were transplanted. The second set was collected in September 2014. The third set of samples will be collected in September 2015 together with the transplanted meso-cosmoses and analyzed simultaneously.

Sampling, processing

Six soil samples were collected at each site using a cylindrical corer of cross-sectional area 10 cm^2 inserted down to a depth of 10 cm (if possible) on 20–21 September 2013 (a) and on 21–22 September 2014 (b). The soil in each sample was weighed, carefully hand-mixed and a part dried to determine the water content. Soil moisture was determined gravimetrically, soil was dried for 48 h at 25 °C and then for 4 h at 105 °C.

Nematodes, enchytraeids, rotifers and tardigrades were isolated from approximately 15 ml of mixed soil, which depending on the soil weighed from 3.75 to 10.02 grams, using a modified Baermann funnel and studied in glycerol on slides. Nematodes (and other animals) in each sub-sample were studied separately and their numbers were adjusted to give the total number per sample and then converted to a per m^2 basis. Altogether 7,860 nematodes were identified to species/genus level. Morphological and morphometric analyses were performed using a Leica Leitz DMRB light microscope equipped with an N PLAN 100×/1.25 immersion oil objective and transmitted light interference contrast, which facilitated the study of structures on the surface of cuticle of the nematodes. The numbers of enchytraeids, rotifers and tardigrades collected were 31, 243 and 510, respectively.

Data analysis

For identifying the nematodes (Table 1) the most recent monographs written by Andrássy (2005, 2007, and 2009) were used. Because Andrássy provides keys to the European fauna, but only the species occurring in Hungary are described in detail, the nematodes were also identified using other studies mostly cited in his books or newer studies such as Geraert's (2008) monograph on Tylenchidae.

The species richness was evaluated using the number of species and the species richness index (Margalef index) $SR=(S-1)/\log_e(N)$ according to Yeates & Bongers (1999), S = the number of species identified, N = the number of individuals identified. To evaluate the diversity of nematodes the genera were counted and the Shannon Index (H'gen), based on natural logarithms, was calculated. The Maturity Index MI and the Plant Parasite Index PPI were calculated according to Bongers (1990). The Sum Maturity Index ∑MI (Yeates 1994) that includes all trophic groups (Wasilewska 1994) and the Heterogeneity Maturity Index HMI (Háněl 1996c) were calculated and used to evaluate the maturity of the nematode assemblages in terms of the *r-K* scale of life history strategies. *C-p* values (1–5) of nematode taxa were used according to Bongers & Bongers (1998).

To study the trophic structure of nematode assemblages the nematode genera were sorted into trophic groups (Háněl 2010) as in Table 2 (bacterivores – B, fungivores – F, root-fungal feeders of the family Tylenchidae – RFF, plant parasites – PP, omnivores – O, predators – P and insect parasites – IP). Proportions of microbivores (B, F, RFF) and plant feeders (RFF, PP) were used to evaluate the participation of the nematodes in decomposition and grazing (direct consumption of primary production) food webs. The ratios (B+F)/PP and (B+F+RFF)/PP were calculated according to Wasilewska (1994, 1996, 1997). PP are Wasilewska's OPP (obligatory plant parasites, which damage their host plants) and RFF are Wasilewska's FPP (facultative plant parasites, which cause no or little damage to their host plants and at least some can feed on fungi). High values for these ratios indicate the preponderance of slow nutrient cycling and mineralization through the detritus food web rather than a rapid flow of matter and energy from autotrophs to obligate plant-feeding heterotrophs through the grazing food web.

Nevertheless, the high population densities of *Aglenchus agricola* recorded in the present study present a problem (Table 2). Yeates et al. (1993) classify *Aglenchus* as plant feeding nematodes in group 1e – epidermal cell and root hair feeders (not plant parasites). This is based on a study by Wood (1973), who reports the feeding habits of *Tylenchus* (*Aglenchus*) *neozelandicus* Egunjobi, 1967, a species recently regarded (Geraert 2008) as a synonym of *Coslenchus costatus* (de Man, 1921). Wood (1973) reports that this species can reproduce when feeding on the roots of seedlings, Lucerne callus tissue and moss, but can only feed but not reproduce on fungi. Brzeski (1998) reports that *A. agricola* is an ectoparasite on the roots of many plants, but does not damage them. Predominance of small fungal feeding *Filenchus* (Okada et al. 2005) in the group of root-fungal feeders is a different situation. Evidently, the species composition should be taken into account when interpreting community indices. For the purpose of the present study and acknowledging the plant feeding habits of *Aglenchus*, the ratio (B+F)/(PP+RFF) was also calculated.

The nematode channel ratio NCR1=B/(B+F) was calculated according to Yeates (2003) and NCR2=B/(B+F+RFF) according to Háněl (2010). Values of these indices greater than 0.5 indicate a greater participation of bacteria than of fungi in the breakdown of detritus; the NCR2 took the fungal-feeding behaviour in Tylenchidae (RFF in the Table 2) into account.

Generally, Wasilewska's indices indicate whether nematodes at a site predominantly feed in detritus or grazing food web, based on the abundance of the different trophic groups. Nematode Channel Ratios indicate the relative participation of either bacteria or fungi in the detritus food web and are constrained to have values between 1 (totally bacterial-mediated decomposition) and 0 (totally fungal-mediated decomposition), which respectively indicate the bacterial-based

Table 1. A preliminary check-list of the species of nematode identified at each of the three sites in the Furkotská dolina Valley of Vyšné Wahlenbergovo Lake (VWL), which is a soil-poor catchment, and at two sites in the Veľká studená dolina Valley of Starolesnianské Lake (SL), which is a soil-rich catchment. Some species could not be identified with certainty because of insufficient material (only a few individuals in poor condition or only juveniles) or the species do not fit available descriptions

	nematodes and sites	VWL 1	VWL 2	VWL 3	SL 1	SL 2
	Monhysterida					
1	*Eumonhystera longicaudatula* (Gerlach et Riemann, 1973)	+	+	+	–	–
2	*Eumonhystera vulgaris* (de Man, 1880)	–	–	–	–	+
3	*Geomonhystera villosa* (Bütschli, 1873)	–	–	–	–	+
4	*Monhystrella* Cobb, 1918 sp.	+	–	–	+	+
	Araeolaimida					
5	*Bastiania uncinata* Andrássy, 1991	+	–	–	+	+
6	*Ceratoplectus armatus* (Bütschli, 1873)	–	+	–	–	–
7	*Metateratocephalus crassidens* (de Man, 1880)	+	+	+	–	+
8	*Plectus acuminatus* Bastian, 1865 s.l.	+	+	+	+	+
9	*Plectus amorphotelus* Ebsary, 1985	–	+	+	–	–
10	*Plectus communis* Bütschli, 1873	+	+	+	+	+
11	*Plectus geophilus* de Man, 1880	+	+	–	–	+
12	*Plectus inquirendus* Andrássy, 1958	–	+	–	–	–
13	*Plectus longicaudatus* Bütschli, 1873	+	+	+	+	+
14	*Plectus magadani* Kuzmin, 1979	+	–	–	–	–
15	*Plectus parietinus* Bastian, 1865	+	+	+	–	+
16	*Plectus parvus* Bastian, 1865	–	–	+	+	–
17	*Plectus rotundilabiatus* Zell, 1993	–	–	–	–	+
18	*Plectus velox* Bastian, 1865	–	+	+	–	–
19	*Rhabdolaimus terrestris* de Man, 1880	+	+	–	+	–
	Rhabditida s.l. Teratocephalina					
20	*Teratocephalus dadayi* Andrássy, 1968	+	+	–	+	–
21	*Teratocephalus lirellus* Anderson, 1969	–	+	–	–	–
22	*Teratocephalus lirellus* Anderson, 1969 / *stratumus* Eroshenko, 1973	+	+	–	+	–
23	*Teratocephalus paratenuis* Eroshenko, 1973	+	+	+	+	+
24	*Teratocephalus terrestris* (Bütschli, 1873)	+	+	–	–	–
25	*Teratocephalus* de Man, 1876 sp.	+	–	–	–	–
	Cephalobina					
26	*Acrobeloides nanus* (de Man, 1880)	–	+	+	+	+
27	*Acrobeloides tricornis* (Thorne, 1925)	+	+	+	+	–
28	*Heterocephalobus elongatus* (de Man, 1880)	+	+	+	+	+
29	*Panagrolaimus rigidus* (Schneider, 1866)	+	+	–	–	+
	Rhabditina					
30	*Bunonema reticulatum* Richters, 1905	+	–	–	–	+
31	*Bursilla monhystera* (Bütschli, 1873)	–	+	+	–	+
32	*Rhabditis terricola* Dujardin, 1845	+	–	+	+	+
33	*Steinernema* Travassos, 1927 dauer larvae	–	+	+	+	+
	Diplogastrina					
34	*Pristionchus lheritieri* (Maupas, 1919)	+	–	–	–	+
	Aphelenchida					
35	*Aphelenchoides breviuteralis* Eroshenko, 1968	+	+	–	–	+
36	*Aphelenchoides conimucronatus* Bessarabova, 1966	+	+	+	+	+
37	*Aphelenchoides curiolis* Gritsenko, 1971	–	–	+	+	+
38	*Aphelenchoides editocaputis* Shavrov, 1967	–	–	–	–	+

39	*Aphelenchoides graminis* Baranovskaya & Haque, 1968	–	–	–	–	+
40	*Aphelenchoides lagenoferrus* Baranovskaya, 1963	–	+	–	–	+
41	*Aphelenchoides macronucleatus* Baranovskaya, 1963	+	+	+	+	+
42	*Aphelenchoides parasubtenuis* Shavrov, 1967	+	+	–	–	–
43	*Aphelenchoides saprophilus* Franklin, 1957	+	+	–	+	–
44	*Aphelenchoides* Fischer, 1894 sp. 1	–	–	–	–	+
45	*Aphelenchoides* Fischer, 1894 sp. 2	–	–	–	–	+
	Tylenchida					
46	*Aglenchus agricola* (de Man, 1884)	+	+	+	+	+
47	*Cephalenchus leptus* Siddiqi, 1963	+	+	–	–	–
48	*Coslenchus costatus* (de Man, 1921)	–	–	–	–	+
49	*Deladenus durus* (Cobb, 1922)	+	+	–	–	–
50	*Ditylenchus dipsaci* (Kühn, 1857)	+	+	–	+	–
51	*Ditylenchus filenchulus* Brzeski, 1991	+	+	+	+	+
52	*Ditylenchus tenuidens* Gritzenko, 1971	–	–	–	–	+
53	*Ditylenchus terricola* Brzeski, 1991	–	+	+	–	–
54	*Ditylenchus valveus* Thorne & Malek, 1968	+	–	–	–	+
55	*Ditylenchus* Filipjev, 1936 sp.	–	–	+	+	–
56	*Filenchus aquilonius* (Wu, 1969)	–	+	–	–	+
57	*Filenchus discrepans* (Andrássy, 1954)	+	+	+	+	+
58	*Filenchus facultativus* (Szczygieł, 1970)	+	+	–	+	–
59	*Filenchus hamatus* (Thorne & Malek, 1968)	–	–	–	–	+
60	*Filenchus misellus* (Andrássy, 1958) s.l.	+	+	+	+	+
61	*Filenchus* Andrássy, 1954 sp. 1	–	+	–	+	–
62	*Filenchus* Andrássy, 1954 sp. 2	–	–	–	–	+
63	*Helicotylenchus pseudorobustus* (Steiner, 1914)	–	–	+	–	+
64	*Helicotylenchus varicaudatus* Yuen, 1964	+	+	–	+	+
65	*Lelenchus leptosoma* (de Man, 1880)	+	+	–	+	–
66	*Malenchus bryophilus* (Steiner, 1914)	–	–	–	–	+
67	*Nagelus leptus* (Allen, 1955)	–	–	–	–	+
68	*Paratylenchus* (*Gracilacus*) *straeleni* (De Coninck, 1931)	–	+	–	+	–
69	*Paratylenchus* (*Paratylenchus*) *microdorus* Andrássy, 1959	–	+	+	+	+
70	*Paratylenchus* (*Paratylenchus*) *projectus* Jenkins, 1956	–	–	–	–	+
71	*Pratylenchus crenatus* Loof, 1960	+	–	+	+	+
72	*Sphaeronema alni* Turkina & Chizhov, 1986 juv.	–	+	–	–	–
73	*Tylenchus davainei* Bastian, 1865	–	+	–	–	–
74	*Tylenchus elegans* de Man, 1876	+	–	–	–	–
75	Tylenchida juv.	–	–	–	–	+
	Enoplida					
76	*Prismatolaimus dolichurus* de Man, 1880	+	+	+	+	+
77	*Prismatolaimus intermedius* (Bütschli, 1873) s.l.	+	+	–	+	–
78	*Tripyla affinis* de Man, 1880	+	+	+	+	+
	Alaimida					
79	*Alaimus arcuatus* Thorne, 1939	+	–	–	–	–
	Mononchida					
80	*Clarkus papillatus* (Bastian, 1865)	–	–	–	–	+
81	*Coomansus menzeli* Loof & Winiszewska-Ślipińska, 1993	+	+	+	–	+
82	*Coomansus zschokkei* (Menzel, 1913)	–	–	–	–	+
	Dorylaimida					
83	*Allodorylaimus* Andrássy, 1986 sp.	–	+	–	–	+
84	*Aporcelaimellus alius* Andrássy, 2002	–	+	–	–	+
85	*Aporcelaimellus amylovorus* (Thorne & Swanger, 1936)	–	+	–	–	–
86	*Aporcelaimellus medius* Andrássy, 2002	–	–	–	+	–
87	*Enchodelus lucinensis* Popovici, 1978	–	+	+	+	–
88	*Enchodelus macrodorus* (de Man, 1880) / *carpaticus* Ciobanu et al., 2010	–	–	–	+	+

Table 1. (continued)

	nematodes and sites	VWL 1	VWL 2	VWL 3	SL 1	SL 2
89	*Enchodelus* Thorne, 1939 sp. (*hopedorus* (Thorne, 1929) group)	+	–	–	–	–
90	*Epidorylaimus agilis* (de Man, 1880)	+	+	+	+	+
91	*Epidorylaimus consobrinus* (de Man, 1918)	+	–	–	+	–
92	*Epidorylaimus humilior* (Andrássy, 1959) / *humilis* (Thorne & Swanger, 1936)	+	+	+	+	+
93	*Epidorylaimus leptosoma* (Altherr, 1963)	+	–	–	+	+
94	*Eudorylaimus brevis* (Altherr, 1952)	+	–	–	+	–
95	*Eudorylaimus discolaimioideus* (Andrássy, 1958)	+	+	+	+	+
96	*Eudorylaimus maritus* Andrássy, 1959 / *carteri* (Bastian, 1865)	–	–	–	–	+
97	*Eudorylaimus pseudobokori* Zell, 1986	–	+	–	–	+
98	*Eudorylaimus stefanskii* (Brzeski, 1960)	–	+	+	+	–
99	*Eudorylaimus* Andrássy, 1959 sp. 1	+	–	–	–	+
100	*Eudorylaimus* Andrássy, 1959 sp. 2	–	+	–	+	–
101	*Heterodorus* Altherr, 1952 juv.	–	+	+	+	+
102	*Metaporcelaimus* cf. *monohystera* (Brzeski, 1964)	+	+	+	+	+
103	*Paravulvus hartingii* (de Man, 1880) juv.	–	+	–	–	–
104	*Tylencholaimus mirabilis* (Bütschli, 1873)	–	+	+	+	–
	Diphtherophorida					
105	*Diphtherophora* cf. *kirjanovae* Ivanova, 1958	+	–	–	+	+
	total number of species	55	64	39	50	65
	SR	6.78	8.59	5.99	7.03	8.52

energy channel (pathway) and the slower fungal-based channel (Yeates 2003). Therefore, for the purpose of this study, Wasilewska's indices were modified in a similar way as follows.

(i) Nematode Food-web Ratio 1: NFR1= (B+F)/(PP+B+F) and
(ii) Nematode Food-web Ratio 2: NFR2= (B+F+RFF)/(PP+B+F+RFF).

Values close to 1 indicate that the nematodes predominantly take part in the detritus food web (with relatively slow mineralization rates of primary production) and values close to 0 suggest that nematodes predominantly take part in the grazing food web (with relatively fast mineralization rates of primary production).

(iii) Nematode Food-web Ratio 3: NFR3=(B+F)/(PP+RFF+B+F) reflects situations similar to those recorded in the present study, such as the predominance of plant feeding nematodes in the group of root-fungal feeders.

To evaluate the condition of the soil food web the Channel Index (CI), the Enrichment Index (EI) and the Structure Index (SI) were calculated according to Ferris et al. (2001). The assessment of the role of omnivores in soil food webs is difficult and the inclusion of neither CI nor EI in the framework for soil food web diagnostics by Ferris et al. (2001) does not make it any easier. The relative scarcity of enrichment opportunists in the area surveyed makes it more difficult to use CI and EI for estimating the role of bacteria and fungi in detritus food webs. Nevertheless, SI and the Basal Index (BI) (Berkelmans et al. 2003) can be used because both the basal and structural components of nematode food webs are well known and abundant. A high BI indicates that the health of an ecosystem is poor, while a high SI indicates a well-regulated, healthy ecosystem.

STATISTICA was used to perform the Analysis of Variance (ANOVA) and related tests, the Cluster Analysis and calculate correlation coefficients. Pearson (*r*) and Spearman (*R*) correlation coefficients were calculated between site altitudes and parameters of nematode assemblages. The nematode abundance data were *ln*(x+1) transformed prior to Cluster Analysis and ANOVA, followed by Fisher LSD post-hoc test at *alpha*=0.05 (the same letters in the Table 2 indicates homogeneous groups of means). The assumption of normality was evaluated using the Kolmogorov-Smirnov & Lilliefors test for normality, and Shapiro-Wilk's W test. If data did not meet the criterion of homogeneity of variances the Kruskal-Wallis ANOVA was also calculated followed by post-hoc multiple comparison of mean ranks of all pairs of groups (homogeneous groups are indicated by the same letters in Table 2). The method of multivariate ordination was selected after testing the length of the gradient in genus data by means of a Detrended Correspondence Analysis (DCA) using detrending by segments in CANOCO for Windows version 4.5 (Ter Braak and Šmilauer, 2002). The length of the gradient in genera abundance along the first axis was 2.145 SD and along the second axis 1.058 SD. Consequently, Principal Components Analysis (PCA) was done using *log*(x+1) transformed genus abundance.

RESULTS

Species richness

A total of 105 species were identified and the numbers at individual sites varied from 39 at VWL3 to 65 at SL2. In the Discussion there are detailed comments on some interesting species. The species richness index SR showed a similar trend (Table 1).

Trophic groups and generic composition of nematode assemblages

The total abundance of nematodes in 2013 varied from 405 to 1,481×10^3 ind.m^{-2}, in 2014 from 515 to 2,762×10^3 ind.m^{-2} (Table 2). The lowest total abundance was recorded at VWL3 mainly because of low population densities of bacterivores and root-fungal feeders. The population densities of plant parasites at VWL1 were markedly lower than at SL2. There was a significantly greater total abundance in 2014 at VWL1 (mainly due to significantly greater population densities of fungivores and root-fungal feeders) and at VWL2 (mainly due to significantly greater population densities of bacterivores). Nevertheless, there were increases in the populations of the majority of the trophic groups except for omnivores and predators at VWL1. The abundance of root-fungal feeders was significantly positively correlated with the altitude of the site (r=+0.775, p<0.01; R=+0.837, p<0.05, n=10). The abundance of plant parasites showed a slightly negative

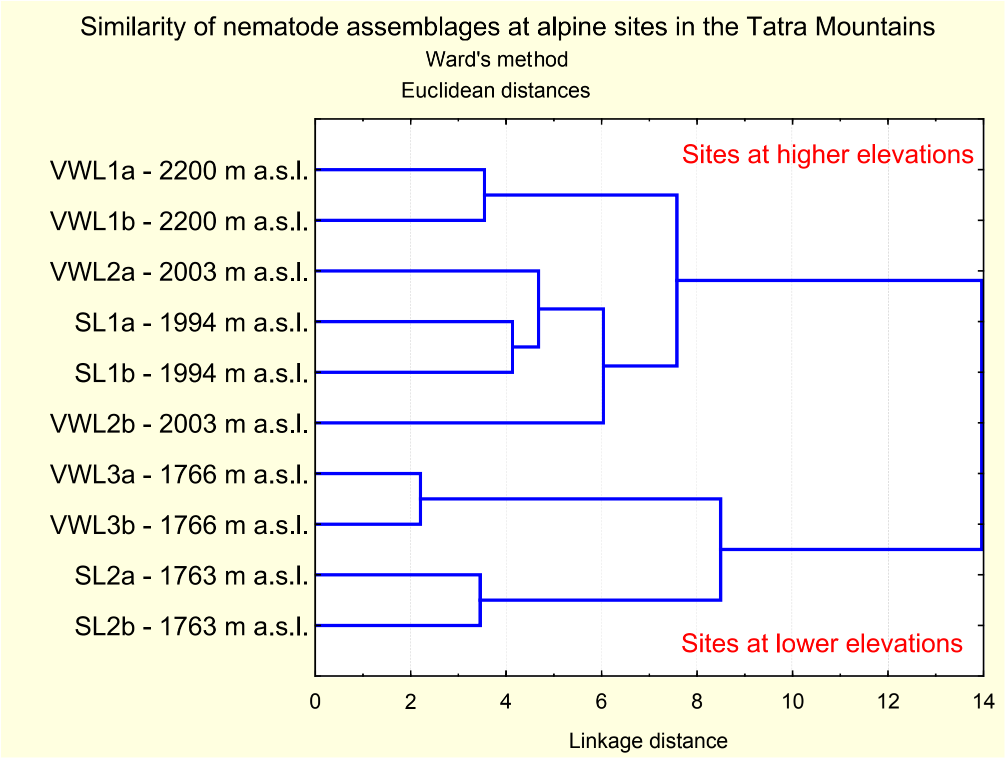

Fig. 1. Dendrogram based on cluster analysis of the *ln*(x+1) transformed abundance of nematode genera. For an explanation of site abbreviations see Material and Methods, a = year 2013, b = year 2014. Ward's method and Euclidean distances.

Table 2. Mean abundance (n=6) of nematode trophic groups with standard errors SE ($\times 10^3$ ind.m^{-2}) and results of a one-way ANOVA (F and p values). Kruskal-Wallis ANOVA (H and p values) was also calculated for trophic groups where violations of assumptions of normality and/or homogeneity of variances were detected. Mean abundance (n=6) of nematode genera and those with a D≥4.5% are in bold italics. Site abbreviations are explained in the Material and methods, "a" stands for the year 2013 and "b" the year 2014

nematodes and sites	VWL 1a	VWL 1b	VWL 2a	VWL 2b	VWL 3a	VWL 3b	SL 1a	SL 1b	SL 2a	SL 2b
bacterivores	511.1	1006.0	149.8	447.1	141.2	121.2	232.8	343.0	294.3	534.4
SE	81.6	360.8	18.5	169.5	23.3	17.1	78.7	63.4	90.2	120.1
$F_{(9,50)}=5.70, p<0.01$	ba	a	d	cb	d	d	dc	cb	dcb	ba
$H_{(9,N=60)}=31.57, p<0.01$	yz	z	y	yz	y	y	yz	yz	yz	yz
Plectus Bastian, 1865	***124.6***	***617.8***	***76.5***	***144.0***	***101.4***	***71.5***	***52.0***	***128.8***	***167.6***	***364.6***
Acrobeloides Cobb, 1924	***321.7***	***260.5***	***34.7***	***101.2***	13.9	***29.5***	***115.4***	***154.2***	***89.0***	52.3
Teratocephalus de Man, 1876	24.9	40.2	19.5	79.4	1.1	2.3	4.6	15.0	–	3.3
Heterocephalobus Brzeski, 1960	9.5	17.5	12.1	41.7	1.0	8.3	40.4	9.6	2.2	13.7
Panagrolaimus Fuchs, 1930	2.6	24.9	–	52.9	–	–	–	–	7.5	52.1
Rhabdolaimus de Man, 1880	21.3	4.5	1.4	5.7	–	–	9.0	20.0	–	–
Prismatolaimus de Man, 1880	–	15.5	4.2	14.5	–	1.9	4.0	13.7	–	1.8
Rhabditis Dujardin, 1845	–	1.2	–	–	15.7	–	2.0	–	7.5	17.6
Metateratocephalus Eroshenko, 1973	4.8	5.9	–	1.3	7.9	3.4	–	–	1.5	12.7
Bastiania de Man, 1876	–	6.8	–	–	–	–	5.3	–	–	4.2
Eumonhystera Andrássy, 1981	–	2.7	–	2.4	–	1.9	–	–	3.1	2.8
Geomonhystera Andrássy, 1981	–	–	–	–	–	–	–	–	10.2	–
Bursilla Andrássy, 1976	–	–	–	3.9	–	2.3	–	–	–	3.9
Bunonema Jägerskiöld, 1905	–	3.7	–	–	–	–	–	–	4.1	–
Monhystrella Cobb, 1918	1.5	–	–	–	–	–	–	1.7	–	4.2
Pristionchus Kreis, 1932	–	1.2	–	–	–	–	–	–	1.5	1.3
Alaimus de Man, 1880	–	3.7	–	–	–	–	–	–	–	–
Ceratoplectus Andrássy, 1984	–	–	1.4	–	–	–	–	–	–	–
fungivores	25.3	191.1	120.2	406.4	56.4	48.1	144.1	39.7	87.1	100.8
SE	11.7	127.3	32.9	164.1	21.6	14.6	67.7	11.2	25.1	29.0
$F_{(9,50)}=3.25, p<0.01$	c	b	ba	a	cb	cb	b	cb	b	b
Aphelenchoides Fischer, 1894	18.1	***187.0***	***65.6***	***213.8***	***41.1***	***35.6***	38.2	33.2	***67.5***	78.3
Tylencholaimus de Man, 1876	–	–	32.7	***177.4***	5.0	8.3	***85.3***	–	–	–
Ditylenchus Filipjev, 1936 s.l.1)	–	2.6	21.9	12.6	10.4	4.2	18.6	6.4	19.6	21.2
Deladenus Thorne, 1941	7.2	–	–	2.6	–	–	–	–	–	–
Diphtherophora de Man, 1880	–	1.6	–	–	–	–	2.0	–	–	1.4
root-fungal feeders	434.1	1364.6	293.4	496.4	24.6	50.8	384.1	119.0	90.1	54.4
SE	150.7	316.1	114.5	108.8	10.6	32.7	189.3	36.7	39.0	11.9
$F_{(9,50)}=12.21, p<0.01$	b	a	cb	b	e	e	cb	dc	ed	ed
Aglenchus Andrássy, 1954	***400.7***	***1343.2***	***161.8***	***344.4***	4.3	–	***342.7***	***88.4***	10.1	2.0
Filenchus Andrássy, 1954 s.l.	17.0	3.7	***87.9***	***122.2***	***20.3***	***50.8***	31.4	21.0	***75.4***	48.3
Lelenchus Andrássy, 1954	4.1	–	***43.7***	23.7	–	–	10.0	9.7	–	–
Cephalenchus Goodey, 1972	11.0	17.7	–	1.3	–	–	–	–	–	–
Tylenchus Bastian, 1865	1.2	–	–	4.8	–	–	–	–	–	–
Malenchus Andrássy, 1968	–	–	–	–	–	–	–	–	4.6	–
Coslenchus Siddiqi, 1978	–	–	–	–	–	–	–	–	–	4.1
plant parasites	3.0	16.7	46.4	215.5	57.2	49.9	97.2	89.5	713.5	851.5
SE	1.9	8.3	26.9	174.5	12.4	20.0	12.9	44.8	202.9	454.7
$F_{(9,50)}=8.15, p<0.01$	d	dc	dcb	cb	cb	cb	b	cb	a	a
$H_{(9,N=60)}=33.77, p<0.01$	y	y	yz	yz	yz	yz	yz	yz	z	z
Helicotylenchus Steiner, 1945	–	1.4	1.6	2.6	5.7	1.9	12.0	–	***453.4***	***566.8***
Paratylenchus Micoletzky, 1922	–	–	7.6	***187.4***	***42.9***	***48.1***	***55.3***	***89.5***	***131.2***	***201.2***
Nagelus Thorne et Malek, 1968	–	–	–	–	–	–	–	–	***118.9***	53.0

Sphaeronema Raski et Sher, 1952	–	–	***34.4***	25.6	–	–	–	–	–	–
Pratylenchus Filipjev, 1936	3.0	15.3	–	–	8.6	–	13.3	–	1.8	5.2
Tylenchida juv.	–	–	–	–	–	–	–	–	8.2	25.4
Gracilacus Raski, 1962 [2]	–	–	2.8	–	–	–	16.6	–	–	–
omnivores	132.5	128.2	143.4	232.3	64.0	99.1	295.3	215.8	135.7	186.0
SE	30.5	44.0	24.1	56.3	21.1	21.7	57.5	42.0	31.2	36.5
$F_{(9,50)}=3.09, p=0.01$	cb	dcb	cba	ba	d	dc	a	ba	cb	cba
Eudorylaimus Andrássy, 1959	***90.9***	78.9	***73.9***	38.1	***58.9***	***78.5***	***174.8***	***86.1***	***107.4***	***95.7***
Epidorylaimus Andrássy, 1986	34.0	43.6	8.4	29.8	–	4.0	29.8	***101.8***	4.5	19.0
Aporcelaimellus Heyns, 1965	–	–	***48.9***	***85.8***	–	–	2.0	–	1.8	–
Enchodelus Thorne, 1939	2.8	0.9	3.3	12.7	–	7.6	***79.3***	10.1	8.4	–
Heterodorus Altherr, 1952	–	–	3.8	49.3	2.0	3.8	2.0	17.8	3.0	7.4
Allodorylaimus Andrássy, 1986	–	–	–	5.4	–	–	–	–	7.7	63.9
Metaporcelaimus Lordello, 1965	4.9	4.9	5.1	11.1	3.1	5.2	7.3	–	3.0	–
predators	65.0	55.8	4.7	51.4	48.3	118.2	14.2	9.7	157.4	116.2
SE	16.6	42.6	3.4	27.2	11.7	36.7	10.2	6.7	59.7	33.2
$F_{(9,50)}=6.19, p<0.01$	cba	dc	d	dc	cb	ba	d	d	a	ba
$H_{(9,N=60)}=31.49, p<0.01$	yz	yz	y	yz	yz	yz	yz	y	z	yz
Tripyla Bastian, 1865	***61.0***	54.0	1.4	4.7	***24.4***	***35.6***	14.2	9.7	***79.6***	52.8
Coomansus Jairajpuri et Khan, 1977	4.0	1.9	3.4	44.9	***23.9***	***82.6***	–	–	***77.9***	52.4
Clarkus Jairajpuri, 1970	–	–	–	–	–	–	–	–	–	11.0
Paravulvus Heyns, 1968	–	–	–	1.9	–	–	–	–	–	–
insect parasites [3]	0.0	0.0	0.0	5.4	13.1	28.0	0.0	1.6	3.1	35.7
SE	–	–	–	5.4	10.1	20.6	–	1.6	3.1	24.3
$H_{(9,N=60)}=17.83, p=0.04$	z	z	z	z	z	z	z	z	z	z
Steinernema Travassos, 1927 larvae	–	–	–	5.4	13.1	***28.0***	–	1.6	3.1	35.7
all nematodes	1171.0	2762.3	758.0	1854.4	404.9	515.2	1167.6	818.3	1481.2	1879.1
SE	112.6	800.6	127.1	401.3	51.0	73.7	286.5	114.3	242.8	501.3
$F_{(9,50)}=8.88, p<0.01$	cb	a	dc	ba	e	ed	cb	dc	ba	ba

[1] *Ditylenchus dipsaci* was very rare, therefore all species of *Ditylenchus* are classified as fungivorous.

[2] *Paratylenchus* (*Gracilacus*) *straeleni* differs from other species of *Paratylenchus* in having a very long stylet. For the purpose of distinguishing these two groups of species the subgenera within the genus *Paratylenchus* are considered to be separate genera, see Andrássy (2007).

[3] The very patchy distribution of invasive individuals of *Steinernema* complicates the statistical evaluation of the abundance data.

correlation with the altitudes of the sites ($r=-0.573, p=0.08$; $R=-0.739, p<0.05$). The abundance of insect parasites was negatively correlated with the altitudes of the sites ($r=-0.691, p=0.03$; $R=-0.749, p<0.05$).

The most abundant genus in the area was the epidermal root feeder *Aglenchus* (21.1% of all nematode individuals in the area studied) and *Aglenchus agricola* was present at all sites (Table 1). Nevertheless, the abundance of *Aglenchus* was greater at the high sites (VWL1, VWL2, and SL1) than at the lowest sites (VWL3 and SL2). The second most abundant genus was the bacterivore *Plectus* (14.4% of all individuals) followed by bacterivore *Acrobeloides* (9.2%), plant parasitic *Helicotylenchus* (8.2%) and *Paratylenchus* (6.0%), omnivore *Eudorylaimus* (6.9%) and fungivore *Aphelenchoides* (6.1%).

The abundance of individual nematode genera varied with site and sampling date (Table 2) but the Cluster Analysis (Fig. 1) and Principal Components Analysis (Fig. 2) showed that nematode assemblages at the high elevations differed from those at lower elevations in both years. The similarity of the nematode assemblages was also greater within sites than between sites, except at VWL2.

Community indices

On individual sampling dates the number of species varied from 29 to 58. The numbers of genera varied from 20 to 30 in 2013 and from 19 to 33 in 2014 (Table 3). There were no significant correlations between the number of species, SR or genera and the altitude of a site. The highest values of the Shannon Index H'gen were recorded at VWL2 (2.58–2.74) and the lowest values at VWL1 (1.67–1.95) as a result of the high population densities there of *Aglenchus* and *Plectus*. H'gen was negatively, but insignificantly, correlated with the altitudes of the sites ($r=-0.610$, $p>0.05$; $R=-0.148$, $p>0.05$, $n=10$).

The Maturity Index varied from 2.27 to 3.18 without any obvious relation to the altitudes of the sites. The PPI values were highest at SL2 (2.72) and slightly negatively correlated with the altitudes of the sites ($r=-0.626$, $p=0.05$; $R=-0.689$, $p<0.05$). The PPI/MI ratio varied from 0.65 to

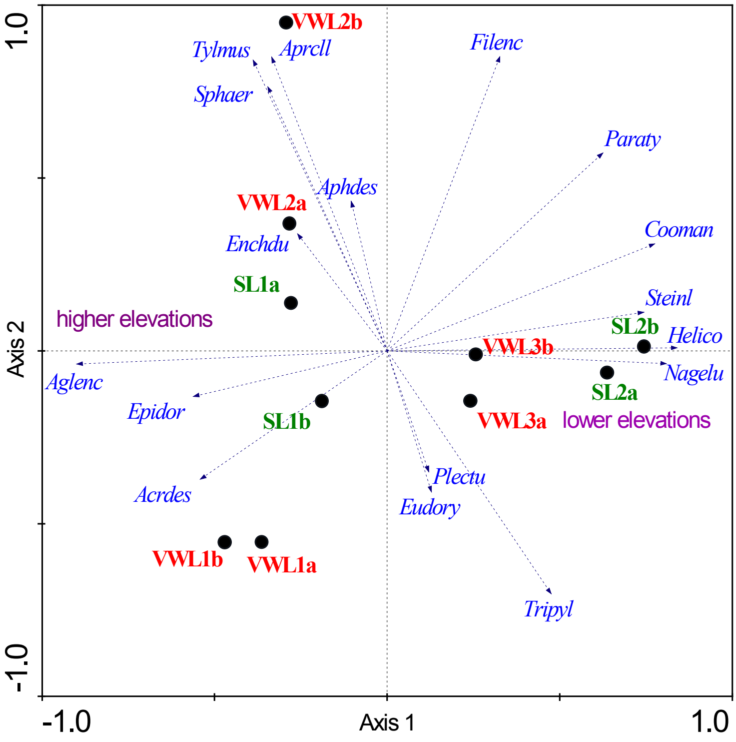

Fig. 2. Biplot from PCA on *log*(x+1) transformed genus abundance. Only genera with D≥4.5% at least one site and sampling date are shown. Eigenvalues of axes 1, 2, 3 and 4 were 0.429, 0.194, 0.159 and 0.075, and the cumulative percentage variance of genus data 42.9, 62.3, 78.2 and 85.7, respectively. Key: For the explanation of site abbreviations see Material and Methods, a = year 2013, b = year 2014. Genera acronyms: *Acrdes* = *Acrobeloides*, *Aglenc* = *Aglenchus*, *Aphdes* = *Aphelenchoides*, *Aprcll* = *Aporcelaimellus*, *Cooman* = *Coomansus*, *Enchdu* = *Enchodelus*, *Epidor* = *Epidorylaimus*, *Eudory* = *Eudorylaimus*, *Filenc* = *Filenchus*, *Helico* = *Helicotylenchus*, *Nagelu* = *Nagelus*, *Paraty* = *Paratylenchus*, *Plectu* = *Plectus*, *Tripyl* = *Tripyla*, *Tylmus* = *Tylencholaimus*, *Sphaer* = *Sphaeronema* juveniles, *Steinl* = *Steinernema* juveniles.

Table 3. Community indices calculated using the mean (n=6) abundances of genera. Site abbreviations are explained in Material and methods, "a" stands for the year 2013 and "b" 2014

indices and sites	VWL 1a	VWL 1b	VWL 2a	VWL 2b	VWL 3a	VWL 3b	SL 1a	SL 1b	SL 2a	SL 2b
nematode diversity and maturity indices										
number of species	31	46	40	58	32	29	39	34	46	50
SR	4.43	5.93	6.37	8.16	5.42	5.03	6.03	5.27	6.92	6.94
number of genera	22	28	25	33	20	22	26	19	30	32
H'gen	1.95	1.67	2.58	2.74	2.47	2.49	2.45	2.41	2.40	2.42
∑MI	2.33	2.14	2.63	2.59	2.56	2.88	2.71	2.60	2.73	2.62
HMI	4.98	3.93	7.09	7.38	6.31	6.85	6.80	6.37	6.39	6.24
MI	2.53	2.27	3.05	2.93	2.67	3.10	3.18	2.81	2.73	2.53
PPI	2.01	2.01	2.11	2.04	2.17	2.02	2.05	2.00	2.72	2.72
PPI/MI	0.79	0.89	0.69	0.70	0.82	0.65	0.65	0.71	1.00	1.07
proportions of nematode trophic groups										
(B+F)/PP	181.36	71.76	5.82	3.96	3.45	3.39	3.88	4.27	0.53	0.75
(B+F+RFF)/PP	328.13	153.57	12.14	6.26	3.88	4.41	7.83	5.60	0.66	0.81
(B+F)/(PP+RFF)	1.23	0.87	0.79	1.20	2.41	1.68	0.78	1.83	0.47	0.70
B/F	20.20	5.26	1.25	1.10	2.50	2.52	1.62	8.64	3.38	5.30
B/(F+RFF)	1.11	0.65	0.36	0.50	1.74	1.23	0.44	2.16	1.66	3.44
nematode food-web and channel ratios										
NFR1	0.99	0.99	0.85	0.80	0.78	0.77	0.80	0.81	0.35	0.43
NFR2	1.00	0.99	0.92	0.86	0.80	0.82	0.89	0.85	0.40	0.45
NFR3	0.55	0.46	0.44	0.55	0.71	0.63	0.44	0.65	0.32	0.41
NCR1	0.95	0.84	0.55	0.52	0.71	0.72	0.62	0.90	0.77	0.84
NCR2	0.53	0.39	0.27	0.33	0.64	0.55	0.31	0.68	0.62	0.77
nematode food-web indices										
CI	70.9	60.5	100.0	50.2	45.0	81.0	87.6	100.0	51.3	24.9
EI	6.9	22.4	29.2	46.8	40.5	24.6	19.7	10.6	32.1	42.6
SI	69.3	50.5	83.6	82.5	77.8	87.5	88.8	80.9	78.6	74.5
BI	30.0	43.3	15.3	15.1	19.3	12.0	10.9	18.7	19.5	21.4

0.89 at VWL1, VWL2, VWL3 and SL1 while at SL2 it varied from 1.00 to 1.07. The ∑MI varied from 2.14 to 2.88 and was significantly negatively correlated with the altitudes of the sites ($r=-0.769$, $p<0.01$; $R=-0.640$, $p<0.05$).

The (B+F)/PP ratio was significantly positively correlated with the altitudes of the sites ($r=+0.705$, $p=0.02$; $R=+0.960$, $p<0.05$) as was the (B+F+RFF)/PP ratio ($r=+0.729$, $p=0.02$; $R=+0.960$, $p<0.05$). The (B+F)/(PP+RFF) ratio showed no association with the altitudes of the sites.

Table 4. Mean abundance (n=6) of other groups of soil fauna collected along with the nematodes ($\times 10^3$ ind.m^{-2}). Site abbreviations are explained in Material and methods, "a" stands for year 2013 and "b" 2014

animals / sites	VWL 1a	VWL 1b	VWL 2a	VWL 2b	VWL 3a	VWL 3b	SL 1a	SL 1b	SL 2a	SL 2b
Enchytraeidae	0.0	6.3	1.8	2.0	0.0	0.0	10.8	24.9	6.0	6.2
Rotifera	18.9	28.2	28.2	85.9	15.6	8.9	55.3	103.9	17.7	34.7
Tardigrada	42.0	167.6	25.6	31.9	37.4	53.3	170.7	119.0	69.5	131.3

The values of NCR2 were slightly negatively correlated with the altitudes of the sites (r=–0.547, p=0.10; R=–0.640, p<0.05). The values of the other indices showed no significant relationships with the altitudes of the sites.

Other soil fauna

The greatest abundance of Enchytraeidae, Rotifera and Tardigrada was recorded at SL1 (Table 4). Rotifera were also abundant at VWL2 in 2014. The abundance of Tardigrada was also high at SL2 and at VWL1 in 2014.

DISCUSSION

Species richness

Šály & Žuffa (1980) and Šály (1983) studied soil nematodes in two meadows in the Gaderská dolina Valley in the Veľká Fatra Mountains. In a typical mountain pasture they report 54 species (SR=7.23) and in a typical mountain meadow 46 species (SR=6.38). These values are within the range recorded in the present study. Other meadow ecosystems studied in the Slovak Republic are mostly located at lower altitudes and have fewer species of nematodes (Lišková & Čerevková 2005, Čerevková 2006, Háněl & Čerevková 2006).

Popovici & Ciobanu (2000) carried out an extensive study of nematode communities in grasslands in Romania. At altitudes from above 1000 to 2270 m a. s. l. the numbers of nematode taxa (genera + species) varied from 46 to 99. Háněl (1994b) report finding 87 species in a mountain meadow (1280 m a. s. l.) in the Krkonoše Mountains in the Czech Republic. However, some sub-alpine and alpine grassland ecosystems in Central Europe have less diversified nematode faunas. In the Italian Alps, Vinciguerra (1988) report finding only 7 to 16 species at altitudes from 1910 to 2250 m a. s. l. But in the Austrian Alps Hoschitz & Kaufmann (2004b) report about 60 nematode genera in a mountain pasture at an altitude of 1961 m a. s. l.

These data indicate that species and generic richness in mountain grassland ecosystems in Central Europe can vary greatly between sites and that further sampling at these sites will yield more species. According to the data of Popovici & Ciobanu (2000) taxonomic richness of nematode assemblages is more dependent on soil type and vegetation than on elevation. Low species and generic richness at VWL3 is difficult to explain and coincides with a low abundance of nematodes (Table 2). This contrasts with a high species richness and abundance of nematodes at SL2, which is at a similar altitude. The greatest PPI/MI ratio (Table 3) was recorded at SL2 and indicates there are more nutrients in soil there than at VWL3, but there is currently no information on the content of soil nutrients in this area. Nevertheless, species richness at the sites studied is sufficient for detecting changes in nematode faunas that can arise as a result of the soil transplantation experiment.

Some nematodes could not be determined based on the available literature or their identity remains uncertain. For example, *Teratocephalus lirellus* might be a group of closely related species (Boström et al. 2000). The cuticle in this (these) species, according to Boström (1989), Karegar et al. (1997; Fig. 2. Iranian population) and Boström et al. (2000), is longitudinally striated by deep incisions and this was clearly visible on some specimens collected at VWL2. But the majority of the specimens collected in the area studied had hardly visible longitudinal striation (or invisible using a light microscope), as described by Karegar et al. (1997, Fig. 1. Belgian population). Using Andrassy's (1984) key they were identified as *Teratocephalus stratumus*. Maybe, *T. stratumus* is a "cryptic species" within the *T. lirellus*-group. The presence/absence of clearly marked longitudinal striae in *Teratocephalus* detectable by means of light microscopy also concerns other species. *Teratocephalus tenuis* Andrássy, 1958 (pp. 12–16) was originally described as lacking longitudinal striation on its cuticle, but Boström & Holovachov (2001) report finding a population in which longitudinal striae are clearly visible.

Another example is the genus *Enchodelus*. According to Andrassy's (2009) key large specimens in SL1 and SL2 are identified as *E. macrodorus*. But closer examination of the specimens revealed that they do not fit the re-description of this species (Guerrero & Peña-Santiago 2007, Guerrero et al. 2008) because they have a long well differentiated tripartite uterus and some other minute differences. These specimens are also similar to *E. carpaticus* Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010 but lack the dorsal mass of cells near cardia and may represent a cryptic species within the *E. macrodorus* group in Guerrero et al. (2008).

In the genus *Eudorylaimus*, Andrássy's keys (1986, 2009) identify specimens with large bodies (L=2.07–2.30 mm) as *E. maritus* with spicules 70–77 µm long. But Zell (1986) described a population of *E. maritus* with a wider range in body lengths (L=1.60–2.30 mm), which overlaps the range of values for *E. carteri* (L=1.35–2.02 mm). Zell's (1986) population was included in the modified key to *Eudorylaimus* (Andrássy 1991). For the topotypes of *E. carteri* described by Loof (1975) L=1.68–1.85 mm and the length of spicules is 64–65 µm. In the specimens studied L=1.59–2.02 mm and the length of spicules is 76–80 µm. Therefore, they may be closer to *E. maritus* than to *E. carteri*, but may also be a cryptic species within the *E. carteri* group. *Allodorylaimus* sp. does not fit any of the European species listed by Andrássy (2009). The above indicate that isolated alpine habitats may harbour endemic (sub)species, which will further enhance the nematode species richness in the Carpathian region. A closer examination of this topic is not within the scope of this paper, but the finding of nematodes that potentially may be species new to science clearly indicate the naturalness of the habitats studied.

Trophic groups and generic composition of nematode assemblages

The most abundant nematode in the area studied was *Aglenchus agricola* but this species dominated (between 10.8% and 48.6% on different dates) only at the sites VWL1, VWL2 and SL1 (i.e. those at the highest elevations). This is in accordance with the dominance of *Aglenchus* in alpine grasslands (2050–2270 m a. s. l.) in Romania (Popovici & Ciobanu 2000). At the lower elevation sites VWL3 and SL2 the low abundance of *A. agricola* is similar to that recorded for this species in the Gaderská dolina Valley in the Veľká Fatra Mountains by Šály & Žuffa (1980). The second abundant genus in the family Tylenchidae is *Filenchus* as is also reported for alpine and subalpine grasslands in Romania (Popovici & Ciobanu 2000). *A. agricola* occurs in various ecosystems in Slovakia (Lišková & Čerevková 2011), but in meadow ecosystems at low altitudes this species is not the most abundant nematode (Lišková & Čerevková 2005, Čerevková 2006, Háněl & Čerevková 2006).

In a mountain meadow (1280 m a. s. l.) in the Krkonoše Mountains (Czech Republic) *A. agricola* makes up 26% of all the nematodes and 47% in a grassy clear-cut (1200 m a. s. l.) left after spruce die-back and salvage logging (Háněl 1994b, 1998).

A similar situation is reported in a southern mountain range in the Czech Republic, The Šumava Mountains. *A. agricola* makes up 79% of all nematodes in a naturally grassy area and occurs in small populations in Norway spruce forests. After clear-cutting of spruce trees damaged by bark beetles and grass completely colonized the site its abundance strongly increased and *A. agricola* became the eudominant species (Háněl 1999, 2004). But the opposite occurred after a windstorm and wildfire destroyed spruce forests in the High Tatras National park; there were low populations of *A. agricola* in undamaged forests, which after this disturbance declined to almost undetectable levels (Čerevková et al. 2013). Why such a common species responds so differently to changes in the environment is an enigma, but as the morphology of the populations at different sites differ

(Brzeski 1988, 1999) they may also differ in their physiology, habitat preferences and ability to compete with other plant-feeding nematodes. Nevertheless, it is likely that *A. agricola* will show response to soil transplantation from one site to another.

According to Yeates et al. (1993) and Bonders & Bongers (1998) RFF and PP they are generally plant feeders, but life-history traits of individual species and genera are very different. *Aglenchus* dominated at the higher elevations (VWL1, VWL2 and SL1) and are epidermal cell and root hair feeders (group 1e) with a *c-p* value of 2. *Filenchus* was dominant at the lower elevations (VWL2, VWL3, and SL2) and also belongs to the group 1e. But *F. discrepans* and *F. misellus* predominated and these small species are fungal feeders (Okada et al. 2005) with *c-p* values of 2. *Paratylenchus*, which occurred at all sites except VWL1, is an ectoparasite (group 1d) with a *c-p* value of 2 but is able to form resting stages (Brzeski & Háněl 1999) unlike the Tylenchidae. *Helicotylenchus* was eudominant (30.2–30.6%) at SL2 and is a semi-endopasite (group 1c) with a *c-p* value of 3. *Nagelus* (2.8–8.0%) was found only at SL2 and is an ectoparasite (group 1d) with a *c-p* value of 3. Invasive larvae of *Sphaeronema* occurred only at VWL2 and this genus is a sedentary parasite (group 1a) with a *c-p* value of 3.

Generally, there is a trend of increasing predominance of plant parasitic nematodes with greater *c-p* values with decreasing altitudes of the sites. However, plant feeding nematodes, sensu lato, were the most dominant or the second most dominant group (after bacterivores) at all sites except for VWL3 in 2014 (with the second most dominant group of predators) and SL1 in 2014 (with the second most dominant omnivores). Maybe, high population densities of predators could account for the low total abundance of all nematodes at VWL3. Consumption of plants by nematodes occurred at all sites and the composition of plant feeding species is a consequence of the development of alpine ecosystems taking millennia. But plant parasites with a *c-p* value of 3 (*Helicotylenchus*, *Nagelus*) were evidently unable to establish abundant populations at high elevations whereas epidermal cell and root hair feeding *Aglenchus* succeeded followed by *Paratylenchus* with a *c-p* value of 2, which is able to form resting stages when food is scarce. The lower abundance of *Aglenchus* at the low elevation sites maybe because this species is outcompeted there by other plant feeding species, but there is no evidence for this. It will be interesting to see how soil transplantation will affect the composition of plant feeding nematode assemblages.

The numbers of bacterivore genera recorded on particular dates at sites varied from 6 to 14. Bacterivore general opportunists with a *c-p* value of 2 (Bongers 1999), *Plectus* and *Acrobeloides*, were dominant at all sites and there was a great variety of species of *Plectus* (Table 1). It is difficult to predict how soil transplantation will affect this genus and the whole diverse spectrum of bacterivore nematodes. But *Acrobeloides tricornis* with a very sharp labial probolae was the only *Acrobeloides* at VWL1 while *A. nanus* with low rounded probolae was found at SL2. At other sites both species occurred and soil transplantation could change their (co)-occurrence. Bacterial communities in alpine meadow soils are sensitive to warming (Wu et al. 2015) and, therefore, a change in the bacterial populations is predicted, which may be reflected in the assemblages of bacterivore nematodes.

Among fungivore nematodes *Aphelenchoides* and *Ditylenchus* (*c-p* value 2) are ubiquitous and species-rich genera but species determination is not easy and that of juveniles often unreliable (Shahina 1996, Brzeski 1998). Their abundance also varied with sampling date and distinguishing natural variations from those induced by soil transplantation is likely to be a difficult task. *Tylencholaimus mirabilis* is a dorylaimid fungivore with a *c-p* value of 4 and is sensitive to disturbance (Yeates et al. 1993, Bonders & Bongers 1998). This species occurred at VWL2, VWL3 and at SL1 in 2013 with a strongly patchy distribution. *T. mirabilis* is relatively rare in grassland ecosystems in the Carpathian region (Popovici 1998, Lišková & Čerevková 2005, Háněl & Čerevková 2006) and most abundant in forests soils (Háněl & Čerevková 2010), but may be absent from climax forest soil exposed for centuries to stress factors such as spells of drought (Háněl 2013b, Schlaghamerský at al. 2014). Its disappearance might therefore indicate a deterioration in the habitat in transplanted blocks of soil. This can, however, concern only this species. Popovici & Ciobanu (2000) list the genus *Tylencholaimus* among genera with maximum occurrence in mountain grasslands in Romania together with *Filenchus*, *Rotylenchus*, *Acrobeloides*, *Plectus*, *Ecphyadophora*, *Paratylenchus* and *Anaplectus*.

The composition and abundance of both omnivore and predacious nematodes strongly suggest that the sites studied are undisturbed natural habitats. *Coomansus menzeli* is the largest (L=2.57–3.34 mm, females and males) of the species recorded in the area studied and was not previously reported from the Slovak Republic (Lišková & Čerevková 2011). *C. menzeli* occurred at all sites except SL1, whereas the smaller *C. zschokkei* (L=2.34 mm, female) was found only at SL2. Disappearance of such large predators and diminishing omnivore-predator nematode guilds is an indicator of ecosystem disturbance (Wasilewska 1997) and might occur as a result of soil transplantation.

The dendrogram produced by the cluster analysis and PCA diagram are self-explanatory. Nematode assemblages at high elevations differed from those at lower elevations in both years. Therefore, transfer of soil meso-cosmoses from a high to a lower altitude could be reflected in the generic composition of their nematode faunas.

Community indices

Naturalness of the sites studied was also highlighted by nematode community indices. High values of SI and low values of EI (Table 3) delimit Quadrant C in the projections of the Structure and Enrichment trajectories according to Ferris et al. (2001). The soil food web is characterised as undisturbed and structured, with moderate enrichment, moderate to high C:N ratio and with fungal decomposition channels. The values of BI are low and thus indicate good ecosystem health (Berkelmans et al. 2003). High values of CI suggest a high activity of the fungal decomposition channel except at VWL2 in 2014, VWL3 in 2013, and SL2 in 2013 and 2014. There were relatively high population densities of *Panagrolaimus* and *Rhabditis* with *c-p* values of 1. But the majority of bacterivores belonged to the genera *Plectus* and *Acrobeloides* with *c-p* values of 2, which are not included in CI. The values of the B/F ratio and NCR1 favour bacterial feeders, which is in accordance with the results of Popovici & Ciobanu (2000), and suggest greater participation of bacteria than fungi in the decomposition of soil organic matter.

Inclusion of root-fungal feeders RFF (family Tylenchidae), facultative plant parasites FPP according to Wasilewska (1994) or non-obligatory plant parasites according to Popovici & Ciobanu (2000), into indices is problematic. *Aglenchus agricola* certainly feeds on plant roots as a migratory ectoparasite but does not damage plants and there are no reports on its pathogenicity. *Coslenchus costatus*, which has similar feeding habits, was very rare at SL2. *Cephalenchus* species can cause some damage to plants (Brzeski 1998) but *C. leptus* occurred only at relatively low populations densities (0.1–0.9% of all nematodes) at VWL1 and VWL2. Feeding habits of *Lelenchus leptosoma* are unknown (Brzeski 1998) but because of its thin and delicate stylet this species may be a fungivore rather than a plant parasite. The small species of *Filenchus* predominating at the sites studied are fungivores (Okada et al. 2005).

Taking the wide variation in the feeding habits of the species in the family Tylenchidae into consideration the proportion (B+F)/(PP+RFF) and NFR3 at VWL1, VWL2 and SL1 can be used to evaluate the participation of nematodes in the detritus and grazing food webs. The values of these community indices indicate that nematodes at these sites participate roughly equally in both food webs. Nevertheless, very high population densities of plant parasites at SL2 indicate strong mineralization of nutrients via grazing at this site while at VWL3 nematodes seem to be more involved in the detritus food web. The species composition of the whole plant-feeding group (RFF+PP) may imply that the plant root production at the highest elevation was lower than at the lowest elevation. Despite low values of EI and high values of CI, which should indicate a greater activity of fungi than bacteria in the soil (Ferris et al. 2001), proportion B/F and NCR1 had values indicating a greater role of bacteria than fungi (except at VWL2). The proportion B/(F+RFF) and NCR2 are correct for site VWL3 (because of the predominance of *Filenchus* in RFF) and these criteria indicate that bacteria are more active in the detritus food web.

It is evident that the information that community indices can provide about the role of nematodes in soils is species-dependent and suffers from an insufficient knowledge of the feeding habits, modes of reproduction and rates of metabolism of individual species. Their biological traits are approximated by various kinds of "weights" applied to abundance data, such as *c-p* values (Bongers 1990, Bongers & Bongers 1988) for calculating various forms of maturity indices and guild-specific weightings in the matrix framework for soil food web diagnostics (Ferris et al. 2001). Most recently, Ferris (2010) and Sieriebriennikov et al. (2014) formulated the metabolic footprint concept to evaluate the role of nematodes in soils using nematode *c-p* class and body weight in a simplified model of nematode production and respiration and carbon flow through a food web. Unfortunately, the metabolic footprint concept omits the temperature-specific coefficient from the calculation of nematode species respiration. This is serious because biotas at different elevations experience different long-term air ambient temperatures and the aim of this study is determine whether there are likely to be changes in alpine ecosystems induced by a simulated short-term increase in the air ambient temperatures. Although the difference in the temperature at the highest and lowest of the sites studied is thought to be at most 3 °C (Kopáček et al. 2014) there were marked differences in the nematode assemblages (Figs 1–2). For current purposes, biomass and metabolic footprint calculations are not included in this pilot survey of nematode assemblages. And the present results are in agreement with Yeates & van der Meulen's (1996) conclusion that it may not be reasonable to expect a global "nematode index" of "soil health" or ecosystem condition.

The values of the Maturity Indices are relatively low because of the prevalence of bacterivores and plant feeders (sensu lato) with *c-p* values of 2. *Cp*-3 plant parasites were abundant at SL2, but no *cp*-4 (Trichodoridae) and *cp*-5 (Longidoridae) species occurred at the sites studied. They are generally rare in grassland ecosystems in the Carpathian region (Popovici 1998, Lišková & Čerevková 2005, Čerevková 2006, Háněl & Čerevková 2006). At the lowest altitude at site SL2 the relatively high values of the PPI/MI ratio indicated a slight nutrient disturbance (enrichment) of the soil food web (Bongers et al. 1997), whereas other sites were rather nutrient poor in comparison. The values of the Shannon index of diversity were relatively low, especially at VWL1 where *Aglenchus agricola*, *Acrobeloides tricornis* and *Plectus* spp. strongly predominated. Nevertheless, abundant populations of omnivores and predators together with high values of SI indicate the naturalness and undisturbed condition of nematode assemblages and the soil environment in the alpine ecosystems studied.

Other soil fauna

The abundance of Enchytraeidae, Rotifera and Tardigrada collectively are within the range of abundance values recorded in different ecosystems in Central Europe where these animals were studied together with nematodes, see e.g. Háněl (2003, 2004).

CONCLUSIONS

Nematode assemblages in all the alpine meadows studied consisted of abundant populations of omnivores and predators, which together with the high values of the Structure Index indicate a natural and undisturbed soil environment. Bacterivore general opportunists (*Plectus*, *Acrobeloides*) were dominant at all sites, but there was a marked gradient in the species composition of plant feeding nematodes sensu lato (root-fungal feeders + plant parasites). Small fungivore *Filenchus* were present at all sites. Epidermal cell and root hair feeding *Aglenchus* predominated at higher elevations. Among plant parasites *Paratylenchus* was present everywhere except at the highest site and *Helicotylenchus* and *Nagelus* predominated at the lowest site. However, the great variety of feeding and life history traits of the plant feeders and patchy distribution of many species complicate the use of nematode community indices for assessing the functioning of soil food webs and the reliable application of univariate statistics. On the other hand, Cluster Analysis and Principal Components Analysis proved to be an effective way of distinguishing nematode assemblages and clearly showed that the nematode fauna at the highest site (ca. 2200 m a. s. l.) differed from that at lowest site (ca. 1760 m a. s. l.). Therefore, we can expect that the transplantation of blocks of soil from high to lower elevations will be, in some way, reflected in the composition of the nematode assemblages.

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REFERENCES

A’Bear A. D., Jones T. H. & Boddy L. 2014: Potential impacts of climate change on interactions among saprotrophic cord-forming fungal mycelia and grazing soil invertebrates. *Fungal Ecology* **10**: 34–43.

Adams G. A. & Wall D. H. 2000: Biodiversity above and below the surface of soils and sediments: Linkages and implications for global change. *BioScience* **50**: 1043–1048.

Andrássy I. 1958: Erd- und Süsswassernematoden aus Bulgarien. *Acta Zoologica Academiae Scientiarum Hungaricae* **4**: 1–88.

Andrássy I. 1984: *Klasse Nematoda* (*Ordnungen Monhysterida*, *Desmoscolecida*, *Araeolaimida*, *Chromadorida*, *Rhabditida*). Berlin: Akademie–Verlag, 509 pp.

Andrássy I. 1986: The genus Eudorylaimus Andrássy, 1959 and the present status of its species (Nematoda: Qudsianematidae). *Opuscula Zoologica Instituti Zoosystematici Universitatis Budapestinensis* **22**: 3–42.

Andrássy I. 1991: The superfamily Dorylaimoidea (Nematoda) – a review. Family Qudsianematidae, II. *Opuscula Zoologica Instituti Zoosystematici Universitatis Budapestinensis* **24**: 3–55.

Andrássy I. 2005: *Free-living Nematodes of Hungary* (*Nematoda Errantia*). *Volume I*. Budapest: Hungarian Natural History Museum & Systematic Zoology Research Group of the Hungarian Academy of Sciences, 518 pp.

Andrássy I. 2007: *Free-living Nematodes of Hungary* (*Nematoda Errantia*). *Volume II*. Budapest: Hungarian Natural History Museum & Systematic Zoology Research Group of the Hungarian Academy of Sciences, 496 pp.

Andrássy I. 2009: *Free-living Nematodes of Hungary* (*Nematoda Errantia*). *Volume III*. Budapest: Hungarian Natural History Museum & Systematic Zoology Research Group of the Hungarian Academy of Sciences, 608 pp.

Bardgett R. D., Bowman W. D., Kaufmann R. & Schmidt S. K. 2005: A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution* **20**: 634–641.

Berkelmans R., Ferris H., Tenuta M. & van Bruggen A. H. C. 2003: Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil managemant. *Applied Soil Ecology* **23**: 223–235.

Boag B. & Yeates G. W. 1998: Soil nematode biodiversity in terrestrial ecosystems. *Biodiversity and Conservation* 7: 617–630.

Bongers T. 1990: The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* **83**: 14–19.

Bongers T. 1999: The Maturity Index, the evolution of nematode life history traits, adaptive radiation and cp-scaling. *Plant and Soil* **212**: 13–22.

Bongers T. & Bongers M. 1998: Functional diversity of nematodes. *Applied Soil Ecology* **10**: 239–251.

Bongers T. & Ferris H. 1999: Nematode community structure as a bioindicator in environmental monitoring. *Trends in Ecology and Evolution* **14**: 224–228.

Bongers T., van der Meulen H. & Korthals G. 1997: Inverse relationship between the nematode maturity index and plant parasite index under enriched nutrient conditions. *Applied Soil Ecology* **6**: 195–199.

Boström S. 1989: The taxonomic position of some teratocephalid nematodes – a scanning electron microscope study. *Revue de Nématologie* **12**: 181–190.

Boström S. & Holovachov O. 2001: Study of Teratocephalidae (Nematoda) from the Ukraine. II. Description of a population of Teratocephalus tenuis Andrássy, 1958 with a discussion of male sexual characters. *Russian Journal of Nematology* **9**: 69–76.

Boström S., Holovachov O. & Susulovsky A. 2000: Study of Teratocephalidae (Nematoda) from the Ukraine. Description of a population of Teratocephalus de Man, 1876 with a compendium on species from the "*lirellus*-group". *Russian Journal of Nematology* **8**: 139–145.

Brzeski M. W. 1998: *Nematodes of Tylenchina in Poland and Temperate Europe*. Warszawa: Muzeum i Instytut Zoologii Polska Akademia Nauk, 397 pp.

Brzeski M. W. 1999: Some Tylenchida (Nematoda) from Greenland. *Journal of Nematode Morphology and Systematics* **2**: 89–106.

Brzeski M. W. & Háněl L. 1999: Paratylenchinae: postembryonic developmental stages of Paratylenchus straeleni (De Coninck, 1931) and P. steineri Golden, 1961 (Nematoda: Tylenchulidae). *Nematology* **1**: 673–680.

Čerevková A. 2006: Nematode communities in three types of grassland in the Slovak Republic. *Helminthologia* **43**: 171–176.

Čerevková A. & Renčo M. 2009: Soil nematode community changes associated with windfall and wildfire in forest soil at the High Tatras National Park, Slovak Republic. *Helminthologia* **46**: 123–130.

Čerevková A., Renčo M. & Cagáň L. 2013: Short-term effects of forest disturbances on soil nematode communities in European mountain spruce forests. *Journal of Helminthology* **87**: 376–385.

Ciobanu M., Popovici I., Guerrero P. & Peña-Santiago R. 2010: Nematodes of the order Dorylaimida from Romania. The genus Enchodelus Thorne, 1939. 3. Species with rounded tail and long odontostyle. *Nematology* **12**: 609–618.

Darby B. J., Neher D. A., Housman D. C. & Belnap J. 2011: Few apparent short-term effects of elevated temperature and increased frequency of summer precipitation on the abundance and taxonomic diversity of desert soil micro- and meso-fauna. *Soil Biology & Bichemistry* **43**: 1474–1481.

Ettema C. H. 1998: Soil nematode diversity: Species coexistence and ecosystem function. *Journal of Nematology* **30**: 159–169.

Ferris H. 2010: Form and function: Metabolic footprints of nematodes in the soil food web. *European Journal of Soil Biology* **46**: 97–104.

Ferris H., Bongers T. & de Goede R. G. M. 2001: A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Applied Soil Ecology* **18**: 13–29.

Franz H. 1950: *Bodenzoologie als Grundlage der Bodenpflege. Mit besonderer Berücksichtigung der Bodenfauna in den Östalpen und im Donaubecken*. Berlin: Akademie-Verlag, 316 pp.

Geraert E. 2008: *The Tylenchidae of the World. Identification of the Family Tylenchidae* (*Nematoda*). Gent: Academia Press, 540 pp.

Gerber K. 1991: Einige Nematoden aus Alpinen Böden in den Hohen Tauern (Österreich). *Linzer Biologische Beiträge* **23**: 661–700.

Guerrero P., Liébanas G. & Peña-Santiago R. 2008: Nematodes of the order Dorylaimida from Andalucía Oriental, Spain. The genus Enchodelus Thorne, 1939. 2. Description of three known species with rounded tail and long odontostyle. *Nematology* **10**: 451–470.

Guerrero P. & Peña-Santiago R. 2007: Redescription of Enchodelus species studied by Thorne in 1939 (Dorylaimida: Nordiidae). *Nematology* **9**: 93–121.

Gupta V. V. S. R. & Yeates G. W. 1997: Soil microfauna as bioindicators of soil health. Pp.: 201–233. In: Pankhurst C. E., Doube B. M. & Gupta V. V. S. R. (eds.): *Biological Indicators of Soil Health*. Wallingford & New York: CAB International, 451 pp.

Háněl L. 1994a: Volně žijící hlístice (Nematoda) SPR Velká kotlina a některých dalších stanovišť v Jeseníkách [Free-living nematodes (Nematoda) of the State Natural Reserve Velká kotlina and some other localities in the Jeseníky Mts.]. *Časopis Slezského Zemského Muzea*, *Série A*, *Vědy Přírodní* **43**: 211–217 (in Czech, with an abstract in English).

Háněl L. 1994b: Půdní hlístice (Nematoda) některých lokalit v Krkonoších [Soil nematodes (Nematoda) of some localities in the Krkonoše Mts.]. *Opera Corcontica* **31**: 105–113 (in Czech, with an abstract in English).

Háněl L. 1996a: Comparison of soil nematode communities in three spruce forests at the Boubín Mount, Czech Republic. *Biologia*, *Bratislava* **51**: 485–493.

Háněl L. 1996b: Soil nematodes in five spruce forests of the Beskydy mountains, Czech Republic. *Fundamental and Applied Nematology* **19**: 15–24.

Háněl L. 1996c: Soil nematodes (Nematoda) in forest ecosystems of the Křivoklátsko Biosphere Reserve, Czech Republic. *Časopis Národního Muzea*, *Řada Přírodovědná* **165**: 91–102.

Háněl L. 1998: Soil nematodes of grassland-meadow ecosystems in the Czech Republic, Central Europe. Pp.: 95–102. In: de Goede R. G. M. & Bongers T. (eds.): *Nematode Communities of Northern Temperate Grassland Ecosystems*. Gießen: Focus Verlag, 338 pp.

Háněl L. 1999: Fauna of soil nematodes (Nematoda) in Trojmezná hora Reserve. *Silva Gabreta* **3**: 89–94.

Háněl L. 2003: Recovery of soil nematode populations from cropping stress by natural secondary succession to meadow land. *Applied Soil Ecology* **22**: 255–270.

Háněl L. 2004: Response of soil nematodes inhabiting spruce forests in the Šumava Mountains to disturbance by bark beetles and clear-cutting. *Forest Ecology and Management* **202**: 209–225.

Háněl L. 2010: An outline of soil nematode succession on abandoned fields in South Bohemia. *Applied Soil Ecology* **46**: 355–371.

Háněl L. 2013a: Free-living nematodes (Nematoda) of the Rokytská slať and the Chalupská slať peat bogs in the Šumava Mts., Czech Republic. P.: 25. In: Tajovský K. (ed.): *12th Central European Workshop on Soil Zoology. Abstract Book*. České Budějovice: Institute of Soil Biology BC AS CR, v.v.i., 66 pp.

Háněl L. 2013b: Distribution of trophic groups of soil nematodes (Nematoda) and soil food web condition in inverse gorges in the České Švýcarsko National Park (Czech Republic). *Acta Societatis Zoologicae Bohemicae* **77**: 87–101.

Háněl L. & Čerevková A. 2006: Diversity of soil nematodes in meadows of the White Carpathians. *Helminthologia* **43**: 109–116.

Háněl L. & Čerevková A. 2010: Species and genera of soil nematodes in forest ecosystems of the Vihorlat Protected Landscape Area, Slovakia. *Helminthologia* **47**: 123–135.

Hoschitz M. 2003: Moss-living nematodes from an Alpine summit (Dachstein, Austria). *Verhandlungen der Zoolologisch-Botanischen Gesellschaft in Österreich* **140**: 93–98.

Hoschitz M. & Kaufmann R. 2004a: Soil nematode communities of Alpine summits – site differentiation and microclimatic influences. *Pedobiologia* **48**: 313–320.

Hoschitz M. & Kaufmann R. 2004b: Nematode community composition in five alpine habitats. *Nematology* **6**: 737–747.

Karegar A., De Ley P. & Geraert E. 1997: Three teratocephalid nematodes from Iran. *Fundamental and Applied Nematology* **20**: 459–471.

Kopáček J., Stuchlík E. & Šantrůčková H. 2014: *Rozlišení vlivů změn v chemismu prostředí a klimatu na biogeochemické procesy a biodiversitu přírodních půd a vod alpinského pásma* [*Disentangling the Effects of Changing Environmental Chemistry and Climate on Biogeochemistry and Biodiversity of Natural Alpine Soils and Waters*]. Unpubl. Project Proposal No. 14-09231S, 43 pp (in Czech and English).

Lišková M. & Čerevková A. 2005: Nematode communities of river banks and adjacent meadows in the Slovak Republic. *Helminthologia* **42**: 223–232.

Lišková M. & Čerevková A. 2011: *Nematodes of the Slovak Republic* (*Free-living*, *Plant and Insect Nematode Species*). Bratislava: VEDA, Publishing House of the Slovak Academy of Sciences, 184 pp.

Lišková M., Čerevková A. & Háněl L. 2008: Nematode communities of forest ecosystems in association with various soil orders. *Russian Journal of Nematology* **16**: 129–142.

Loof P. A. A. 1975: Dorylaimoidea from some subantarctic islands. *Nematologica* **21**: 219–255.

Mosier A. R. 1998: Soil processes and global change. *Biology and Fertility of Soils* **27**: 221–229.

Nielsen U. N., Wall D. H., Adams B. J. & Virginia R. A. 2011: Antarctic nematode communities: observed and predicted responses to climate change. *Polar Biology* **34**: 1701–1711.

Okada H., Harada H. & Kadota I. 2005: Fungal-feeding habits of six nematode isolates in the genus Filenchus. *Soil Biology & Biochemistry* **37**: 1113–1130

Pauli H., Gottfried M., Hohenwallner D., Hülber K., Reiter K., Grabherr G. (eds.) 2001: *GLORIA – Global Observation Research Initiative in Alpine Environments*, *The Multi-Summit Approach*, *Field Manual*, *Third version*. *Annexes I*, *II*, *III*.Vienna: Institute of Ecology and Conservation Biology – University of Vienna, 43 pp.

Popovici I. 1984: Nematode abundance, biomass and production in a beech forest ecosystem. *Pedobiologia* **26**: 205–219.

Popovici I. 1997: Diversity and distribution of terrestrial nematodes in natural ecosystems from the Eastern Carpathians (Romania). *Anuarul Muzeului Naţional al Bucovinei* **14**: 23–33.

Popovici J. 1998: Structure of nematode communities in mountain grasslands from Romania. Pp.: 221–240. In: de Goede R. G. M. & Bongers T. (eds.): *Nematode Communities of Northern Temperate Grassland Ecosystems*. Gießen: Focus Verlag, 338 pp.

Popovici I. & Ciobanu M. 2000: Diversity and distribution of nematode communities in grasslands from Romania in relation to vegetation and soil characteristics. *Applied Soil Ecology* **14**: 27–36.

Ruess L. 1995: Nematode fauna in spruce forest soils: a qualitative/quantitative comparison. *Nematologica* **41**: 106–124.

Ruess L. & Funke W. 1995: Nematode fauna of a spruce stand associated with forest decline. *Acta Zoologica Fennica* **196**: 348–351.

Rusek J. 1993: Air-pollution-mediated changes in Alpine ecosystems and ecotones. *Ecological Applications* **3**: 409–416.

Šály A. 1983: *Voľne žijúce nematódy v SSR* [*Free-Living Nematodes in the Slovak Socialist Republic*]. Bratislava: Veda, Vydavateľstvo Slovenskej akadémie vied, 160 pp (in Slovak, with a summary in English).

Šály A. 1985: Production of free living nematodes in the Protected Landscape Area of the Slovak Paradise. *Ekológia* (*ČSSR*) **4**: 185–209.

Šály A. & Žuffa M. 1980: Voľne žijúce nematódy Gaderskej doliny, Blatnickej doliny, Seleneckej doliny a Štátnej prírodnej rezervácie Padva vo Veľkej Fatre [Nematodes living free in Gader's Valley, Blatnica Valley, Selenec Valley and State Natural Reservation Padva in Veľká Fatra]. *Ochrana Prírody*, *Výskumné práce z ochrany prírody* **3C**: 5–51 (in Slovak, with abstracts in Russian, German and English).

Šály A. & Žuffa M. 1985: Voľne žijúce hlístovce (Nematoda) Štátnej prírodnej rezervácie Suchý v Chránenej krajinnej oblasti Malá Fatra [Free-living nematodes of the State Nature Reserve Suchý in the Protected Territory Malá Fatra]. *Ochrana Prírody* **6**: 79–93 (in Slovak, with abstracts in Russian, English and German).

Schlaghamerský J., Devetter M., Háněl L., Tajovský K., Starý J., Tuf I. H. & Pižl V. 2014: Soil fauna across Central European sandstone ravines with temperature inversion: From cool and shady to dry and hot places. *Applied Soil Ecology* **83**: 30–38.

Shahina F. 1996: A diagnostic compendium of the genus Aphelenchoides Fischer, 1894 (Nematoda: Aphelenchida) with some new records of the group from Pakistan. *Pakistan Journal of Nematology* **14**: 1–32.

Sieriebriennikov B., Ferris H. & de Goede R. G. M. 2014: NINJA: An automated calculation system for nematode-based biological monitoring. *European Journal of Soil Biology* **61**: 90–93.

Ter Braak C. J. F. & Šmilauer P. 2002: *CANOCO Reference Manual and CanoDraw for Windows User's Guide*: *Software for Canonical Community Ordination* (*version 4.5*). Ithaka, NY: Microcomputer Power, 500 pp.

van der Putten W. H., Bardgett R. D., de Ruiter P. C., Hol W. H. G., Meyer K. M., Bezemer T. M., Bradford M. A., Christensen S., Eppinga M. B., Fukami T., Hemerik L., Molofsky J., Schädler M., Scherber C., Strauss S. Y., Vos M. & Wardle D. A. 2009: Empirical and theoretical challenges in aboveground–belowground ecology. *Oecologia* **161**: 1–14.

Verhoef H. A. & Brussaard L. 1990: Decomposition and nitrogen mineralization in natural and agroecosystems – the contribution of soil animals. *Biogeochemistry* **11**: 175–211.

Vinciguerra M. T. 1988: Nematodi di ambienti forestali ed alpini delle Dolomiti [Nematodes from forest- and alpine environments of the Dolomites]. *Studi Trentini di Scienze Naturali*, *Acta Biologica* **64** Suppl.: 467–480 (in Italian, with an abstract in English).

Wasilewska L. 1974: Analysis of a sheep pasture ecosystem in the Pieniny Mountains (the Carpathians). XIII. Quantitative distribution, respiratory metabolism and some suggestion on production of nematodes. *Ekologia Polska* **22**: 651–668.

Wasilewska L. 1994: The effect of age of meadows on succession and diversity in soil nematodes nematode communities. *Pedobiologia* **38**: 1–11.

Wasilewska L. 1996: The influence of acid rain on soil nematode communities: a comparison of contaminated habitats in the belt of the Karkonosze and Izerskie Mountains (south-west Poland) with uncontaminated areas in other regions of Poland. *Ekologia Polska* **44**: 73–110.

Wasilewska L. 1997: Soil invertebrates as bioindicators, with special reference to soil-inhabiting nematodes. *Russian Journal of Nematology* **5**: 113–126.

Wilson M. J. & Kakouli-Duarte T. (eds.) 2009: *Nematodes as Environmental Indicators*. Wallingford, UK: CAB International, 326 pp.

Wood F. H. 1973: Nematode feeding relationships. Feeding relationships of soil-dwelling nematodes. *Soil Biology & Biochemistry* **5**: 593–601.

Wu J., Xiong J., Hu C., Shi Y., Wang K. & Zhang D. 2015: Temperature sensitivity of soil bacterial community along contrasting warming gradient. *Applied Soil Ecology* **94**: 40–48.

Yeates G. W. 1994: Modification and qualification of the nematode maturity index. *Pedobiologia* **38**: 97–101.

Yeates G. W. 2003: Nematodes as soil indicators: functional and biodiversity aspects. *Biology and Fertility of Soils* **37**: 199–210.

Yeates G. W. & Bongers T. 1999: Nematode diversity in agroecosystems. *Agriculture*, *Ecosystems and Environment* **74**: 113 – 135.

Yeates G. W., Bongers T., de Goede R. G. M., Freckman D. W. & Georgieva S. S. 1993: Feeding habits in soil nematode families and genera – and outline for soil ecologists. *Journal of Nematology* **25**: 315–331.

Yeates G. W. & van der Meulen H. 1996: Recolonization of methyl-bromide sterilized soils by plant and soil nematodes over 52 months. *Biology and Fertility of Soils* **21**: 1–6.

Zell H. 1986: Nematoden eines Buchenwaldbodens. 6. Die Dorylaimen (Nematoda, Dorylaimida). *Carolinea* **44**: 91–118.

Žuffa M. & Šály A. 1986: Náčrt voľne žijúcich hlístovcov Štátnej prírodnej rezervácie Šrámková [Free-living nematodes of the State Nature Reserve Šrámková]. *Ochrana Prírody* **7**: 301–315 (in Slovak, with abstracts in Russian, English and German).