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Distribution of trophic groups of soil nematodes (Nematoda) and soil food web condition in inverse gorges in the České Švýcarsko National Park (Czech Republic)

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Abstract. Trophic groups of soil nematodes were studied in three gorges (Hauschengrund HG, Brtnický potok BP and Kachní potok KP) in the České Švýcarsko National Park. Soil samples were collected from the bottom, the middle and the uppermost parts (zones) of the sides of the gorges in June and October 2008, 2009 and 2010. Gorges themselves had no significant effect on the total nematode abundance and trophic groups except for plant parasites (low abundance in KP) and omnivores (greater abundance in BP). Sampling date significantly affected the abundance of fungivores and root-fungal feeders, and the abundance of all nematodes. Zonation affected the abundance of all trophic groups. Root-fungal feeders and fungivores were most abundant on the slopes, predators and insect parasites mostly occurred at the bottoms of the gorges. Cluster analysis indicates that the zonation has a marked effect on the trophic structure of nematode assemblages, although there were many overlaps between-zones associated with seasonal fluctuations in fungivores and root-fungal feeders. Bacterivores, fungivores, root-fungal feeders and omnivores were significantly negatively, and plant parasites and predators significantly positively correlated with soil bulk density. The decrease in soil bulk density generally corresponded with the accumulation of soil organic matter and decrease in soil pH in the upper parts of the gorges. Ratios between nematode trophic groups indicate greater participation of bacteria than fungi in the detritus food web and greater rate of nutrient mineralization via the grazing food web at the bottoms than on the slopes of the gorges. Greater trophic diversity of nematode assemblages at the bottoms of the gorges coincided with greater species and generic richness.

Key words. Soil zoology, ecology, Nematoda, trophic group, soil food web, forest, inverse gorge, Bohemian Switzerland National Park, Czech Republic.

INTRODUCTION

Nematodes are a diverse group of soil micro-fauna (Boag & Yeates 1998) and feed on a great variety of soil organisms (Yeates et al. 1993). Feeding habits combine with different life-history strategies of species on an *r*/*K* scale and so it is possible to distinguish various functional guilds of soil nematodes, which occur in different segments of the soil food web (Bongers & Bongers 1998). Abundance of trophic groups and ratios between trophic groups are good indicators of activity of bacterial- and fungal-based energy channels in detritus food webs and root-based energy channels in grazing food webs (Wasilewska 1997, Ferris et al. 2001, Yeates 2003). Therefore, nematodes can indicate changes in soil food web conditions during build-up ecosystem development in primary and secondary succession towards climax (de Goede et al. 1993, Austin et al. 2009, Háněl 2001, 2010a) as well as senescence and ecosystem decline (Williamson et al. 2005).

The landscape of the České Švýcarsko National Park is mostly covered with climax forest ecosystems, which are little affected by human intervention. Geologically, this territory was a plateau of cretaceous sandstones partly disintegrated by tertiary folding and volcanism. As

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a result of weathering and erosion the landscape developed a diverse relief intersected by numerous gorges in the recent quaternary. A preliminary survey of soil nematodes (Háněl 2010b) revealed that a relatively poor nematode fauna of smaller species inhabited the top parts of the gorges (remnants of the primary plateau). At the bottoms of the gorges (secondary, geologically younger structures) the nematode fauna is richer and frequently includes larger species. The data also indicates a high abundance of fungivorous nematodes at the tops of the gorges whereas at the bottoms the trophic structure of nematode assemblages was more balanced. Nevertheless, the abundance of nematode trophic groups can undergo greater seasonal fluctuations than the richness of nematodes. Therefore, the period of the research was extended.

The aim of this part of the study was: (i) to evaluate the trophic composition of nematode assemblages from the tops to the bottoms of the gorges and (ii) to assess soil food web conditions in the gorges as indicated by the nematodes.

MATERIAL AND METHODS

The area of the České Švýcarsko National Park (Bohemian Switzerland NP) is 79.25 km^2. Parent rocks are mainly cretaceous sandstones susceptible to weathering, which results in landscape relief of an alternating pattern of horizontal plateaux, vertical valleys and narrow gorges, and dissected transitional surfaces. The climate is generally temperate with mean annual air temperatures of 6–8ºC and precipitation of about 600–900 mm, but often with temperature inversions due to the diverse relief of the landscape. The bottoms of the gorges are colder than their tops. Soils are mostly arenic podzols and depending on local conditions acid cambisols and rankers with accumulation of raw humus. Pine forests cover the tops of the plateaux, beech and spruce the lower parts of the sides and deciduous alluvial forests at the bottoms of some inverse gorges (Culek 1996).

Nematodes were studied in three inverse gorges Hauschengrund (HG), Brtnický potok (BP) and Kachní potok (KP). The localities cited in the text will be abbreviated as indicated above. The numbers 1 and 5 each indicate five samples collected from the uppermost parts (zones) of the sides of gorges on the dates specified below. Similarly, the numbers 2 and 4 each indicate five samples taken from the middle parts of the sides of the gorges. The number 3 indicates five samples collected from the bottoms of the gorges. There is a permanent stream in BP3, whereas HG3 and KP3 have periodical streams. Details on localities were briefly summarised in my previous paper (Háněl 2010b, Table 1). Sampling dates were 24–25 June 2008 (*a*), 14–15 October 2008 (*b*), 24 June 2009 (*c*), 5–6 October 2009 (*d*), 22–23 June 2010 (*e*) and 5–6 October 2010 (*f*).

The soil samples were taken using a cylindrical soil corer of cross-sectional area 10 cm^2 inserted down to a depth of 10 cm (if possible). The soil in each sample (five per zone, 75 on each sampling date, total n=450) was weighed, carefully mixed and a part was dried to determine the water content. Soil moisture was determined gravimetrically, soil was dried for 48 h at 25 °C, than for 4 h at 65 °C and finally for 4 h at 105 °C. Soil bulk density was expressed in grams of soil per cm^3 after drying at 105 °C. Chemical analyses of soil samples collected in autumn 2008 were done by AGROLA Ltd. using standardized methods of Zbíral (1995).

Nematodes were isolated from approximately 15 ml of mixed soil, which according to sample properties represented 3.0 to 10 grams of the substrate, using modified Baermann funnels and mounted in glycerol on slides (Háněl 2010b). Nematodes in each sample (total sample n=450) were studied separately. Then the nematode numbers were adjusted to give the total number per sample and converted to a per m^2 basis for each zone (mean of five samples) and sampling date (total zone & date n=90). Altogether 103,894 nematode specimens were determined to species/genus level.

Nematodes were sorted into the following trophic groups: bacterivores (B), fungivores (F), root-fungal feeders (RFF), plant parasites (PP), omnivores (O), predators (P) and insect parasites (IP). These abbreviations are used in the text. Ratios between trophic groups used to evaluate soil food web condition were calculated for each zone and sampling date as follows. Marked increases in the values of Nematode Channel Ratios NCR=B/(B+F) (Yeates 2003) and NCR2= B/(B+F+RFF) (Háněl 2010a) indicate greater participation of bacteria than fungi in the detritus food web. Decreasing values of (B+F)/PP, and (B+F+RFF)/PP ratios (Wasilewska 1997, 2004) can indicate faster nutrient and energy cycling via a grazing food web with abundant plant-feeding nematodes. Trophic diversity index $T=1/\sum(p_i)^2$ in which p_i is the proportion of trophic group i in the nematode community was calculated according to Heip et al. (1988) in Freckman & Ettema (1993). High values of the index T indicate a more balanced trophic structure of nematode populations.

Statistical analyses were performed using STATISTICA (StatSoft 2001). A great spatio-temporal variability in soil nematodes and soil properties seriously complicated the application of statistical tests to evaluate differences between gorges and their parts. Data transformations, which were applied to meet ANOVA assumptions, such as logarithmic for abundance, square-root for richness, arcsine for proportions, were not always effective. To make analyses manageable

Table 1. Mean values of gravimetric soil moisture (moisture %) and soil bulk density (BD g/cm^3) in individual zones in the inverse gorges (HG, BP and KP). One way ANOVA was performed on untransformed data, $F_{(14,435)}$. The same letters (a, b, c, d, e, f, g) indicate homogeneous groups of means detected by Fisher LSD post-hoc test at *alpha* = 0.05. Because Levene's test detected heterogeneity of variances a Kruskal-Wallis ANOVA (K-W ANOVA, H(14,N=450)), followed by post-hoc multiple comparison of mean ranks of all pairs of groups, was calculated and homogeneous groups are indicated by the same letters (u, w, x, y, z). Other soil parameters are data from a single survey, carried out in autumn 2008, Ca, Mg, K, Na, and Pv (water-soluble phosphorus) are expressed in mg per kg of dry soil. pH = pH/$CaCl_2$

zones	moisture %			BD g/cm^3			C_{ox} %	pH	Ca	Mg	K	Na	Pv
ANOVA	F=4.95; p<0.01			F=10.5; p<0.01									
Levene's test	F=3.49; p<0.01			F=2.71; p<0.01									
K-W ANOVA	H=66.6; p<0.01			H=111.4, p<0.01									
HG1	xyz	28.9	de	wxyz	0.67	de	9.00	2.80	58	5	22	10	5
HG2	wxyz	35.4	bc	uwxy	0.79	cd	10.80	2.73	110	10	29	10	5
HG3	wxy	38.9	ab	uwxy	0.77	cd	9.89	3.46	212	101	83	10	5
HG4	wxyz	36.4	ab	uwx	0.84	bc	5.61	3.02	50	5	15	10	5
HG5	xyz	30.1	cde	xyz	0.59	ef	15.30	2.72	108	11	35	10	5
BP1	wxy	38.7	ab	z	0.42	g	20.30	2.69	81	7	50	10	5
BP2	xyz	30.3	cde	wxyz	0.68	de	7.94	2.83	51	5	31	10	5
BP3	z	27.3	e	u	1.00	a	4.70	3.83	165	22	57	10	9
BP4	wxyz	38.6	ab	xyz	0.55	efg	21.10	2.88	50	19	150	10	6
BP5	wx	38.2	ab	z	0.41	g	21.70	2.76	78	15	77	10	6
KP1	wxyz	34.2	bcd	xyz	0.61	ef	10.60	2.79	197	16	41	10	5
KP2	w	42.6	a	yz	0.50	fg	14.10	2.80	87	13	50	10	5
KP3	yz	27.4	e	uw	0.98	ab	3.87	3.90	174	29	49	10	19
KP4	wxyz	37.9	ab	wxyz	0.64	def	10.30	2.82	65	15	56	10	6
KP5	z	27.2	e	xyz	0.61	ef	20.50	2.80	163	27	107	11	5

untransformed soil gravimetric moisture and soil bulk density data and ln(x+1) transformed nematode data were used in ANOVA, cluster analysis and Pearson correlation coefficient r. If the heterogeneity of variances in ANOVA was detected, data were also analysed by means of non-parametric statistics. Non-parametric tests (Kruskal-Wallis ANOVA, Spearman correlation coefficient R) were carried out using untransformed data.

RESULTS

Soil properties

The mean soil moisture of all 450 samples was 34.1%. In individual samples the moisture varied from 6.5% to 73.5% but did not significantly differ between gorges (HG 33.9%, PB 34.6%, KP 33.9%). Soil moisture significantly differed between sampling dates (one-way ANOVA: $F_{(5,444)}$=9.34, p<0.01; Levene's test: $F_{(5,444)}$=0.23, p=0.95). The significantly lowest soil moisture was that on the first sampling date (June 2008; 26.6%). The greatest moisture of 39.1% was recorded in October 2010 and was significantly greater than on other sampling dates. An exception was the moisture in June 2009 (38.2%), which also differed significantly from that recorded in October 2008 (32.1%). Soil moisture in individual zones was significantly different. Nevertheless, heterogeneity of variance was detected and Kruskal-Wallis ANOVA was performed. There is a detailed report in Table 1, which shows that the highest values of soil moisture were recorded at the bottom of gorge HG, while the bottoms of the BP and KP gorges had the lowest values of soil moisture (also the zone KP5).

The mean bulk density of soil of all 450 samples was 0.67 g×cm^{-3} and varied from 0.09 (only organic material) to 1.85 g×cm^{-3} (almost only sand with some roots) in individual samples and dif-

fered significantly between gorges (HG 0.73[a], PB 0.61[b], KP 0.67[ab]; one-way ANOVA: $F_{(2,447)}$=4.75, p=0.01; Levene's test: $F_{(2,447)}$=2.12, p=0.12). The effect of sampling date was insignificant. Soil bulk density in individual zones was significantly different but heterogeneity of variance was detected and data were also analyzed using Kruskal-Wallis ANOVA. There is a detailed report in Table 1. The greatest soil bulk density was recorded at the bottoms of gorges BP and KP. Soil bulk density was significantly negatively correlated with gravimetric soil moisture in individual samples (r=–0.65, p<0.01, n=450) and zones (r=–0.45, p<0.01, n=90).

Values of other soil parameters recorded in a single survey are in Table 1. C_{ox} was lower at the bottoms than on the slopes of the gorges, except in zones HG4 and HG1. Spearman rank correlation coefficients R (n=15, p<0.05) indicate that soil C_{ox} is significantly negatively correlated with soil bulk density (R=–0.89) and soil pH (R=–0.68). Soil pH is significantly positively correlated with soil bulk density (R=+0.67). Significant positive correlation coefficients were recorded between soil Mg and K (R=+0.76) and Mg and Ca (R=+0.68).

Soil temperature at a depth of 5 cm was measured at the same time as the soil samples were collected. Mean temperatures in °C on the different sampling dates and in the different zones were as follows: HG1 – 13.0, HG2 – 12.1, HG3 – 11.7, HG4 – 11.8, HG5 – 13.1; BP1 – 11.2, BP2 – 10.8, BP3 – 11.4, PB4 – 11.3, BP5 – 11.2; KP1 – 12.5, KP2 – 12.1, KP3 – 11.6, KP4 – 12.6, KP5 – 13.2. These data indicate that the soil at the bottoms of gorges HG and KP were somewhat cooler than on the slopes but such a trend in BP could not confirmed.

Nematode trophic groups and indices

The mean abundance of all soil nematodes in the area studied was $3{,}489\times10^3$ ind×m^{-2} and did not differ significantly between gorges (HG 3,105, BP 3,512 and KP $3{,}851\times10^3$ ind×m^{-2}). In individual samples the abundance of nematodes, when converted to a per square metre basis, ranged from 225 to $55{,}780\times10^3$ ind×m^{-2}. The greatest population densities of soil nematodes occurred on date *b* in October 2008 ($6{,}226\times10^3$ ind×m^{-2}), the lowest on date *e* in June 2010 ($1{,}829\times10^3$ ind×m^{-2}) and the difference was statistically significant (one-way ANOVA, $F_{(5,84)}$=4.42, p<0.01; Levene's test: $F_{(5,84)}$=1.98, p=0.09).

The mean abundance of bacterivores was 757, fungivores 963, root-fungal feeders 1,420, plant parasites 135, omnivores 203, predators 10 and insect parasites 2×10^3 ind×m^{-2}. The abundance of the different trophic groups mostly did not differ between gorges except for a slight but significant variation in the abundance of plant parasites (46–180×10^3 ind×m^{-2}; one-way ANOVA, $F_{(2,87)}$=6.23, p<0.01; Levene's test: $F_{(2,87)}$=4.25, p=0.02) and omnivores (167–252×10^3 ind×m^{-2}; one-way ANOVA, $F_{(2,87)}$=3.17, p<0.05; Levene's test: $F_{(2,87)}$=1.39, p=0.26). A greater abundance of plant parasites was recorded in BP and HG than KP, and greater abundance of omnivores in BP than in HG and KP.

Significant variations between sampling dates were recorded for fungivores (270–$2{,}437\times10^3$ ind×m^{-2}; one-way ANOVA, $F_{(5,84)}$=3.22, p=0.01; Levene's test: $F_{(5,84)}$=0.94, p=0.46) and root--fungal feeders (595–$2{,}409\times10^3$ ind×m^{-2}; one-way ANOVA, $F_{(5,84)}$=3.62, p<0.01; Levene's test: $F_{(5,84)}$=1.72, p=0.14). Their minimum and maximum abundance coincided with that recorded for all nematodes, i.e. on sampling dates *e* and *b*. Two-way ANOVA detected no interaction between gorge and sampling date for any trophic group and all nematodes.

Table 2 gives the mean abundance of nematode trophic groups and all nematodes in individual zones of the inverse gorges. Bacterivores, fungivores and root-fungal feeders generally were more abundant in the upper and middle zones than in the bottom zone. Plant parasites, predators and insect parasites were most abundant in bottom zones. The abundance of omnivores was less variable. Table 3 shows the dominance of the most abundant genera. The greatest values of dominance for the genera *Acrobeloides*, *Wilsonema*, *Aphelenchoides*, *Tylolaimophorus* and *Filenchus*

Table 2. Mean abundance (x 10^3 ind.m^{-2}) of nematode trophic groups in individual zones in the inverse gorges (HG, BP and KP). One way ANOVA was performed on *ln*(x+1) transformed abundance data, $F_{(14,75)}$. The same letters (a, b, c, d, e, f, g, h, i) indicate homogeneous groups of means detected by Fisher LSD post-hoc test at *alpha* = 0.05. When Levene's test detected heterogeneity of variances a Kruskal-Wallis ANOVA (K-W ANOVA, $H(14,N=90)$), followed by post-hoc multiple comparison of mean ranks of all pairs of groups, was also calculated and homogeneous groups are indicated by the same letters (y, z)

zones in gorges	bacterivores		fungivores		root-fungal feeders		plant parasites		omnivores		predators			insect parasites			all nematodes	
ANOVA	F=3.03; p<0.01		F=7.67; p<0.01		F=4.22; p<0.01		F=13.7; p<0.01		F=3.09; p<0.01		F=17.6; p<0.01			F=1.64; p=0.09			F=2.24; p=0.01	
Levene's test	F=1.38; p=0.18		F=1.94; p=0.04		F=1.41; p=0.17		F=1.77; p=0.06		F=1.60; p=0.10		F=7.83; p<0.01			F=5.11; p<0.01			F=1.17; p=0.32	
K-W ANOVA			H=44.5; p<0.01								H=64.7; p<0.01			H=25.0; p=0.03				
HG1	765	bc	y 849	abc	729	bcde	103	cd	119	d	zy 2		def	z 3		abc	2571	abc
HG2	465	cd	zy 394	cdef	3094	a	109	de	144	bcd	zy 0.2		ef	z 0		c	4207	abc
HG3	428	cd	zy 261	ef	546	cde	417	ab	233	abc	zy 41		b	z 12		a	1937	cd
HG4	346	d	zy 289	def	1906	a	28	efgh	158	bcd	z 0		f	z 0		c	2727	abc
HG5	784	bcd	y 1313	ab	1571	abcde	228	bc	179	bcd	zy 8		cde	z 1		bc	4086	abc
BP1	2278	a	y 2209	a	654	def	86	de	416	a	z 0		f	z 0		c	5643	ab
BP2	577	cd	zy 584	bcde	1387	ab	47	def	110	d	z 0		f	z 1		c	2705	abc
BP3	554	cd	z 44	g	225	f	755	a	238	ab	y 81		a	z 12		ab	1910	cd
BP4	430	cd	zy 357	cdef	1154	abcde	6	i	135	bcd	z 0		f	z 0		c	2082	cd
BP5	764	bc	y 1142	ab	2944	a	8	ghi	363	a	z 0		f	z 0		c	5221	ab
KP1	626	cd	zy 728	bcde	1124	abcde	34	efgh	175	bcd	zy 1		def	z 0		c	2689	bcd
KP2	794	bcd	y 1254	ab	1582	abcd	20	fghi	384	ab	z 0		f	z 0		c	4034	abc
KP3	541	cd	zy 206	f	500	ef	105	cd	99	d	zy 14		c	z 0		c	1466	d
KP4	578	cd	zy 816	abcd	2160	a	61	efg	112	cd	z 0		f	z 0		c	3727	abc
KP5	1417	ab	y 4003	a	1718	abc	10	hi	178	bcd	zy 10		cd	z 0		c	7336	a

Table 3. Dominance of the most important genera (% of the nematodes in a zone belonging to a particular genus) belonging to the trophic groups bacterivores, fungivores, root-fungal feeders and plant parasites in the inverse gorges (HG, BP, KP); *Plectus* Bastian, 1865, *Wilsonema* Cobb, 1913, *Acrobeloides* Cobb, 1924, *Rhabditis* Dujardin, 1845, *Aphelenchoides* Fischer, 1894, *Tylolaimophorus* de Man, 1880, *Tylencholaimus* de Man, 1876, *Filenchus* Andrássy, 1954, *Malenchus* Andrássy, 1968, *Aglenchus* Andrássy, 1954, *Paratylenchus* Micoletzky, 1922, *Helicotylenchus* Steiner, 1945, *Rotylenchus* Filipjev, 1936, *Trichodorus* Cobb, 1913

zones	bacterivores	fungivores	root-fungal feeders	plant parasites
HG1	*Plectus* 8.3	***Aphelenchoides* 24.6**	***Filenchus* 25.1**	*Paratylenchus* 4.0
	Wilsonema 5.8	*Tylolaimophorus* 6.3	*Malenchus* 1.0	*Helicotylenchus* <0.1
	***Acrobeloides* 11.0**			
HG2	*Plectus* 3.0	*Aphelenchoides* 5.9	***Filenchus* 19.0**	*Paratylenchus* 2.6
	Wilsonema 1.3	*Tylolaimophorus* 2.9	***Malenchus* 53.4**	
	Acrobeloides 4.3		*Aglenchus* <0.1	
HG3	*Plectus* 5.1	*Aphelenchoides* 6.1	***Filenchus* 20.3**	*Paratylenchus* 0.2
	Wilsonema 0.8	*Tylolaimophorus* 1.7	*Malenchus* 5.1	***Helicotylenchus* 19.7**
	Acrobeloides 3.0	*Tylencholaimus* 4.7	*Aglenchus* <0.1	*Rotylenchus* 0.1
	Rhabditis 1.1*			*Trichodorus* 0.2
HG4	*Plectus* 3.2	*Aphelenchoides* 5.7	***Filenchus* 35.8**	*Paratylenchus* 0.7
	Wilsonema 1.6	*Tylolaimophorus* 3.5	***Malenchus* 30.9**	*Helicotylenchus* <0.1
	Acrobeloides 3.8		*Aglenchus* 0.5	*Rotylenchus* 0.2
HG5	*Plectus* 4.5	***Aphelenchoides* 27.2**	***Filenchus* 30.4**	*Paratylenchus* 5.6
	Wilsonema 5.4	*Tylolaimophorus* 3.7	*Malenchus* 6.5	
	Acrobeloides 6.8			
BP1	*Plectus* 9.2	***Aphelenchoides* 27.5**	***Filenchus* 11.4**	*Paratylenchus* 1.5
	***Wilsonema* 13.6**	***Tylolaimophorus* 10.8**	*Malenchus* 0.1	
	Acrobeloides 8.2			
BP2	*Plectus* 7.5	***Aphelenchoides* 16.0**	***Filenchus* 47.6**	*Paratylenchus* 1.7
	Wilsonema 4.9	*Tylolaimophorus* 4.5	*Malenchus* 3.5	
	Acrobeloides 5.1			
BP3	*Plectus* 5.6	*Aphelenchoides* 1.6	*Filenchus* 3.4	***Helicotylenchus* 11.5**
	Wilsonema 0.9	*Tylolaimophorus* 0.1	*Malenchus* <0.1	***Rotylenchus* 21.4**
	Acrobeloides 2.1		*Aglenchus* 5.4	*Trichodorus* 6.0
	Rhabditis 5.9*			
BP4	*Plectus* 4.7	***Aphelenchoides* 13.9**	***Filenchus* 49.7**	*Paratylenchus* 0.2
	Wilsonema 3.4	*Tylolaimophorus* 1.8	*Malenchus* 3.7	*Helicotylenchus* <0.1
	Acrobeloides 7.2		*Aglenchus* 0.9	
BP5	*Plectus* 2.3	***Aphelenchoides* 15.0**	***Filenchus* 52.3**	*Paratylenchus* 0.2
	Wilsonema 4.4	*Tylolaimophorus* 6.1	*Malenchus* 4.1	
	Acrobeloides 7.0			
KP1	*Plectus* 4.2	***Aphelenchoides* 23.2**	***Filenchus* 38.3**	*Paratylenchus* 1.3
	Wilsonema 5.5	*Tylolaimophorus* 2.0	*Malenchus* 1.0	
	***Acrobeloides* 10.6**			
KP2	*Plectus* 3.6	***Aphelenchoides* 27.9**	***Filenchus* 35.7**	*Paratylenchus* 0.3
	Wilsonema 8.0	*Tylolaimophorus* 2.5	*Malenchus* 2.7	
	Acrobeloides 6.2		*Aglenchus* <0.1	
KP3	***Plectus* 18.3**	*Aphelenchoides* 8.1	***Filenchus* 24.2**	*Paratylenchus* 1.1
	Wilsonema 1.2	*Tylolaimophorus* 3.6	*Malenchus* 4.0	*Helicotylenchus* 3.5
	Acrobeloides 6.5	*Tylencholaimus* 0.4	*Aglenchus* 4.6	*Rotylenchus* 0.8
				Trichodorus 0.6
KP4	*Plectus* 2.1	***Aphelenchoides* 13.9**	***Filenchus* 50.4**	*Paratylenchus* 1.6
	Wilsonema 2.9	*Tylolaimophorus* 7.1	*Malenchus* 6.8	*Helicotylenchus* <0.1
	Acrobeloides 8.6			
KP5	*Plectus* 1.4	***Aphelenchoides* 53.2**	***Filenchus* 22.8**	*Paratylenchus* 0.1
	Wilsonema 3.9	*Tylolaimophorus* 0.5	*Malenchus* 0.4	
	***Acrobeloides* 12.5**			

* in other zones, except for HG3 and BP3, the dominance of *Rhabditis* was lower than 1% or the genus was absent.

Table 4. Mean values of ratios between nematode trophic groups, trophic diversity index T and mean numbers of species and genera in individual zones in the inverse gorges (HG, BP and KP). One way ANOVA was performed on *ln*(x+1) transformed data, $F_{(14,75)}$ except for (B+F)/PP and (B+F+RFF)/PP with $F_{(14,65)}$ because plant parasites were absent from some zones and the ratios could not be calculated. The same letters (a, b, c, d, e, f, g, h) indicate homogeneous groups of means detected by Fisher LSD post-hoc test at *alpha* = 0.05. When Levene's test detected heterogeneity of variances a Kruskal-Wallis ANOVA (K-W ANOVA, $H(14,N=90)$, or $H(14,N=80)$ for (B+F)/PP and (B+F+RFF)/PP), followed by post-hoc multiple comparison of mean ranks of all pairs of groups, was also calculated and homogeneous groups are indicated by the same letters (x, y, z); K-W = K-W ANOVA

zones	NCR		NCR2		(B+F)/PP		(B+F+RFF)/PP		T		genera		species	
ANOVA	F=4.49; p<0.01		F=7.26; p<0.01		F=10.1; p<0.01		F=12.8; p<0.01		F=6.25; p<0.01		F=21.1; p<0.01		F=16.2; p<0.01	
Levene' test	F=2.07; p=0.02		F=1.47; p=0.15		F=1.85; p=0.05		F=2.40; p=0.01		F=1.15; p=0.33		F=0.58; p=0.87		F=1.13; p=0.35	
K-W	H=36.6; p<0.01				H=54.5; p<0.01		H=56.6; p<0.01							
HG1	zy	0.47 cde	0.32	cde	zy	20.47 bcd	zyx	28.23 def	3.14	bcde	16.8	cdef	24.5	cdef
HG2	zy	0.55 bcde	0.19	fg	zy	28.55 bcd	zyx	89.01 cd	1.96	h	18.2	cd	27.7	cde
HG3	zy	0.63 bc	0.36	bcd	z	2.96 ef	zy	5.48 gh	4.12	a	36.2	a	54.0	a
HG4	zy	0.53 bcde	0.16	g	zy	27.12 bc	yx	104.71 bc	2.21	gh	19.5	c	29.0	c
HG5	z	0.42 de	0.26	cdefg	zy	12.12 cd	zyx	20.60 ef	3.43	abcd	15.8	def	23.8	cdef
BP1	zy	0.54 bcde	0.48	b	y	228.36 a	yx	262.83 bc	2.87	cdef	15.0	ef	23.7	def
BP2	zy	0.56 bcde	0.23	defg	zy	29.68 bc	zyx	67.81 cd	2.63	efg	16.5	cdef	25.0	cdef
BP3	y	0.92 a	0.69	a	z	0.88 f	z	1.16 h	3.52	abc	35.2	a	49.7	a
BP4	zy	0.57 bcd	0.25	defg	y	160.23 a	x	482.56 ab	2.67	efg	17.2	cde	29.0	cd
BP5	z	0.41 de	0.20	efg	y	181.27 a	x	493.06 a	2.83	def	14.2	f	22.3	f
KP1	zy	0.48 cde	0.23	defg	zy	42.07 bc	zyx	72.63 cde	2.96	cdef	15.8	def	24.0	cdef
KP2	z	0.40 e	0.24	defg	y	160.99 a	x	250.04 ab	3.10	bcde	16.7	cdef	25.8	cdef
KP3	zy	0.69 b	0.39	bc	zy	10.98 de	zyx	18.13 fg	3.81	ab	26.8	b	40.3	b
KP4	zy	0.46 de	0.19	efg	zy	146.35 ab	yx	381.70 abc	2.51	efg	16.2	def	24.8	cdef
KP5	zy	0.45 de	0.30	cdef	zy	86.32 ab	yx	109.81 abcd	2.45	fgh	15.2	ef	23.2	ef

Table 5. Pearson correlation coefficients *r* between soil moisture and soil bulk density and parameters of nematode assemblages (abundance of trophic groups, numbers of species and genera, and community indices) for all soil samples (*n*=450) and for composite samples (consisting of five samples taken from each zone in the gorges) on the different sampling dates (total zone & date *n*=90). Statistically significant correlation coefficients ($p<0.05$) are in italics. n.d. = not determined

	individual samples (*n*=450)		zone & date samples (*n*=90)	
	moisture	bulk density	moisture	bulk density
bacterivores	+0.04	*–0.20*	+0.01	*–0.30*
fungivores	+0.05	*–0.33*	+0.06	*–0.51*
root-fungal feeders	*+0.17*	*–0.17*	+0.16	*–0.24*
plant parasites	–0.04	*+0.26*	–0.04	*+0.39*
omnivores	*+0.16*	*–0.19*	*+0.26*	*–0.29*
predators	*–0.13*	*+0.21*	*–0.29*	*+0.43*
insect parasites	*–0.11*	+0.08	–0.17	+0.18
all nematodes	*+0.11*	*–0.24*	+0.09	*–0.34*
genera	+0.08	+0.09	–0.13	*+0.54*
species	*+0.11*	–0.02	–0.09	*+0.46*
NCR	n.d.	n.d.	–0.04	*+0.40*
NCR2	n.d.	n.d.	–0.12	*+0.24*
(B+F)/PP	n.d.	n.d.	[1)]*+0.26*	[1)]*–0.49*
(B+F+RFF)/PP	n.d.	n.d.	[1)]*+0.28*	[1)]*–0.45*
T	n.d.	n.d.	–0.08	+0.15

[1)] *n*=80 because plant parasites were absent from some zones

were recorded in the upper zones of the gorges. *Malenchus* evidently dominated in the middle zones of the gorge Hauschengrund. Some genera reached their greatest dominance at the bottoms of the gorges, such as *Plectus* in KP3, *Rotylenchus* and *Trichodorus* in BP3 and *Helicotylenchus* in HG3 and BP3. *Eudorylaimus* Andrássy, 1959 was the only dominant omnivore in nematode assemblages.

The greatest values of NCR and NCR2 and lowest values of the ratios (B+F)/PP and (B+F+RFF)/PP were recorded mainly at the bottoms of the gorges. The greatest values of trophic diversity index T and the numbers of nematode genera and species were recorded at the bottoms of the gorges (Table 4). The index T was significantly positively correlated with the abundance of plant parasites (r=+0.41, n=90, $p<0.01$), predators (r=+0.41), insect parasites (r=+0.30) and significantly negatively with root-fungal feeders (r=–0.59) and all nematodes (r=–0.46). The numbers of species and genera were significantly positively correlated with the T index (r=+0.42 and +0.43, respectively).

Cluster analysis depicted three large groups (Fig. 1). Cluster A mostly included records for bottom zones, Cluster B mostly middle zones, whereas Cluster C encompassed a greater part of the upper zones. Individual gorges were represented by similar numbers of zones in individual clusters and each cluster included all sampling dates.

Correlation between nematodes and soil moisture

In individual samples (*n*=450) root-fungal feeders, omnivores, all nematodes and the number of species were significantly positively correlated with soil moisture, while predators and insect parasites were significantly negatively correlated. Across all zones and sampling dates (*n*=90) omnivores were significantly positively correlated with soil moisture and predators significantly negatively. (B+F)/PP and (B+F+RFF)/PP were significantly positively correlated with soil moisture (Table 5).

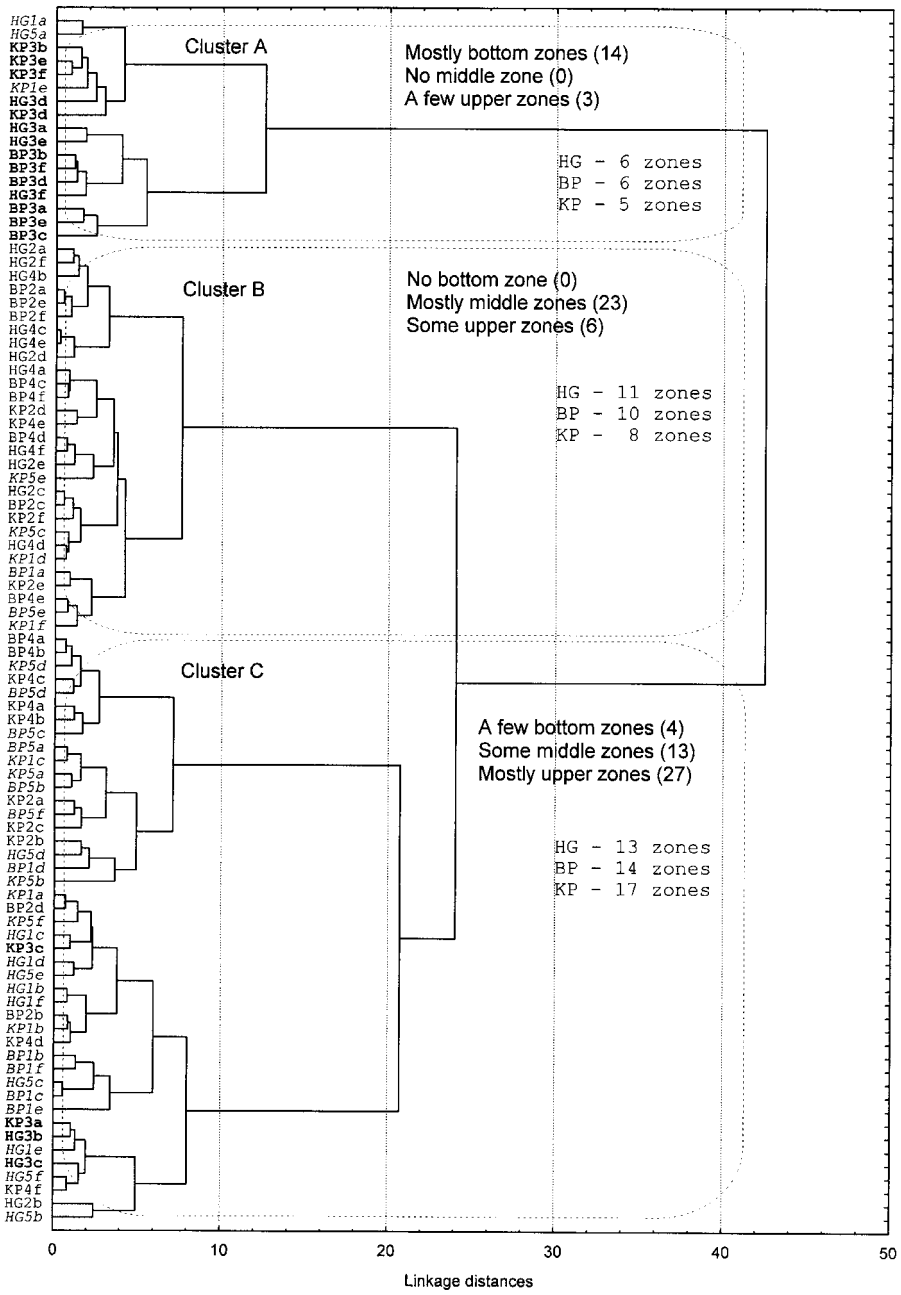

Fig. 1. Dendrogram based on cluster analysis of the *ln*(x+1) transformed abundance of nematode trophic groups in individual zones (1, 2, 3, 4, 5) and sampling dates (a, b, c, d, e, f) in the inverse gorges Hauschengrund (HG), Brtnický potok (BP) and Kachní potok (KP). Bottom zones are in bold, upper zones in italics and middle zones in normal type. Ward's method and Euclidean distances.

Table 6. Spearman correlation coefficients *R* (*n*=15) between mean values of the parameters of soil properties (Table 1, moist = soil moisture, BD = soil bulk density) and mean values of the parameters of nematode assemblages (abundance of trophic groups, numbers of species and genera, and community indices). Statistically significant correlation coefficients ($p<0.05$) are in italics

	moist	BD	C_{ox}	pH	Pv	K	Mg	Ca	Na
bacterivores	–0.09	*–0.66*	+0.48	*–0.67*	–0.28	+0.08	–0.18	+0.05	+0.37
fungivores	+0.09	*–0.79*	*+0.69*	*–0.80*	–0.47	+0.05	–0.30	–0.16	+0.43
root-fungal feeders	+0.19	–0.31	+0.45	–0.44	–0.22	–0.14	–0.36	–0.40	+0.19
plant parasites	–0.20	*+0.57*	*–0.55*	+0.14	+0.07	–0.27	+0.07	+0.46	–0.43
omnivores	+0.40	–0.49	+0.47	–0.41	–0.22	+0.34	+0.09	+0.26	+0.06
predators	*–0.59*	*+0.53*	–0.38	+0.33	+0.13	+0.13	*+0.59*	*+0.77*	+0.26
insect parasites	–0.26	+0.39	–0.43	+0.29	–0.09	–0.06	+0.03	+0.19	–0.18
all nematodes	+0.15	*–0.62*	*+0.69*	*–0.80*	–0.45	<+0.01	–0.36	–0.18	+0.43
genera	–0.05	*+0.80*	*–0.70*	*+0.77*	+0.23	–0.11	+0.25	+0.19	–0.31
species	–0.08	*+0.73*	*–0.65*	*+0.80*	+0.30	<+0.01	+0.31	+0.17	–0.37
NCR	–0.17	*+0.68*	*–0.56*	*+0.63*	+0.36	+0.06	+0.31	+0.22	–0.25
NCR2	–0.25	+0.09	–0.16	+0.23	+0.21	+0.34	+0.41	+0.42	+0.12
(B+F)/PP	*+0.53*	*–0.83*	*+0.74*	*–0.54*	–0.10	+0.28	–0.23	–0.42	+0.12
(B+F+RFF)/PP	+0.51	*–0.72*	*+0.72*	–0.41	+0.04	+0.29	–0.20	*–0.56*	+0.12
T	–0.05	+0.12	–0.30	+0.28	+0.23	+0.16	+0.43	*+0.53*	–0.31

As concerns the mean values in Tabs 1–2 (*n*=15) predators were significantly negatively correlated with soil moisture, whereas (B+F)/PP was significantly positively correlated (Table 6).

Correlation between nematodes and soil bulk density

In individual samples (*n*=450) plant parasites and predators were significantly positively correlated with soil bulk density. Bacterivores, fungivores, root-fungal feeders, omnivores, and all nematodes were significantly negatively correlated. Across all zones and sampling dates (*n*=90) plant parasites, predators, the number of genera, and number of species were significantly positively correlated with soil bulk density. Bacterivores, fungivores, root-fungal feeders, omnivores and all nematodes were significantly negatively correlated. NCR and NCR2 were significantly positively correlated with soil bulk density while (B+F)/PP and (B+F+RFF)/PP were significantly negatively correlated (Table 5).

As concerns the mean values in Tabs 1–2 (*n*=15) plant parasites, predators, the number of genera, and number of species were significantly positively correlated with soil bulk density. Bacterivores, fungivores and all nematodes were significantly negatively correlated. NCR was significantly positively correlated with soil bulk density while (B+F)/PP and (B+F+RFF)/PP were significantly negatively correlated (Table 6).

Correlation between nematodes and soil chemical parameters

Fungivores and all nematodes were significantly positively correlated with C_{ox}, plant parasites, the number of genera and the number of species were significantly negatively correlated (Table 6). The number of genera and the number of species were significantly positively correlated with soil pH, while bacterivores, fungivores and all nematodes were significantly negatively correlated. Predators were significantly positively correlated with Mg and Ca.

NCR was significantly positively correlated with soil pH and significantly negatively with C_{ox}. (B+F)/PP was significantly positively correlated with C_{ox} and significantly negatively with pH. (B+F+RFF)/PP was significantly positively correlated with C_{ox} and significantly negatively with Ca. Trophic diversity index T was significantly positively correlated with Ca.

DISCUSSION

It is known that over a large-scale altitudinal gradients spanning hundreds of metres forest vegetation, soils and soil nematode faunas change markedly (Solov'eva 1986, Kozlovsky 2002, Háněl & Čerevková 2010). On the slopes of narrow gorges and in ravines, which experience temperature inversions, there occur different zones of vegetation and soils within several tens of metres of one another from the top to the bottom, but very little is known about whether there are corresponding changes in soil faunas (Schlaghamersky et al. 2012). A preliminary survey (Háněl 2010b) indicated that the nematode faunas at the bottoms of gorges were distinctly different from those on the slopes and that different trophic relationships existed in the nematode communities in the different zones. The more comprehensive study presented here supports these results. Gorges did not differ significantly in total nematode abundance and trophic groups, except for plant parasites (because of a low abundance of Hoplolaimidae in KP) and omnivores (*Eudorylaimus* was most abundant in BP). The abundance of fungivores and root-fungal feeders and of all nematodes depended significantly on date sampled. The abundance of all trophic groups depended on the zonation. Consequently, cluster analysis indicated a marked association between zonation and the trophic structure of nematode assemblages although there were many overlaps between-zones that may to a great extent be attributed to seasonal fluctuations in the numbers of fungivores and root-fungal feeders.

Nematode relationships with soil moisture were meagre, which is in accordance with Sohlenius & Boström (2001), although moisture was significantly negatively correlated with soil bulk density. Soil organic material from the tops of the gorges was often so dry that it floated on water in Baermann's funnels but contained abundant populations of nematodes. This is possibly because different species of nematodes have different requirements for soil water and temperature for feeding and reproduction (Sohlenius 1985) as discussed below. There is a negative correlation between microbivorous nematodes (bacterivores, fungivores, root-fungal feeders) and omnivores and soil bulk density, whereas for plant parasites and predators this correlation appeared to be positive. The decrease in soil bulk density is associated with an accumulation in soil organic matter and decrease in soil pH in the upper parts of the slopes in gorges, with some exceptions in the Hauschengrund gorge. Ruess & Funke (1992) report that root and fungal feeders (within the genera *Aphelenchoides*, *Filenchus*) and bacterial feeders (*Acrobeloides*, partly *Wilsonema*) are adapted to living in acid coniferous soil. Their findings accord with the dominant position of these genera in nematode assemblages on the slopes (Table 3), which affects the ratios between trophic groups.

NCR (Yeates 2003) indicates a greater relative participation of bacteria than fungi in the detritus food web at the bottoms (especially in BP and KP) than on the slopes of gorges. Inclusion of root-fungal feeders in NCR2 (Háněl 2010a) resulted in lower values of this index than NCR, which indicates a dominant role of fungi in the detritus food web at all the sites sampled in this study, except for BP3. However, inclusion of RFF (Tylenchidae) in NCR2 was justified because the majority of the Tylenchidae belonged to *Filenchus* and *Malenchus*. Small species of *Filenchus* (*F. misellus* (Andrássy, 1958) and *F. discrepans* (Andrássy, 1954)) are fungal feeders (Okada et al. 2005) and juvenile *Malenchus* feed on fungi and the adults on root hairs (Magnusson 1983).

It is interesting that fungal (hyphal) feeding Dorylaimida were rare and only *Tylencholaimus mirabilis* (Bütschli, 1873) occurred at high population densities in HG3. On the other hand the hyphal feeding *Tylolaimophorus* (according to Yeates et al. 1993) of the order Diphtherophorida, occurred in all zones. Nevertheless, the food requirements of this genus are insufficiently known and Arpin (1973) also suggests it might have symbiotic relationships with nitrogen fixing bacteria in the intestinal granular bodies in *T. typicus* de Man, 1880. The high population densities of *Ty-*

lolaimophorus in the area studied may be a rather uncommon phenomenon. In most of the forest ecosystems previously studied in the Czech Republic (Bartošová & Háněl 1994, Háněl 1993, 1994, 1996ab, 1998, 2000, 2008, 2010a) fungivorous Dorylamida prevail over Diphtherophorida or the last named were absent. An exception to this rule are climax spruce forests in the Šumava Mountains (Háněl 1996c, 2002, 2004).

The absence or a very low abundance of Ba-1 bacterivores (*r*-strategists with short life cycles) on the slopes of the gorges (except in a few samples) is in agreement with Bongers & Bongers (1998) hypothesis that the Ba-1 guild in advanced successional stages can disappear. On the other hand Ba-1 bacterivores are abundant in climax deciduous forests (Háněl 2010a) and wet coniferous forests (Háněl 1996a, 2004) in the Czech Republic. The scarcity of Ba-1 bacterivores high up the sides of the gorges can therefore be a result of the presence there of nutrient poor sandy soils on sandstones, prevalence of coniferous litter resistant to decomposition and accumulation of raw humus on sun-exposed dry sites. This is indicated by the abundant populations of *Wilsonema schuurmansstekhoveni* (De Coninck, 1931), with anterior body structures adapted to sweep up bacteria from the surface of flat particles (De Ley & Coomans, 1997), on the slopes of the gorges. At the bottom of the Brtnický potok Gorge (BP3) the relatively high dominance of *Rhabditis* may indicate ± continuous nutrient enrichment supplied by the cold stream, which flows all the year round, and an abundance of nutrient-rich litter. In other gorges streams flow only in spring after snow melt or after flooding when the flow of water down the slopes carries off nutrients.

The nematode data thus suggests fast nutrient mineralization via a detritus food web at the bottoms of the gorges with more active bacteria-based energy channel (especially in BP3) than on the slopes, where a fungal-based energy channel predominates. Lower values of the ratios (B+F)/PP and (B+F+RFF)/PP also indicate a higher rate of nutrient mineralization via a grazing food web (root-based energy channel) at the bottoms than on the slopes of the gorges (Wasilewska 1997, 2004). The low temperatures at the bottoms of sun-shaded gorges limit evaporation of water from soil, which is important for continuous nematode activity.

Nevertheless, we cannot say that soil biological activity at the bottoms of the gorges was greater than on the slopes. Some nematodes can be active in soil with very low values of matric potential (Yeates et al. 2002). More nematodes live on the slopes than at the bottoms and are mostly fungivores + root-fungal feeders that feed on metabolically active mycelium (Sohlenius & Wasilewska 1984). Sohlenius & Boström (2001) report a higher proportion of fungal feeders during the warm and dry season and an increase in bacterial feeders during the wet and cold winter in pine forests; fungi require less water than bacteria to grow. Dry conditions are favourable for fungivorous Aphelenchoididae and to a less extent fungivorous Tylenchidae (Bouwman & Zwart 1994). A fungus-fungivore dominated energy channel and mycorrhiza become established in successively mature ecosystems that are characterized predominantly by detritus web like food chains with closed mineral cycles (Odum 1969, Bardgett et al. 2005). Fungal-feeding nematodes excrete less NH_4^+-N than bacterial-feeding nematodes (Ingham et al. 1985) and mycorrhizal symbionts are better able to exploit nutrients (N, P) from dead nematodes than saprotrophs (Perez-Moreno & Read, 2001).

Communities of soil organisms, even taking possible N_2-fixation by *Tylolaimophorus typicus* into consideration, seem to be more adapted to the retention of nutrients in the system on the slopes than at the bottoms of the gorges. However, soil biological activity can be intermittent (and difficult to estimate) due to the incidence of warm and dry periods and only some organisms are able to reproduce under such conditions (nematode richness was less on the slopes). Considering plant parasites a good indicator of this kind of intermittent activity can be the occurrence of *Paratylenchus* on the slopes. Species of this genus can adopt a non-feeding resting stage and so survive adverse environmental conditions (Brzeski & Háněl 1999). *Helicotylenchus* and *Rotylenchus* (at

least those in our study, Háněl 2010b) are not able to adapt to stressful environments on the slopes and only occur in high population densities at the bottoms of the gorges.

The greater trophic diversity of the nematode communities at the bottoms of the gorges is clearly associated with a greater species and generic richness, and greater abundance of predators (mostly Mononchida) and plant parasites (mostly Tylenchida). Detritus soil food webs, affected by nematodes, have basically three trophic levels (microbes, microbivorous nematodes and predatory nematodes) at the bottoms and two levels (microbes and microbivorous nematodes) on the slopes. Mononchid predators can feed on various nematodes from all trophic groups (Bilgrami et al. 1986) and also on bacteria (Yeates 1987). There is a chance that the individuals of more abundant species are frequently attacked and this can result in greater values of the trophic diversity index T. However, vulnerability of prey to predation and different and indirect pathways for their control are hard to trace (Mikola & Setälä 1998). In the inverse gorges studied greater species richness at the bottoms very likely reflects the less harsh environment there than on the slopes.

Nematode faunas in the Czech Republic are usually richer and include more predators in deciduous than in coniferous forests (Háněl 1996a, b, 2008). These findings accord with the greater nematode richness at the bottom of the Brtnický potok Gorge compared to that in coniferous soil higher up the gorge sides. Nevertheless, the very low nematode richness and greater populations of fungivores + root-fungal feeders than bacterivores might also indicate some degree of ecosystem senescence (Williamson et al. 2005) at the tops of the slopes of the gorges. Although ecosystem functioning is considered to be robust and species extinction rare because of the reduced top-down control cascading to the base of detritus food webs in soils (Laakso & Setälä 1999ab) organisms in the fungal pathway are less resistant to disturbance than those in the bacterial pathway (Hedlund et al. 2004). Recovery of ecosystems from severe disturbance could therefore take longer high up the sides of the gorges than at the bottoms.

Nonetheless, the functional aspects of trophic diversity and faunistic richness of the nematode assemblages studied are difficult to assess. The negative associations between species and genus richness with soil C_{ox} and positive associations with soil pH are similar to that found in an altitudinal gradient (from 400 to 1100 m a.s.l.) of forest ecosystems in the Vihorlat Mts (Háněl & Čerevková 2010). Altitudinal gradient in the gorges studied did not exceed 60 m from the bottom to the top but the range of variation in C_{ox} values was similar (4.6–22.1% in Vihorlat, 3.9–21.7% in České Švýcarsko). On the other hand, nematode richness in the Vihorlat Mts is negatively associated with increase in soil moisture at high altitudes where the climate is cold. In the inverse gorges the colder bottoms had a greater nematode richness than the warmer tops. Thus the relationships between soil food conditions and functioning and taxonomic richness of soil communities can vary under different (micro) climates and ranges in soil temperature and fluctuations in moisture.

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