Acta Soc. Zool. Bohem. **82**: 27–46, 2018
ISSN 1211-376X

A shift in the trophic structure of assemblages of soil nematodes in a Central European woodland – an indication of a forest maturing or climate warming?

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Received 24 August 2018; accepted 26 October 2018
Published 27 December 2018

Abstract. Soil nematodes were studied in oak-hornbeam, oak and beech climax forests in the Protected Landscape Area and Biosphere Reserve Křivoklátsko in Central Bohemia, Czech Republic. This study was carried out in the years 1994–1995 (Period 1) and 2006–2007 (Period 2). In Period 1 the mean total precipitation per year was 664.5 mm and mean air temperature 8.4 °C. In Period 2 these values were 449.0 mm and 9.0 °C. The abundance of root-fungal feeders, fungivores (F) and bacterivores (B) were significantly greater in Period 2 than in Period 1. The abundance of plant parasites (PP), omnivores, predators and insect parasites did not differ significantly between the two Periods. Shannon diversity index H'gen significantly decreased as a result of abundant microbivore populations in Period 2. The values of PPI significantly decreased because of a high abundance of *Filenchus* and some reduction of PP with *c-p* values greater than 2. (B+F)/PP ratio significantly increased in Period 2 because of a significant increase in the abundance of B and F. No significant differences between the two Periods were found in the values of the Maturity indices, NCR, EI, SI, BI and CI, indicating no deterioration in nematode assemblages. Principal Component Analysis of genera revealed that although the composition of nematode assemblages in individual forests overlapped the samples from Period 1 and Period 2 were in two separate groups. Very likely, warmer and drier years caused the changes observed in nematode assemblages but they could also result from natural long-term variations in climax systems. The abundance of Tardigrada was significantly higher in Period 2.

Key words. Soil zoology, ecology, Nematoda, trophic group, community composition, Enchytraeidae, Rotifera, Tardigrada, forest, Bioshere Reserve Křivoklátsko, Czech Republic, climate change.

INTRODUCTION

The Protected Landscape Area and Bioshere Reserve Křivoklátsko is one of the most valuable natural areas in the Czech Republic in which about 62% of the area is covered with forests (Ložek et al. 2005). An apposite and succinct characterization of this piece of natural beauty is summarised by Ložek (2011) as follows. "In the context of Central European hill countries, the Křivoklát Area is a woodland landscape which has been continuously covered by forest since the prehistoric times. Due to mild dry climate as well as varied soil and relief conditions it is characterised by a high biodiversity that has not been disturbed by human impact. At present, it represents one of the last areas with a number of well-preserved semi-natural ecosystems within the zone of Central European hill countries."

The climate at Křivoklátsko is moderately warm and moderately dry with mean air temperatures of 7–8 °C. Sum of precipitation per year is about 500–550 mm, but only about 350 mm falls in the vegetative period and mostly in July (Ložek et al. 2005). Increase in air temperatures accompanied by a decrease in precipitation can result in a more arid climate, which can potentially effect above-ground and below-ground parts of ecosystems. These changes in climate may combine

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Presented at the 13th Central European Workshop on Soil Zoology, České Budějovice, Czech Republic, 13–15 April 2015

with ungulate browsing and result in a higher level damage to plants as, for example, reported by Černý et al. (2011), but how they influence soil and soil biota is poorly known.

Extensive research on the flora and macro-fauna in ecosystems at Křivoklátsko has a long tradition but the soil micro-fauna has received little attention. Balík (1996) studied soil and moss testate amoebae and Háněl (1996a) simultaneously investigated soil nematodes in three climax forests at Benešův luh, Červený kříž and Tři skalky. The first part of this research was done in 1994–1995 within enclosures established in 1993 to protect the sites from ungulate grazing and other disturbance. The study of nematodes was continued in 2006–2007, within the enclosures and also in forests without enclosures. In this second period the research was also aimed at studying the effect of browsing and uprooting by ungulates, which results in visible damage to aboveground vegetation and may have consequences for below-ground biota. The results were only partly published (Háněl 2009), nevertheless, they also reveal that the abundance of nematodes within enclosures was greater than in 1994–1995. Results of studies on soil microfauna were briefly evaluated by Háněl (2011).

Nematodes are the most abundant multicellular animals (Bongers & Ferris 1999), an important component of soil systems and highly taxonomically and functionally diverse (Boag & Yeates 1998, Bongers & Bongers 1998, Ettema 1998). They are useful indicators of soil condition, dynamics of soil processes and the effects of human disturbance on ecosystems (Wasilewska 1997, Yeates 2007, Wilson & Kakouli-Duarte 2009). Recent studies show that nematodes are also potentially good bioindicators of climate change (Porazinska et al. 2002, Hoschitz & Kaufmann 2004, Landesman et al. 2011). The problem is that nematode responses to climate warming were mostly studied in a few short-term (not longer than one decade) manipulative experiments (Freckman & Virginia 1997, Sohlenius & Boström 1999ab, Ruess et al. 1999a, b, Bakonyi & Nagy 2000, Papatheodorou et al. 2004, Bakonyi et al. 2007, Darby et al. 2011, Stevnbak et al. 2012, Dong et al. 2013, Song et al. 2014, Thakur et al. 2014). Climate manipulation induce changes in soil nematode communities but it is difficult to generalize the results. In cold climates, it seems that atmospheric warming favours microbivores that increase the rate of mineralization and can reduce the numbers of species of omnivores and predators, which in some cases can negatively affect the diversity of nematodes. In temperate and warm climates, the manipulation of soil temperature and moisture can affect nematodes in a complicated and less predictable way and in high-mountain ecosystems the exposure of the site can significantly affect nematode faunas (Hoschitz & Kaufmann 2004). A serious potential problem associated with climate warming is the spreading of soil-borne plant parasitic nematodes over larger areas and the resultant increase in their pest potential (Tiilikkala 1991, Boag et al. 1991, 1997, Neilson & Boag 1996, Yeates et al. 1998, Colagiero & Ciancio 2011).

Nielsen et al. (2014) surveyed the family structure in assemblages of nematodes at 12 sites in various types of ecosystems along a latitudinal gradient (68°N to 77°S) on six continents. This indicates that the family composition is related to mean annual rainfall and temperature, and that climate might be a good predictor of the structure of local assemblages. According to the Intergovernmental Panel on Climate Change, by 2100, atmospheric CO_2 concentration is predicted to reach 540–970 ppm, accompanied by globally differential temperature increases in the range 1.1–6.4 °C and temperate regions are generally predicted to become warmer and wetter (A'Bear et al. 2014). A meta-analysis of the data from published studies on climate manipulation reveal that climate change affects the abundance of soil invertebrates in different ways depending on the climatic treatment, taxonomic group and in the case of nematodes, feeding guild. Nematode abundance is not affected by temperature overall. But feeding guilds display different responses; plant feeders decrease whereas fungivores and carnivores increase in abundance with increasing temperature and their response to drought is rather neutral. Because in the Křivoklátsko area air

Table 1. Physico-chemical characteristics of the soils at the sites studied

forest type periods (1,2)	oak-hornbeam forest (C) 1994–1995 (1)	 2006–2007 (2)	oak forest (Q) 1994–1995 (1)	 2006–2007 (2)	beech forest (F) 1994–1995 (1)	 2006–2007 (2)
moisture %	27.8	18.5	40.2	23.0	26.6	20.4
temperature °C	8.1	12.2	10.0	12.3	9.1	11.1
C_{ox} %	1.64	2.82	8.30	13.97	2.15	3.94
pH (H_2O)	4.83	4.41	4.92	4.76	4.82	4.43
pH (KCl)	4.17	3.39	4.32	3.37	4.08	3.40

temperature was lower and precipitation greater in 1994–1995 than in 2006–2007, which was reflected in soil moisture and temperature (Table 1), it is likely there were changes in the nematode assemblages. Therefore, this paper analyses in detail the responses of nematodes in enclosures to changes in climate. Having evaluated the effects of climate the next paper will concentrate on the changes in nematode faunas that can be attributed to ungulate browsing.

MATERIAL AND METHODS

Study sites

This study was carried out in the Křivoklátsko Protected Landscape Area and Biosphere Reserve, Central Bohemia, Czech Republic. It covers an area of 62,792 ha. The region is characterized by a moderately warm and moderately dry climate with long-term (1961–1990) average air temperatures of 7–8 °C and precipitation totals of 500–600 mm. It borders an area in the north-west with an average air temperature of 8–9 °C and annual precipitation of 400–500 mm. This may indicate that Křivoklátsko will become more arid if surface air temperatures actually rise as predicted by global-warming models. In the area studied the mean total precipitation per year in 1994–1995 (Period 1) and in 2006–2007 (Period 2) were 664.5 mm and 449.0 mm, respectively (meteorological station Křivoklát). The mean air temperatures in Periods 1 and 2 were 8.4 C and 9.0 °C, respectively (meteorological station Zbiroh).

Original plant cover was mostly composed of deciduous oak-hornbeam, beech and oak forests (Kolbek et al. 1997, Kolbek 2011). Soil types were mostly cambisols along with cambic leptosols and luvisols on Proterozoic and Paleozoic silicate parent rocks and local Neogene and Quaternary deposits (Vorel & Stárková 2011, Žigová 2011). To record the long-term changes in woodland ecosystems fenced enclosures measuring 50×120 m or 50×60 m were established in 1993 at three localities with representative forest types of Central European woodland. The enclosures protected parts of the forests from ungulate grazing and uprooting, tree cutting and disturbance by tourists. The forests studied (Kolbek & Vítková, 1999) were as follows:

C (Carpinion): Oak-hornbeam forest in the alliance *Carpinion* Issler 1931 emend. Mayer 1937 (association *Melampyro nemorosi-Carpinetum* Passarge 1957) located at Benešův luh, which borders on the Vůznice Nature Reserve, 50°02'22.9"N, 14°00'32.5–34.9"E, 430 m a. s. l., soil type polygenetic oligotrophic cambisol on fossil pseudogleysol, parent rock proterozoic slates, enclosure 50×60 m. Dominant trees *Quercus petraea* (Mattusch.) Liebl. with *Fagus sylvatica* L. and *Carpinus betulus* L., dense shrub of *C. betulus* with some *Tilia* sp. A dense growth of grass and herbaceous plants covered about 60% of the area in Period 1 (1994–1995) and less, 30–40%, in Period 2 (2006–2007), when the shrubs were taller and denser.

Q (Quercion): Xerothermic oak forest in the alliance *Quercion pubescenti-petraeae* Braun-Blanquet 1931 (association *Potentillo albae-Quercetum* Libbert 1933) in the Červený kříž Nature Reserve, NW of the village Nový Jáchymov, 49°59'32.2"N, 13°55'51.9"E, 420 m a. s. l., soil type ranker cambisol (cambic leptosol), parent rock proterozoic slates, enclosure 50×120 m. Dominant trees *Quercus petraea*, shrubs scarce, understorey grass-herbaceous plant cover about 50–60% in Period 1 and about 70% in Period 2.

F (Fagion): Submontaneous herbaceous plant-rich beech forest in the alliance *Fagion* Luquet 1926, suballiance *Eu-Fagenion* Oberdofer 1957 em. Tüxen in Oberdofer et Tüxen 1958 (association *Tilio cordatae-Fagetum* Mráz 1960 em. Moravec 1977) located at Tři skalky, NW of the village Kublov, 49°57'52.8"N, 13°53'09.1"E, 470 m a. s. l., soil type oligotrophic to mesotrophic cambisol locally polygenetic, parent rock proterozoic slates, enclosure 50×120 m. Dominant tree *Fagus sylvatica* L., shrubs scarce, understorey grass-herbaceous cover 70–80% in Period 1 and about 50% in Period 2.

Sampling and processing

The studies were carried out during two periods. In Period 1 the samples were collected on 4 May 1994 (date 1a), 18 October 1994 (1b), 30 May 1995 (1c) and 25 October 1995 (1d). In Period 2 the samples were collected on 10 May 2006 (2a), 26 October 2006 (2b), 15 May 2007 (2c) and 25 September 2007 (2d). Thus the combination of letters, number codes, localities and time. For instance, C[1a] is oak-hornbeam forest with samples collected in Period 1 (year 1994) in spring (month May – a). C[2d] is oak-hornbeam forest with samples collected in Period 2 (year 2007) in autumn (month September – d), etc.

Within enclosures (established in 1993) samples were collected from the corners and the centre of the 8×8 m square in each forest on each sampling date. At each sampling point two cylindrical cores (10 cm apart) of cross-sectional area 10 cm^2 down to a depth of 10 cm were collected. In Period 1 the soil of all the samples was carefully hand-mixed into one bulked sample in the field and four ten gram sub-samples were used to extract nematodes and other animals (enchytraeids, rotifers and tardigrades) in the laboratory. This simplified procedure was used to characterize the nematode (and other) fauna in three areas, Křivoklátsko (Háněl 1996a), Velká kotlina (Háněl 1996b) and Voděradské bučiny (Háněl 2013a), which were each surveyed simultaneously by collecting large numbers of samples. In Period 1 soil faunas outside the enclosures were not studied because (i) the vegetation in fenced areas (established in 1993) did not differ from that outside and (ii) it was technically very difficult to extend the scope of the soil fauna study.

As an effect of fencing the vegetation within and without enclosures became gradually different (Kolbek & Vítková, 1999). On receiving further financial support from the Czech Science Foundation the soil studies in enclosures were resumed and plots of 8×8 m were staked out outside the enclosures and their soil faunas were also sampled. In Period 2 the soil in the two cores collected at each sampling point was mixed and eight grams of mixed soil was used for studying the soil fauna. Thus, in Period 2 five independent samples were collected from each square plot which were used to statistically compare the nematode faunas on different dates in different enclosures and the surrounding forest. Data on nematodes collected outside the enclosures in Period 2 are not included in this study and were partly published elsewhere (Háněl 2009). The amount of soil used for studying the nematodes and other faunas was 40 g for each plot at each sampling date in both Periods and thus suitable for the evaluation of community structure and comparing taxonomic richness. The generic composition of nematode assemblages studied in 1994–1995 widely overlaps (Háněl 1996a) that of individual plots, which are considered to be independent replicates within the Křivoklátsko woodland despite the fact the dominant trees differed.

The soil sampled was thoroughly mixed and nematodes were isolated from sub-samples using a modified Baermann funnel, fixed in 3% formaldehyde and studied in glycerol on slides using light microscopy. In total, 22,643 nematodes, 159 enchytraeids, 1,042 rotifers, and 950 tardigrades were examined. Nematodes were counted and determined, to species or genus level, simultaneously.

Soil temperature was measured on the dates sampled at a depth of 5 cm. Soil moisture on these dates was determined gravimetrically and expressed as percentage of water in wet soil. Soil was dried for 48 hours at 25 °C and then for 4 hours at 105 °C. Soil chemical parameters were obtained from the Institute of Soil Biology's internal databases.

Data analysis

To evaluate the trophic structure of nematode assemblages the nematodes were sorted into trophic groups as, e.g., explained by Háněl (2010) and presented in Table 2. Proportions of various microbivore (B, F, RFF) and plant feeding (RFF, PP) nematodes were used to assess the relative participation of the nematodes in the detritus and primary production consumption food webs. The nematode channel ratio NCR1=B/(B+F) was calculated according to Yeates (2003) and NCR2=B/(B+F+RFF) according to Háněl (2010). High values of these indices indicate a greater participation of bacteria than fungi in the breakdown of detritus and the NCR2 also takes the fungal-feeding behaviour of Tylenchidae into account. The ratio (B+F)/PP was calculated according to Wasilewska (1997) and high values of this ratio indicate slower nutrient cycling and mineralization of a detritus food web than the rapid flow of matter and energy from autotrophs to obligate plant-feeding heterotrophs.

To evaluate the diversity of nematodes the number of genera was counted and the natural logarithm of the proportions of abundances of the different genera used to calculate a Shannon Index (H'gen). The Maturity Index (MI) and the Plant Parasite Index (PPI) were calculated according to Bongers (1990). The Sum Maturity index (∑MI) was calculated according to Yeates (1994) and the Heterogeneity Maturity Index (HMI) according to (Háněl 1996a) and used to evaluate the maturity of nematode assemblages in terms of the *r-K* scale of life history strategies.

To provide soil food web diagnostics the nematode functional guilds that combine feeding preferences (Yeates et al. 1993), life-history traits on a *r-K* scale and derived colonizer-persister groups (Bongers 1990) were used to calculate the Enrichment Index (EI), Structure Index (SI) and Channel Index (CI) according to Ferris et al. (2001). Weightings of nematode taxa were used as suggested by these authors. The weightings for the taxa not included in the Ferris' et al. (2001) paper were derived from *c-p* values set by Bongers (1990). The Basal Index (BI) was calculated according to Berkelmans et al. (2003). A shift in the values of those indices indicate a change has occurred in soil food web condition over the period between the two sampling periods in the forests studied.

STATISTICA was used to perform the Analysis of Variance (ANOVA) and related tests, and the Cluster Analysis. The nematode abundance data were *ln*(x+1) transformed prior to the analysis of variance and cluster analysis. Assumption of normality was evaluated using Kolmogorov-Smirnov & Lilliefors tests for normality, and Shapiro-Wilk's W test. The homogeneity of variances was tested using Levene's test. The community indices (Table 4) were analyzed without transformation and because some data did not meet ANOVA assumptions a Kruskal-Wallis ANOVA was also performed. Principal Components Analysis (PCA) was done using *log*(x+1) transformed genus abundance in CANOCO for Windows version 4.5. PCA was selected after testing the length of the gradient in the genus data using a Detrended Correspondence Analysis (DCA) and detrending by segments (Ter Braak & Šmilauer 2002). The length of the gradient in genera abundance along the first axis was 1.582 SD and along the second axis 1.501 SD.

RESULTS

Trophic groups of nematodes

Bacterivores were the most abundant trophic group, making up 41.3% of all the nematodes. Tables 2 and 3 show that the abundance of bacterivores was significantly greater in Period 2 than Period 1. Nevertheless, this effect was mainly due to bacterivorous populations of *Plectus*, *Rhabditis*, *Acrobeloides* and *Wilsonema* in oak-hornbeam forest (Table 2). The abundance of fungivores (18.8% of all nematodes) and root-fungal feeders (21.5%) was significantly greater in Period 2 than Period 1 (Table 3). The increase in fungivore abundance was less marked in oak forest and that of root-fungal feeders in oak-hornbeam forest, for which a one-way ANOVA with post-hoc Fisher LSD test did not reveal significant differences (Table 2). Generally, the abundance of these three trophic groups (mostly microbivores) was greater in Period 2 than Period 1, although in some forests this difference was not statistically significant. As a consequence of the abundance of microbivores the abundance of all nematodes in the soil was significantly greater in Period 2 than Period 1 (Table 3).

The greatest abundance of plant parasites was recorded in oak-hornbeam forest. Plant parasites were less abundant in all forests in Period 2 (Table 2) but in general this decrease was not statistically significant (Table 3). But as some plant parasitic genera were not present in the soil of the forests studied or far less abundant (except for *Xenocriconemella macrodora* (Taylor, 1936) in C[2]) in Period 2 (Table 2), the decline in the abundance of plant parasites should be considered biologically significant.

There were no significant differences in the abundance of omnivores and predators. The abundance of insect parasites was greatest in the oak forest. The lowest abundance of insect parasites was recorded in the beech forest in Period 2 (Table 2), but the overall effect in this Period across all sites was statistically insignificant (Table 3).

The dendrogram based on the cluster analysis of the *ln*(x+1) transformed abundance of nematode trophic groups is shown in Fig. 1. The upper cluster contains eleven samples from Period 2 and four from Period 1. The lower cluster contains eight samples from Period 1 and one from Period 2. The upper cluster includes mostly samples from oak-hornbeam (C) and oak (Q) forest. The lower cluster includes mostly samples from beech forest (F), where the abundance of nematodes in Period 1 was relatively low (Table 2).

Generic composition of nematode assemblages

The most abundant and dominant genera in the area studied were *Filenchus* (17.2% of all the nematodes; mainly fungivorous *F. misellus* (Andrássy, 1958) and *F. discrepans* (Andrássy, 1954)), *Aplelenchoides* (12.2%; several species) and *Plectus* (12.1%; mainly *P. parietinus* Bastian, 1865 and *P. acuminatus* Bastian, 1865) (Table 2). *Rhabditis* (9.3%; *R. terricola* Dujardin, 1845) dominated in all forests (i.e. > 5.0% of all nematodes) except for Q[2]. *Tylencholaimus* (4.6%; mainly *T. mirabilis* (Bütschli, 1873)), which was dominant in all forests in Period 2.

Other genera were dominant (D > 5.0%) in some forests and Periods, however, their contribution to the total number of individuals was lower than 5.0%. These were *Acrobeloides* (4.9%; *A. nanus* (de Man, 1880) in C[2] and F[1]), *Metateratocephalus* (2.1%; mainly *M. crassidens* (de Man, 1880) in Q[1]), *Malenchus* (3.5%; mainly *M. acarayensis* Andrássy, 1968 in F[1]), *Paratylenchus* (2.4%; mainly *P. straeleni* (De Coninck, 1931) in C[1] and F[1]), *Helicotylenchus* (1.8%; mainly *H. pseudorobustus* (Steiner, 1914) in C[1] and F[1]) and *Aporcelaimellus* (2.7%; *A. obtusicaudatus* (Bastian, 1865) in C[1]).

The dendrogram based on the cluster analysis of *ln*(x+1) transformed abundance of nematode genera is shown in Fig. 2. The upper cluster consists of ten samples from Period 1 and five from Period 2. The lower cluster consists of seven samples from Period 2 and two from Period 1. Both clusters contain samples from the three forests. Evidently, the generic composition of nematode assemblages in different forests overlapped but the effect of Period upon these assemblages was detectable.

The Principal Components Analysis of nematode assemblages resulted in a similar picture (Fig. 3). All samples from Period 1 (except for Q[1a]) are in part A of the ordination diagram and

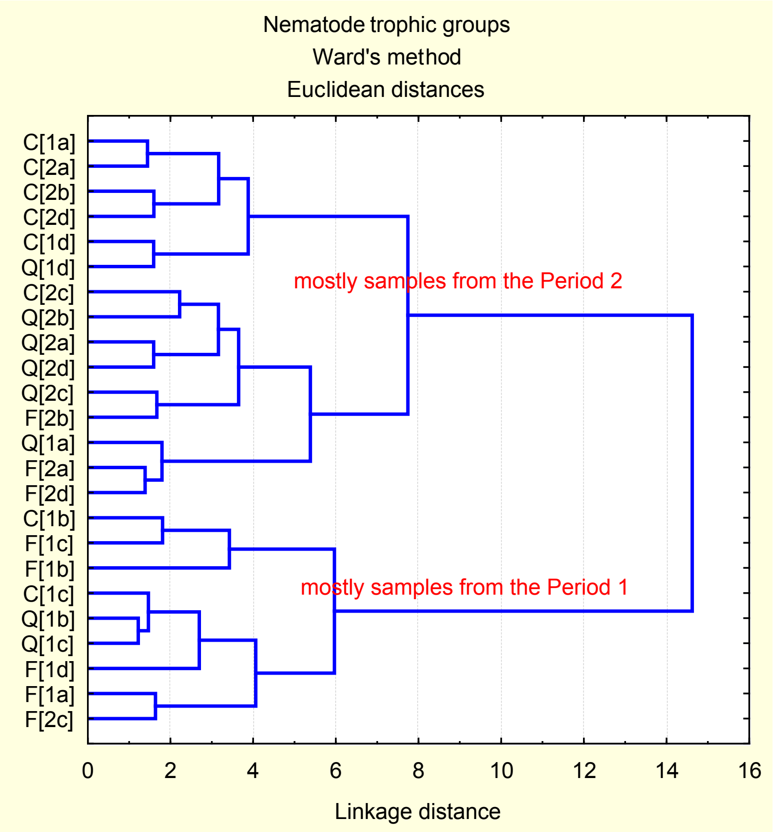

Fig. 1. Dendrogram based on cluster analysis of *ln*(x+1) transformed abundances of the nematode trophic groups. Ward method and Euclidean distances. For an explanation of samples codes see Material and Methods.

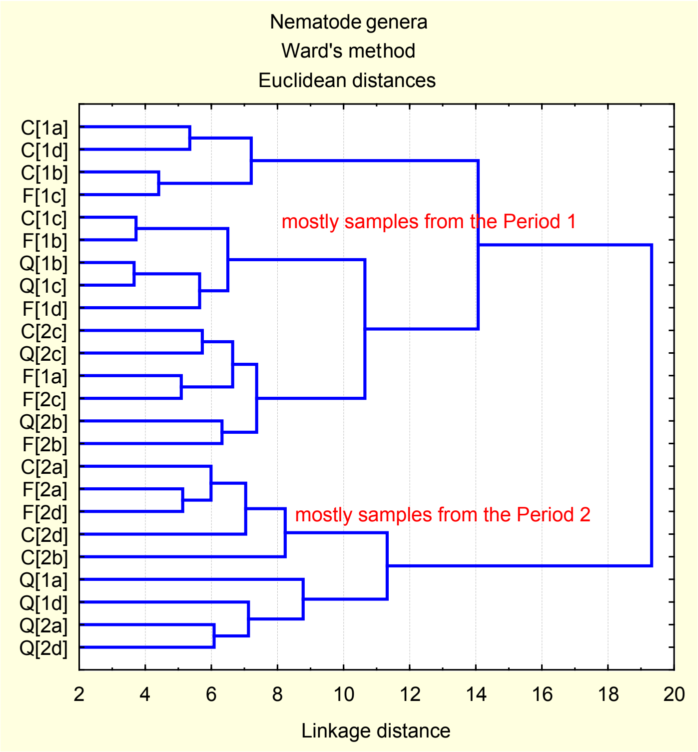

Fig. 2. Dendrogram based on cluster analysis of *ln*(x+1) transformed abundances of nematode genera. Ward method and Euclidean distances. For an explanation of samples codes see Material and Methods.

all samples from Period 2 are in part B of the diagram. Composition of nematode assemblages in the three forests overlapped, the effect of the Period was evident, but positions of individual samples indicate that the variance in the generic data cannot be explained only by the effect of Period.

Diversity, maturity and food web condition indices

Table 4 shows that the greatest generic richness was recorded in oak forest and lowest in beech forest and it did not differ significantly between Periods. Shannon diversity index, H'gen, was significantly less in Period 2 because of the predominance of microbivore genera.

Maturity indices ∑MI, MI and HMI did not differ significantly, either between forests or Periods. PPI was significantly lower in Period 2 than Period 1. This was because the abundance of plant parasites (with *c-p* values greater than 2, except for *Paratylenchus*) was lower and that of root-fungal feeders (with *c-p* value of 2) was higher in all of the three forests in Period 2 (Table 2). PPI was highest in the oak-hornbeam forest, but because of the patchy distribution of different plant parasitic species with varying *c-p* values only the Kruskal-Wallis ANOVA detected that the PPI differed significantly in the oak-hornbeam forest and beech forest.

PPI/MI ratio was higher in the oak-hornbeam forest than in oak and beech forests (Table 4) because of a high abundance of *H. pseudorobustus* and *X. macrodora* with p-c values of 3. Wasi-

Table 2. Mean abundance ($\times 10^3$ ind.m^{-2}) of nematodes in the oak-hornbeam (C), oak (Q) and beech (F) forests in the Period 1994–1995 [1] and Period 2006–2007 [2]. Standard errors SE, *F*-values and *p*-values for the one-way ANOVA with post-hoc Fisher LSD tests (the same letters denote homogeneous groups of means, *alpha*=0.05) are given for different trophic groups. If Fisher LSD tests revealed the groups were heterogeneous and the ANOVA was insignificant a Tukey HSD post-hoc test was also used. Dominant genera (D>5.0%) are in bold italics. abbrev. = abbreviation

nematodes and sites	abbrev.	C[1]	C[2]	Q[1]	Q[2]	F[1]	F[2]
bacterivores	B	770.9	2328.0	1138.3	1293.3	603.1	1085.3
SE (*n*=4)		239.5	441.2	450.9	103.9	169.5	265.1
$F_{(5,18)}$=2.817, p=0.047		bc	a	bc	ab	c	abc
Plectus Bastian, 1865 + *Chiloplectus* Andrássy, 1984	*Plectu*	***205.4***	***519.0***	***240.6***	***555.4***	***168.0***	***430.0***
Rhabditis Dujardin, 1845	*Rhabdi*	***138.9***	***813.4***	***200.8***	131.7	***121.1***	***228.9***
Acrobeloides Cobb, 1924	*Acrdes*	104.4	***287.4***	92.7	144.8	***107.8***	114.9
Wilsonema Cobb, 1913	*Wilson*	17.7	238.7	11.3	10.9	26.8	68.3
Metateratocephalus Eroshenko, 1973	*Metate*	39.2	67.5	***165.8***	34.7	26.9	33.0
Eucephalobus Steiner, 1936	*Euceph*	69.1	35.6	41.2	56.8	61.0	9.9
Teratocephalus de Man, 1876	*Terato*	11.5	51.9	70.5	46.8	8.6	40.5
Prismatolaimus de Man, 1880	*Prisma*	30.7	49.0	35.2	35.4	9.9	19.6
Ceratoplectus Andrássy, 1984	*Cerato*	6.4	57.5	22.7	24.6	8.0	23.9
Tylocephalus Crossman, 1933	*Tyloce*	–	33.0	4.4	72.6	1.6	19.1
Heterocephalobus Brzeski, 1960	*Heceph*	13.5	25.7	13.6	33.9	6.3	9.6
Bursilla Andrássy, 1976	*Bursil*	21.2	3.0	49.7	3.6	7.8	1.9
Eumonhystera Andrássy, 1981	*Eumonh*	25.1	8.5	35.9	2.2	10.7	4.8
Anaplectus De Coninck et Schuurmans Stekhoven, 1933	*Anaple*	13.8	7.8	17.9	32.9	10.1	1.5
Alaimus de Man, 1880	*Alaimu*	24.2	14.5	7.8	3.2	15.2	18.2
Prodesmodora Micoletzky, 1923	*Prodes*	–	26.4	35.0	12.4	–	7.5
Monhystrella Cobb, 1918	*Monrel*	4.1	26.7	12.5	14.5	–	23.1
Bastiania de Man, 1876	*Bastia*	20.3	18.2	27.6	6.0	1.6	3.0
Cephalobus Bastian, 1865	*Cephal*	16.3	1.9	12.6	14.4	1.6	–
Panagrolaimus Fuchs, 1930	*Panagr*	5.4	11.5	4.6	11.9	–	3.9
Geomonhystera Andrássy, 1981	*Geomon*	–	2.3	20.3	12.3	–	–
Cervidellus Thorne, 1937	*Cervid*	3.2	12.5	3.0	5.6	1.1	1.8
Deficephalobus De Ley et Coomans, 1990	*Defice*	–	5.6	–	3.7	–	8.9
Bunonema Jägerskiöld, 1905	*Bunone*	–	6.6	–	1.9	–	3.2
Achromadora Cobb, 1913	*Achrom*	–	–	–	6.9	–	4.1
Odontolaimus de Man, 1880	*Odonto*	–	0.6	–	6.5	–	0.7
Pristionchus Kreis, 1932	*Pristi*	–	–	–	–	6.0	1.6
Cylindrolaimus de Man, 1880	*Cylind*	–	–	4.0	1.2	1.6	–
Chiloplacus Thorne, 1937	*Chilop*	–	0.7	2.5	–	–	3.4
Acrobeles Linstow, 1877	*Acrobe*	0.5	–	3.2	2.5	–	–
Ereptonema Anderson, 1966	*Erepto*	–	2.3	–	3.2	–	–
Amphidelus Thorne, 1939	*Amphid*	–	–	3.0	0.6	1.6	–
fungivores	F	314.8	1046.5	396.1	898.5	119.2	516.0
SE (*n*=4)		151.5	302.9	251.3	341.1	27.7	147.4
$F_{(5,18)}$=3.164, p=0.032		bc	a	bc	ab	c	ab
Aphelenchoides Fischer, 1894	*Aphdes*	***257.0***	***658.9***	***250.3***	***613.2***	***89.7***	***271.9***
Tylencholaimus de Man, 1876	*Tylmus*	24.6	***271.2***	98.9	***225.9***	7.1	***181.2***
Ditylenchus Filipjev, 1936	*Dityle*	30.2	101.1	35.4	50.0	17.9	57.3
Deladenus Thorne, 1941	*Delade*	–	3.8	–	4.5	–	2.7
Tylolaimophorus de Man, 1880	*Tylola*	–	4.3	2.1	–	3.0	1.5
Aphelenchus Bastian, 1865	*Apchus*	3.1	–	1.2	3.2	1.5	–
Paraphelenchus Micoletzky, 1922	*Paraph*	–	–	8.2	0.4	–	–
Funaria ? Van der Linde, 1983 juv.	*Funar?*	–	2.3	–	–	–	–
Tylenchida juv.	*Tyjuvs*	–	4.9	–	1.3	–	1.4

root-fungal feeders	RFF	322.5	1016.4	306.0	831.5	233.3	1050.3
SE (n=4)		101.8	351.6	116.6	128.2	78.9	544.9
$F_{(5,18)}$=2.906, p=0.043		abc	a	bc	a	c	ab
Filenchus Andrássy, 1954	*Filenc*	***233.1***	***887.0***	***157.9***	***687.4***	***152.1***	***893.8***
Malenchus Andrássy, 1968	*Malenc*	82.7	80.2	101.5	115.3	***73.9***	153.1
Lelenchus Andrássy, 1954	*Lelenc*	3.2	5.2	16.1	27.6	2.3	2.0
Cephalenchus Goodey, 1972	*Celenc*	2.0	44.0	–	–	–	–
Aglenchus Andrássy, 1954	*Aglenc*	–	–	30.5	1.2	3.4	–
Coslenchus Siddiqi, 1978	*Colenc*	–	–	–	–	1.5	1.4
Tylenchus Bastian, 1865	*Tylenc*	1.5	–	–	–	–	–
plant parasites	PP	389.1	277.5	76.0	30.2	223.1	75.4
SE (n=4)		125.2	147.1	33.0	15.2	142.6	43.0
$F_{(5,18)}$=2.162, p=0.104		a	ab	ab	b	ab	b
Tukey HSD		a	a	a	a	a	a
Paratylenchus Micoletzky, 1922	*Paraty*	***158.0***	54.2	7.8	1.0	***123.6***	75.4
Helicotylenchus Steiner, 1945	*Helico*	***168.7***	2.9	53.1	11.0	***83.6***	–
Xenocriconemella De Grisse et Loof, 1965	*Xenocr*	35.0	219.2	3.0	17.1	3.4	–
Pratylenchus Filipjev, 1936	*Pratyl*	25.1	–	3.9	1.2	8.2	–
Tylenchorhynchus Cobb, 1913	*Tylrhy*	–	–	5.9	–	–	–
Longidorus Micoletzky, 1922	*Longid*	1.8	1.2	1.5	–	–	–
Rotylenchus Filipjev, 1936	*Rotyle*	0.5	–	0.8	–	2.6	–
Criconemoides Taylor, 1936	*Crimel*	–	–	–	–	1.6	–
omnivores	O	222.5	244.3	203.5	242.0	131.0	318.8
SE (n=4)		95.2	52.5	64.0	48.8	44.1	89.9
$F_{(5,18)}$=0.993, p=0.449		a	a	a	a	a	a
Eudorylaimus Andrássy, 1959	*Eudory*	66.8	119.7	93.4	83.1	51.8	103.5
Aporcelaimellus Heyns, 1965	*Aprcll*	***115.1***	81.2	73.6	86.8	43.0	77.3
Mesodorylaimus Andrássy, 1959	*Mesodo*	24.7	30.1	20.3	40.0	8.3	124.8
Crassolabium Yeates, 1967	*Crasso*	2.1	7.4	8.1	24.3	13.0	12.4
Dorydorella Andrássy, 1987	*Dorydo*	7.1	1.7	3.1	–	7.5	–
Pungentus Thorne & Swanger, 1936	*Pungen*	6.8	0.8	1.0	–	7.3	–
Microdorylaimus Andrássy, 1986	*Microd*	–	–	4.0	3.5	–	–
Allodorylaimus Andrássy, 1986	*Allodo*	–	–	–	4.3	–	–
Metaporcelaimus Lordello, 1965	*Metapo*	–	3.5	–	–	–	0.8
predators	P	63.0	33.4	103.6	64.8	44.5	46.2
SE (n=4)		22.1	15.6	49.0	19.4	32.3	17.3
$F_{(5,18)}$=1.131, p=0.380		a	a	a	a	a	a
Prionchulus Cobb, 1916	*Prionc*	17.9	27.7	12.8	38.7	8.7	14.2
Clarkus Jairajpuri, 1970	*Clarku*	41.3	4.2	35.2	7.3	28.2	2.3
Tripyla Bastian, 1865	*Tripyl*	0.5	–	25.9	11.8	7.5	–
Paractinolaimus Meyl, 1957	*Paract*	–	–	–	–	–	29.7
Mylonchulus Cobb, 1916	*Mylonc*	–	–	17.3	7.0	–	–
Coomansus Jairajpuri et Khan, 1977	*Cooman*	1.6	1.5	9.0	–	–	–
Tobrilus Andrássy, 1959	*Tobril*	1.8	–	1.0	–	–	–
Seinura Fuchs, 1931	*Seinur*	–	–	1.5	–	–	–
Iotonchus Cobb, 1916 juv.	*Iotonc*	–	–	0.9	–	–	–
insect parasites	IP	98.6	93.1	76.7	140.1	26.9	5.8
SE (n=4)		39.7	28.3	40.5	62.4	17.4	2.3
$F_{(5,18)}$=3.471, p=0.023		ab	ab	ab	a	bc	c
Steinernema Travassos, 1927 dauer larvae	*Daurla*	98.6	90.8	76.7	140.1	26.9	5.8
Tylenchida juv.	*Tyjuvs*	–	2.4	–	–	–	–
all nematodes		2181.4	5039.2	2300.2	3500.3	1381.0	3097.8
SE (n=4)		648.2	1153.4	856.4	332.6	314.8	717.2
$F_{(5,18)}$=2.559, p=0.064		bc	a	bc	ab	c	abc
Tukey HSD		a	a	a	a	a	a

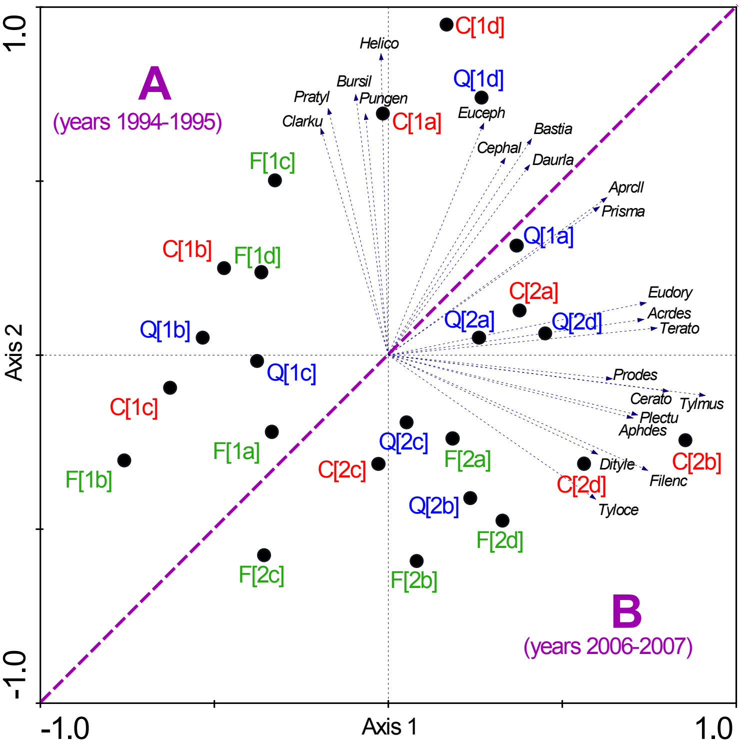

Fig. 3. Biplot from a PCA based on *log*(x+1) transformed genus abundance. Eigenvalues of the axes 1, 2, 3 and 4 were 0.275, 0.153, 0.106 and 0.078, and cumulative percentage variance of genus data 27.5, 42.9, 53.5 and 61.3, respectively. Inclusion rule for the fitness of the different genera ranged from 40% to 100% (which was passed by 22 genera). Abbreviations of the names of the genera are in Table 2 and an explanation of sample codes in Material and Methods.

lewska's (1997) ratio (B+F)/PP was significantly higher in Period 2. Other indices did not differ significantly either between forests or Periods.

Other soil fauna

The abundance of enchytraeids was slightly greater in Period 1 than Period 2 ($p<0.10$). Neither forest type nor period affected the abundance of rotifers. The abundance of tardigrades was significantly higher in oak forest than in beech and oak-hornbeam forest and in Period 2 than in Period 1 (Table 3).

DISCUSSION

Changes induced by Climate warming?

From the beginning of the determination and counting of the nematodes collected in the warmer and drier Period 2 (2006–2007) it was obvious that there were more microbivore nematodes than there were in samples collected ca. 10 years previously (Háněl 1996a). This difference proved to be statistically significant (Table 3). The increase in microbivore nematodes was also recorded

Table 3. Mean values of the abundance ± SE (×10^3 ind.m^{-2}) of nematodes, enchytraeids, rotifers and tadigrades at different localities and in different forest types (C, Q and F) and in two consecutive time periods (1 and 2) analyzed using a Two-way ANOVA (significant *F*-values and *p*-values in bold italics). The means of groups (C-Q-F or 1-2) with the same letters do not differ significantly according to a post hoc Fisher LSD test, *alpha* = 0.05

	locality (forest type)			period		two-way ANOVA (*F*-values)					
	C	Q	F	1	2	locality		period		L×P	
	oak-hornbeam	oak	beech	1994–1995	2006–2007						
n	8	8	8	12	12	$F_{(2,18)}$	*p*	$F_{(1,18)}$	*p*	$F_{(2,18)}$	*p*
Nematoda total	3610.3±816.6 a	2900.3±482.0 a	2239.4±486.5 a	1954.2±359.2 b	3879.1±491.3 a	1.154	0.338	***10.321***	***0.005***	0.083	0.921
bacterivores	1549.4±375.0 a	1215.8±216.2 a	844.2±171.9 a	837.5±175.3 b	1568.8±227.9 a	1.671	0.216	***8.942***	***0.008***	0.901	0.424
fungivores	680.7±209.1 a	647.3±217.9 a	317.6±102.2 a	276.7±95.5 b	820.3±159.5 a	1.478	0.255	***12.830***	***0.002***	0.017	0.984
root-fungal feeders	669.4±214.3 a	568.7±127.7 a	641.8±298.0 a	287.2±53.7 b	966.1±201.4 a	0.223	0.803	***14.005***	***0.002***	0.039	0.962
plant parasites	333.3±91.9 a	53.1±18.9 b	149.2±74.4 ab	229.4±69.7 a	127.7±56.6 a	***4.026***	***0.036***	2.527	0.129	0.117	0.891
omnivores	233.4±50.5 a	222.7±38.0 a	224.9±58.4 a	185.7±38.9 a	268.4±36.3 a	0.096	0.909	3.242	0.089	0.766	0.479
predators	48.2±13.7 a	84.2±25.5 a	45.3±17.0 a	70.4±20.3 a	48.1±9.9 a	1.763	0.200	0.322	0.576	0.904	0.423
insect parasites	95.9±22.6 a	108.4±36.5 a	16.4±9.0 b	67.4±20.1 a	79.7±26.6 a	***7.732***	***0.004***	0.020	0.891	0.935	0.411
Enchytraeidae	22.9±6.5 a	31.3±9.4 a	25.4±7.9 a	35.8±7.5 a	17.3±3.5 a	0.208	0.814	3.600	0.074	0.140	0.870
Rotifera	195.8±64.9 a	167.2±34.3 a	143.9±40.2 a	133.4±29.8 a	204.5±44.0 a	0.324	0.727	2.180	0.157	1.535	0.242
Tardigrada	104.7±31.6 b	202.1±42.9 a	92.1±49.5 b	72.1±20.2 b	193.9±40.0 a	***4.952***	***0.019***	***11.466***	***0.003***	0.460	0.638

outside the enclosures. Moreover, a preliminary study showed that the higher abundance of root--fungal feeders + fungivores indicate a greater activity of fungi outside than inside enclosures (Háněl 2009). In the present study NCR values were higher in Period 1 than Period 2 but generally the difference was insignificant (p>0.05). Nevertheless, Kruskal-Wallis ANOVA of NCR1 resulted in p=0.083 and two-way ANOVA of NCR2 a p=0.095. This is an indication that in the enclosures fungi played greater part in soil matter breakdown in Period 2 than Period 1 although the statistical significance of the difference in Nematode Channel Ratios was relatively low.

A much better indication of increased fungal activity is the increase in the abundance of *Tylencholaimus* (*c-p* value 4) in all three forests in Period 2 (Table 2). These *K*-strategist fungivorous nematodes of the order Dorylaimida usually occur in undisturbed forest soils and have lower growth rates than the *r*-strategist fungivorous Aphelenchida (Magnusson 1983, Okada et al. 2005b). *Tylencholaimus* species reproduce readily on Deuteromycotina and Basidiomycota but attempts to establish cultures on seedling roots, algae, moss, bacteria and nematodes failed (Wood 1973). Thus, it is likely that these *K*-strategist Dorylaimida fungivores need a more stable fungus production than *r*-strategist Aphelenchida fungivores, which have a relatively short life cycle (one to several weeks). *K*-strategist Dorylaimida omnivores are not affected by this constraint because they can feed on a variety of soil organisms. European temperate forests are sub-optimal for mycelial growth and decay, as they rarely reach 20 °C and high temperatures favour fungi (A'Bear et al. 2014). And as indicated by abundant fungivore nematodes, the recorded decline in soil moisture only had a slightly negative effect upon fungal activity.

Trophic structure of nematodes assemblages thus changed during the course of about 10 years between Period 1 and Period 2, with the latter being characterized by lower precipitation and higher air temperatures, which resulted in a lower soil moisture and higher soil temperature (Table 1). As recorded in the České Švýcarsko National Park the abundance of microbivores and especially fungivores and root-fungal feeders in soil exposed to dry spells increases but the species and generic richness decreases (Háněl 2013b, Schlaghamerský et al. 2014). In the Křivoklátsko woodland generic richness did not change significantly between the two Periods and the Shannon diversity index was slightly but significantly lower in Period 2 (which resulted from increased populations of microbivores). Maturity indices (∑MI, MI, and HMI) and food web condition indices (EI, SI, BI, and CI) did not change significantly.

According to Ferris et al. (2001) the increase in CI should indicate an increase in the participation of fungi in the soil food web but it only includes bacterivores with *c-p* values of 1 and fungivores with *c-p* values of 2. Therefore, CI is not fully applicable to systems with abundant populations of bacterivores with *c-p* values greater than 1, abundant populations of fungivores with *c-p* values greater than 2 and abundant populations of root-fungal feeders dominated by small fungal-feeding *Filenchus* (Okada et al. 2005a). Nevertheless, like other food web indices CI indicated no significant difference in weighted guild proportions between the two Periods.

These facts indicate that increase in temperature between Period 1 and Period 2 affected nematode assemblages (greater populations of microbivores and especially those of fungivores + root-fungal feeders) but had no detrimental effect upon them (diversity indices, maturity indices and food web condition indices remained unaffected). SI was almost always greater than 50 (except for Q[2b] and F[1b]), which is an indication of undisturbed natural woodland (Čerevková & Renčo 2009, Tomar & Ahmad 2009) and the abundance of omnivores and predators did not differ between the Periods indicating the soil environment did not worsen (Wasilewska 1997).

In Period 2 the increase in the abundance of fungivores (from 2.3× to 4.3×) and root-fungal feeders (from 2.7× to 4.5×) was greater than that in the abundance of bacterivores (from 1.1× to 3.0×) (Table 2), but the NCR1 and NCR2 values indicated that the bacterial channel still functioned efficiently (Table 4). EI, which depends on the abundance of bacterivores with *c-p* values of 1,

Table 4. Mean values of nematode community indices ± SE for different localities and different forest types (C, Q and F) in two consecutive time periods (1 and 2) analyzed using a Two-way ANOVA (significant *F*-values and *p*-values in bold italics) and Kruskal-Walis ANOVA (*H*-values in bold italics when $p < 0.05$). The means of groups (C-Q-F or 1-2) with the same letters do not differ significantly according to a post hoc Fisher LSD test, *alpha* = 0.05 (Two-way ANOVA)

	locality (forest type)			period		two-way ANOVA (*F*-values) and Kruskal-Wallis ANOVA (*H*-values)							
	C	Q	F	1	2	locality			period			L×P	
	oak-hornbeam	oak	beech	1994–1995	2006–2007								
n	8	8	8	12	12	$F_{(2,18)}$	*p*	$H_{(2,N=24)}$	$F_{(1,18)}$	*p*	$H_{(1,N=24)}$	$F_{(2,18)}$	*p*
nematode diversity and maturity indices													
genera	36.63±2.28 a	41.63±1.71 a	29.75±2.56 b	33.92±2.52 a	38.08±1.84 a	***7.589***	***0.004***	***10.578***	2.780	0.113	2.530	0.568	0.576
H'gen	2.71±0.10 a	2.79±0.14 a	2.55±0.14 a	2.85±0.08 a	2.52±0.11 b	1.083	0.360	2.220	***5.952***	***0.025***	***4.320***	0.350	0.709
∑MI	2.22±0.08 a	2.34±0.04 a	2.33±0.07 a	2.33±0.05 a	2.27±0.05 a	1.031	0.377	1.996	0.567	0.461	0.120	1.686	0.213
MI	2.25±0.10 a	2.41±0.05 a	2.50±0.09 a	2.37±0.07 a	2.38±0.08 a	1.908	0.177	2.715	0.002	0.963	0.053	3.305	0.060
PPI (+)	2.18±0.05 a	2.10±0.03 a	2.07±0.05 a	2.18±0.04 a	2.05±0.02 b	2.286	0.131	***6.905***	***7.989***	***0.011***	***5.653***	0.008	0.992
PPI/MI	0.98±0.03 a	0.87±0.02 b	0.85±0.04 b	0.93±0.03 a	0.88±0.04 a	***5.136***	***0.017***	***6.405***	2.070	0.167	1.333	3.183	0.066
HMI	6.41±0.38 a	6.86±0.40 a	6.29±0.41 a	6.91±0.31 a	6.12±0.29 a	0.622	0.548	1.580	3.206	0.090	2.430	0.667	0.526
proportions of the different nematode trophic groups and channel ratios													
(B+F)/PP (+)	19.21±10.83 a	81.30±34.43 a	67.89±36.17 a	14.31±4.54 b	97.96±29.97 a	1.609	0.228	5.505	***7.910***	***0.012***	***7.680***	0.821	0.456
NCR1	0.72±0.04 a	0.71±0.06 a	0.73±0.06 a	0.77±0.04 a	0.67±0.04 a	0.046	0.955	0.155	2.435	0.136	3.000	0.528	0.598
NCR2	0.55±0.03 a	0.55±0.05 a	0.54±0.07 a	0.60±0.03 a	0.50±0.05 a	0.013	0.987	0.380	3.114	0.095	2.253	1.201	0.324
nematode food-web indices													
EI (++)	66.83±3.85 a	63.57±4.52 a	58.47±2.50 a	65.94±3.00 a	59.99±3.03 a	1.710	0.209	2.535	2.560	0.127	2.083	***3.693***	***0.045***
SI	65.38±3.18 a	71.10±5.59 a	69.15±4.61 a	70.61±3.81 a	66.48±3.51 a	0.477	0.628	3.120	0.720	0.407	0.333	3.004	0.075
BI	19.54±1.77 a	19.40±3.41 a	20.92±2.30 a	18.59±2.20 a	21.31±1.85 a	0.127	0.881	0.245	0.999	0.331	0.653	3.110	0.069
CI	21.03±5.52 a	21.10±7.41 a	23.95±8.33 a	18.21±4.86 a	25.85±6.30 a	0.052	0.950	0.095	0.818	0.378	1.920	0.702	0.509

(+) Levene's test detected heterogeneity of variances for "Period" and "Locality×Period".

(++) EI values in oak forest (Q) were significantly higher in Period 1 than Period 2. In the beech forest (F) the EI values were higher in Period 1 than Period 2, whereas in oak-hornbeam forest (C) they were higher in Period 2 than Period 1.

was almost always greater than 50 (except for C[1b], Q[2c] and F[2b]). In the graphic presentation based on Ferris et al. (2001) the values of EI and SI intersect in Quadrant B, which according to the Table 4 in their paper indicates low to moderate disturbance, N-enriched environment, balanced decomposition channels, low C:N ratio and a maturing food web.

The most abundant bacterivores were *Plectus* and *Rhabditis*. Postma-Blaauw et al. (2005) report that the interaction between *Bursilla monhystera* (Bütschli, 1873) (Rhabditidae s.l.) and *Plectus parvus* Bastian, 1865 in a microcosm experiment strongly affects the composition of the bacterial community, increases the bacterial biomass and soil N mineralization. Combinations with *Acrobeloides nanus* had less prominent effects on microcosm properties. Fu et al. (2005) report that the effect of *Cruznema tripartitum* (Linstow, 1906) (Rhabditidae s.l.) upon bacteria and carbon mineralization is stronger than that of *Acrobeloides bodenheimeri* (Steiner, 1936). Species of *Acrobeloides* require less abundant bacterial populations than Rhabditidae to reproduce (Ilieva-Makulec 2001) and are drought resistant (Demeure et al. 1979). This can explain the decrease in the abundance of *Rhabditis* and increase in that of *Acrobeloides* in the oak forest where the decrease in soil moisture was most marked and soil carbon accumulated (Table 1). The decrease in the abundance of *Metateratocephalus* in the oak forest might also be due to the decrease in soil moisture, although *M. crassidens* can survive in arid or semi-arid habitats (Andrássy 2005).

Nevertheless, the overall changes in bacterivore nematodes in the oak forest were relatively small as almost all the genera recorded in Period 1 were also recorded in Period 2, but the lower precipitation and higher air temperature in the latter period could have had a more marked effect on the nematode assemblages. In a microcosm experiment Bouwman & Zwart (1994) found that dry conditions favour fungivorous Aphelenchoididae and to a less extent fungivorous Tylenchidae. Dry conditions did not affect epistrate-grazing bacterivore Cephalobidae but the numbers of suspension-feeding bacterivore Rhabditidae were reduced. Griffiths et al. (1995) confirm that as soil matrix potential decreases there is a greater proportion of fungal-feeding nematodes and Cephalobidae tend to predominate over Rhabditidae. Plectidae are successful in stressed natural environments (Yeates 2003) and *Plectus* was more abundant in Period 2.

This accounts for the fact that *Acrobeloides nanus*, *Plectus* (mainly the smaller species) and *Wilsonema schurmansstekhoveni* (De Coninck, 1931) are dominant bacterivores on the slopes and top parts of the gorges in the České Švýcarsko National Park (Háněl 2013b), which are drier than the wetter bottoms of the gorges where *Rhabditis* occurs. In addition, fungivores, *Aphelenchoides* and *Tylolaimophorus* dominate high up the slopes of the gorges and *Tylencholaimus mirabilis* only occurs in the wetter bottoms. That *Filenchus* accompanied by *Malenchus* are dominant on the slopes and top parts of the gorges is in agreement with the findings that *Filenchus* was most abundant in Period 2 and that of *Malenchus* did not change except for the beech forest (Table 2). If climate becomes more arid we can expect similar changes in the Křivoklátsko woodland, in particular a decrease in the abundance of *Rhabditis* and *Tylencholaimus* and predominance of *W. schhurmasstekhoveni* over *W. otophorum* (de Man, 1880) (both species occurred in both Periods). Prolonged drought could cause a decrease in the abundance of *Wilsonema*, *Aphelenchoides*, Tylenchidae and Criconematidae, while that of Cephalobidae and Qudsianematidae might not be so strongly affected as is reported by Landesman et al. (2011) in an oak-pine forest in USA.

A more arid environment could result in a change in the trophic structure of the nematodes similar to that reported in semiarid shrub land in which bacterivores (*Cephalobus*, *Plectus*, *Cervidellus*) dominate followed by omnivores (*Eudorylaimus*, *Thonus*) and there are fewer fungivores and root-fungal feeders, but nevertheless there is a relatively high generic richness (Bakonyi et al. 2007). A more detailed prediction would be speculative. For example, the experimental warming of winter wheat fields in a subtropical monsoon climatic zone in China favoured bacterivores and fungivores (including *Filenchus*), whereas the abundance of plant parasites, such as *Heli-*

cotylenchus, decreased and that of carnivores/omnivores remained almost unchanged, and there were no significant changes in the EI and SI values (Song et al., 2014). This picture is similar to that recorded in the present study, however in the wheat fields in China bacterivores and plant parasites dominate the nematode community as they also do in agroecosystems in the Czech Republic (Háněl 2003a). Mean values of SI (22.57–24.40) are much lower than those recorded in the present study, whereas the values of EI (66.05–66.55) are very similar to those in Table 4. But in agroecosystems in a temperate semi-humid monsoon climate zone in China warming did not have a significant effect on the abundance of nematodes, abundance of individual feeding groups or functional indices, whereas tillage was the most important factor accounting for the differences in the nematode communities (Dong et al. 2013).

In a temperate-boreal forest ecotone in Minnesota, USA, the abundance of nematode trophic groups did not differ among experimental warming treatments. Nevertheless, the ratio of microbial feeding and plant feeding nematodes (i.e. (B+F)/PP) increases significantly with warming and that of PPI decreases significantly (Thakur et al. 2014), which is consistent with the results of the present study (Table 4). In a dry, Danish heathland in which soil temperature and soil moisture were modified for eight years (Stevnbak et al. 2012) the abundance of root herbivores (most abundant group), bacterivores and fungivores in the 0–3 cm layer decreased similarly in the drought and heat treatments. *Helicotylenchus* (*c-p* value 3) remained the dominant plant parasites in the Danish heathland, but in the Křivoklátsko woodland this genus was less abundant in the drier and warmer Period 2 and absent in the beech forest (Table 2). Community indices thus can change (or remain unchanged) in response to climate change in a similar way in very different ecosystems and different soil nematode faunas and local conditions should always be taken into account. Sylvain et al. (2014) report that along a large-scale gradient of ecosystems (mesic, xeric and arid grasslands, and a polar desert) responses of nematodes to experimentally manipulated soil moisture differed from those reported in individual ecosystems. Along the large-scale gradient the abundance of nearly all nematodes (except for bacterivores) increases with increase in available soil moisture, while within ecosystems the abundance of all trophic groups decreased with increase in the availability of moisture (as did Shannon diversity and species evenness) and the proportions of the different trophic groups also differed.

Natural long-term variations in climax systems?

There is however another explanation of the recorded changes. EI and SI values were high in the forests studied and according to Ferris et al. (2001) this indicates a maturing of the soil food web. A good indicator of ecosystem maturing in Central Europe is the increase in the abundance and dominance of the genus *Filenchus*, especially the small species, such as *Filenchus misellus* and *Filenchus discrepans* groups (Wasilewska 1970, Brzeski 1995, Háněl 1996c, 2001, 2003b, 2010). This can be accompanied by an increase in species and generic richness. Thus, the greater abundance of *Filenchus* in Period 2 could simply reflect the fact that the forest ecosystems are older. Drier conditions could further account for the statistically significant difference in the abundance of root-fungal feeders.

Populations of omnivores and predators increase with succession over periods of several tens of years and then can decrease or fluctuate in abundance in (sub)climax stages. High populations of plant parasites can occur in the early successional stages and then decline (Háněl 1996c) or change in species composition (Háněl 2003b, 2010) in older successional stages. *Helicotylenchus pseudorobustus* feeds on various plants (Krall' 1990) and its decline in oak-hornbeam forest and absence from beech forest can be a consequence of the decrease in under storey plant cover in Period 2. *Paratylenchus straeleni* (slim species, *c-p* value 2) and *Xenocriconemella macrodora* (stout species, *c-p* value 3) prefer to feed on the roots of shrubs and trees (Ivanova 1976, Brzeski

& Háněl 2000, Eroshenko & Volkova 2005). In the oak-hornbeam forest they changed places in the assemblage of plant parasitic nematodes (Table 2). But it is impossible to say whether this was due to the warmer and drier conditions in Period 2 or to unknown changes in root-growth dynamics and possible competition between these two species. Competition between *Paratylenchus* and *Helicotylenchus* (*c-p* value 3) is affected by drought but it is more likely that a longer growing season probably benefits the larger long-lived root herbivores with *c-p* values of 3 or more (Stevnbak et al. 2012). They may be right. Climax systems are in a state of dynamic equilibrium in which the different components may vary from time to time and include drier and wetter periods but the whole system remains in balance.

Changes in the abundance of omnivores and predators are insignificant although *Aporcelaimellus*, *Eudorylaimus* and *Mesodorylaimus* are sensitive to moisture levels in sandy soils (McSorley 2012). Thus, the *K*-strategist part of the nematode assemblages indicates there is "nothing detrimental in the woodland soils at Křivoklátsko". Also the differences in the abundance of bacterivores in the oak-hornbeam forest can be accounted for without implying it might be due to global warming. The shrub layer increased in height to that of young trees (up to 6–7 metres) and very likely produced more leaf litter. The abundance of species of *Wilsonema* and *Tylocephalus auriculatus* (Bütschli, 1873) were also higher and as pointed out by De Ley & Coomans (1997) Wilsonematinae are specialist feeders of bacteria attached to flat micro surfaces, which decomposing leaves in soil provide in abundance. And the low carbon content in the soil in the oak-hornbeam forest (Table 1) indicate that most of the organic litter had been decomposed and mineralized and the significant role of Rhabditidae in carbon mineralization is discussed above. On the other hand, there was an accumulation of carbon in the soil in the oak forest, where the total abundance of bacterivores did not differ significantly and the abundance of *Rhabditis* was slightly lower (although the most striking decrease was recorded for *Metateratocephalus*, the biology of which is poorly known).

Despite differences in the genera the compositions of the nematode assemblages in individual forests overlapped, and as in the ordination diagram (Fig. 3) the effect of Period is clearly visible. This indicates that the soil nematodes in the woodland at Křivoklátsko, as a whole, responded to a Factor "X", which at least partly coincides with the change in climate that occurred in the area over the period studied. And this also indicates that soils in this area continued in their long-term development that over millennia results in soils in which the composition of the soil biota is relatively stable, but locally modified by changes in the dominant trees and cover of grasses and herbaceous plants, which can change over periods as short as a century.

In terms of the effect on other soil faunas, the abundance of Enchytraeidae was slightly lower ($p<0.10$) in Period 2, which might be related to the lower soil moisture. The increased abundance of tardigrades probably reflected the increased abundance of nematodes, which they often feed on (Hallas & Yeates 1972). Moreover, less precipitation may favour some tardigrades (Morgan 1977) that are adapted to anhydrobiosis and individual species that differ in their tolerance of desiccation (Wright 1989).

CONCLUSIONS

It is very likely that the warmer and drier years stimulated an increase in the abundance of fungivorous, root-fungal feeding and some bacterivore nematodes. But this mild local climate warming had no detrimental effect on the composition of the nematode assemblages, which indicated there was no degradation of the soil. Nevertheless, changes recorded in the nematode assemblages could also have resulted from natural long-term variations in climax systems. Therefore, long-term studies are necessary for testing the hypothesis that climate warming actually occurred in the area studied and affected both the forest soils and their biota.

Acknowledgements

The study was supported by Grant No. 526/06/1384 (Long-term changes of invertebrate assemblages in deciduous woodland soil as affected by ungulate grazing) from the Czech Science Foundation (GAČR). I thank Dr Karel Tajovský for information on the characteristics of the sites. The English of this manuscript was kindly checked and improved by Professor Anthony F. G. Dixon (Norwich, UK).

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