Zoological Studies **51**(5): 619-626 (2012)

Zoological Studies

Soil Nematode Abundance and Diversity in Different Forest Types at Changbai Mountain, China

Min Zhang[1,2,3], Wen-Ju Liang[1], and Xiao-Ke Zhang[1,*]

[1]*State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China*
[2]*Vegetable Research Institute, Liaoning Academy of Agricultural Sciences, Shenyang 110161, China*
[3]*Graduate University of Chinese Academy of Sciences, Beijing 100049, China*

(Accepted January 13, 2012)

Min Zhang, Wen-Ju Liang, and Xiao-Ke Zhang (2012) Soil nematode abundance and diversity in different forest types at Changbai Mountain, China. *Zoological Studies* **51**(5): 619-626. Soil nematode communities were investigated in the O and A horizons of soils in 4 typical forest types (mixed coniferous-broadleaf forest (MCB), dark-coniferous spruce-fir forest (DCSF), dark-coniferous spruce forest (DCS), and Ermans birch forest (EB)) along an elevational gradient at Changbai Mt., China. Sixty-two genera were identified in this study. Results showed that soil nematode abundance and diversity significantly differed among the different forest types along an elevational gradient. A horizon effect was stronger on nematode abundance than on diversity. Fungivores were found to be the dominant trophic group and comprised approximately 45%-63% of total nematodes. Nematode assemblages had the greatest diversity, maturity, and generic richness under the MCB. Forest types could be distinguished through a canonical correspondence analysis of nematode genera. Forest type and elevation were crucial to the distribution of soil nematode communities at Changbai Mt. The soil C:N ratio, microbial biomass carbon, and pH were important factors affecting soil nematode communities.
http://zoolstud.sinica.edu.tw/Journals/51.5/619.pdf

Key words: Abundance, Diversity, Forest type, Soil horizon, Soil nematodes.

Soil nematode communities and their structural changes were found to be one of the best biological tools for assessing soil processes and plant conditions in terrestrial ecosystems (Wang et al. 2009, Pen-Mouratov et al. 2010). In natural and plantation forest ecosystems, their diverse assemblages play important roles and have considerable influences on ecosystem functioning (Yeates 2003, Bakonyi et al. 2007). Yeates (2007) considered nematode assemblages to be the most diverse in forest ecosystems, and their changes could be related to changes in food resource availability and environmental conditions. Plant species in forest ecosystems have important roles in determining the composition of the soil biota via both above- and belowground resource inputs and by altering abiotic conditions (Keith et al. 2009).

The Changbai Mountain Natural Reserve, protected by UNESCO since 1980, is one of the best preserved areas in China. It is one of the most diverse temperate forest ecosystems in Asia and is seldom affected by anthropogenic activities. The vertical forest vegetation distribution of Changbai Mt. typically changes with elevational variations. The elevational gradient is among the most powerful “natural experiments” for testing ecological and evolutionary responses of biota to environmental changes (Körner 2007, Zhu et al. 2010). Háněl and Čerevková (2010) suggested that the richness of soil nematodes was correlated with elevation in forest ecosystems of the Vihorlat (Slovakia). Although there are some studies on

*To whom correspondence and reprint requests should be addressed. Tel: 86-24-83970359. Fax: 86-24-83970300.
E-mail:zxk@iae.ac.cn

soil nematode abundance and diversity in forest ecosystems (Yeates 2007, Háněl 2008, Tomar and Ahmad 2009, Tong et al. 2010), data on nematode faunal variations with forest types at different elevations are relatively scare. Moreover, the distribution of nematode assemblages was more related to regional effects, and soils of different forest types contained differing taxa and populations of nematodes (Yeates 2007). The objectives of this research were to investigate soil nematode abundance and diversity in different forest types along an elevational gradient at Changbai Mt., China and analyze potential factors that impact soil nematodes.

MATERIALS AND METHODS

Study sites

The Changbai Mountain Natural Reserve (41°23'-42°36'N, 126°55'-129°00'E) is located in Jilin Province, Northeast China. This area has a typical temperate continental monsoon climate. Along an increasing elevational gradient from 720 to 2691 m above sea level, the annual mean temperature changes from 3 to -7°C, and the annual mean precipitation increases from 679 to 1330 mm, with most of this occurring in July and Aug. The variety of vegetation types, climate characteristics, and soil types were well reported in previous studies (Zhao et al. 2004, Gong et al. 2007, Zhang et al. 2011). Four typical forest types along the elevational gradient on the northern slope of Changbai Mt. were chosen in this study (Zhang et al. 2011).

(1) A mixed coniferous-broadleaf forest (MCB) (42°24'N, 128°06'E) was sampled at 760 m. The annual mean temperature is 2.6°C, the annual mean precipitation is 691 mm, the O horizon is at 0-11 cm in depth with clay loam, and the A horizon is at 11-25 cm in depth with sandy clay loam. Tree species are dominated by a mixture of coniferous *Pinus koraiensis* and broadleaf *Quercus* spp. and *Acer* spp. on Albi-Boric Argosols. (2) The dark-coniferous spruce-fir forest (DCSF) (42°09'N, 128°08'E) was sampled at 1250 m, the annual mean temperature is 0.3°C, the annual mean precipitation is 811 mm, the O horizon is at 0-12 cm in depth with silty loam, and the A horizon is at 12-30 cm in depth with loamy sand. Tree species are dominated by *Abies nephrolepis* and *Picea jezoensis* on Bori-Udic Cambosols. (3) The dark-coniferous spruce forest (DCS) (42°05'N, 128°04'E) was sampled at 1680 m, the annual mean temperature is -2.3°C, the precipitation is 967 mm, the O horizon is at 0-8 cm in depth with silty loam, and the A horizon is at 8-32 cm in depth with loamy sand. Tree species are dominated by *Picea jezoensis* on Umbri-Gelic Cambosols. (4) The Ermans birch forest (EB) (42°03'N, 128°04'E) was sampled at 1950 m, the annual mean temperature is -3.3°C, the precipitation is 1038 mm, the O horizon is at 0-19 cm in depth with sandy loam, and the A horizon is at 19-36 cm in depth with sandy loam. Tree species are dominated by *Betula ermanii* on Permi-Gelic Cambosols.

Soil sampling

In each forest type, soil samples were collected from 4 independent replicates (10 × 10 m) at random on 18 June 2009. After removing the aboveground plant debris, soil samples were taken using a soil corer (5 cm in diameter) and separated into the O and A horizons in the field. Each soil sample was a composite comprised of 6 cores. Visible roots and organic residue were removed from the samples. Then the samples were stored in individual plastic bags, kept at 4°C, and processed within 1 wk. Fresh soils were used to analyze soil moisture, microbial biomass carbon, and nematodes, and air-dried ones were used to analyze the other soil properties. Soil properties including soil moisture, pH, soil total organic carbon (TOC; by the potassium dichromate heating method), and total nitrogen (by the Kjeldahl method) were determined by standard methods (McGill and Figueiredo 1993, Rowell 1994). Microbial biomass carbon was measured using the chloroform fumigation and extraction method (Vance et al. 1987).

Extraction and identification of soil nematodes

Nematodes were extracted from 100 g of fresh soil by a modified cotton-wool filter method (Liang et al. 2009). Abundances of nematodes were expressed as individuals per 100 g (ind./100 g) of dry soil, and at least 150 nematodes from each sample were identified to genus level using an inverted compound microscope. Nematodes were divided into 4 trophic groups according to the feeding habits and life history characteristics (Yeates et al. 1993): bacterivores, fungivores, omnivores-carnivores and plant parasites. Although feeding habits of the Tylenchidae are unclear (Yeates et al. 1993), they were allocated to fungivores in this study since recently growing evidence appears to support this (Neher et al. 2005, Okada et al. 2005, Yeates 2007).

Nematode community analyses

The following nematode community indices were calculated: (1) Simpson's index for dominance (λ); (2) the Shannon-Weaver diversity index (H'); (3) richness (SR); (4) evenness (J'); (5) the modified maturity index (ΣMI); and (6) the nematode channel ratio (NCR) (Yeates and Bongers 1999, Yeates 2003).

Statistical analyses

Nematode abundances were ln(x + 1)-transformed, and relative abundances of trophic groups were transformed as the arcsine of the square root prior to the statistical analysis for normality of the data. All data were analyzed through a two-way analysis of variance (ANOVA) to determine the effects of forest type, horizon, and their interaction. Multiple comparisons were conducted by Duncan's multiple-range tests among forest types. All statistical analyses were performed using SPSS (vers.13.0; SPSS, Chicago, IL, USA). Differences at the $p < 0.05$ level were considered statistically significant. Relationships between the community structure and environmental parameters were analyzed by a canonical correspondence analysis (CCA) using CANOCO software (ter Braak and Šmilauer 2002). In order to depict associations among the nematode taxa and between nematodes and environmental factors, forest types were treated as a nominal (0, 1) environmental variable.

RESULTS

Nematode abundance and community composition

The total nematode abundance was significantly affected by the forest type, horizon, and their interaction ($p < 0.05$). The highest abundance (3367 ind./100 g dry soil) was found in the O horizon under the MCB, and the lowest (355 ind./100 g dry soil) was in the A horizon under the DCS (Table 1).

There were similar patterns between the abundance of trophic groups and total nematodes among forest types and between horizons (Table 1). Abundances of trophic groups were significantly higher under the MCB and EB than under the DCSF and DCS ($p < 0.05$) for both the O and A horizons, with the exception of bacterivores and omnivores-carnivores in the A horizon. A significant difference in the abundance of each trophic group was found between horizons with the exception of plant parasites ($p < 0.05$). Far fewer plant parasites were found in the DCSF and DCS than in the MBC and EB, and no plant parasites were present in half of the sampling sites of the DCSF. Only under the MCB were proportions of plant parasites, bacterivores, and omnivores-carnivores significantly affected by the horizon, with higher values for bacterivores and omnivores-carnivores and lower values for plant parasites in the O horizon (Fig. 1). Fungivores were found

Table 1. Abundances of total nematodes and their trophic groups (mean ± S.E.) (individuals/100 g dry soil) in the O and A horizons in different forest types at Changbai Mountain. MCB, mixed coniferous-broadleaf forest; DCSF, dark-coniferous spruce-fir forest; DCS, dark-coniferous spruce forest; EB, Ermans birch forest

Soil nematode	Horizon	MCB	DCSF	DCS	EB
Total abundance	O	3367 ± 363	1086 ± 164	664 ± 146	3139 ± 358
	A	1265 ± 102	470 ± 64	355 ± 49	737 ± 176
Bacterivores	O	728 ± 89	318 ± 46	216 ± 55	475 ± 109
	A	168 ± 27	166 ± 39	105 ± 32	139 ± 48
Fungivores	O	1827 ± 216	677 ± 150	280 ± 42	2010 ± 357
	A	584 ± 139	254 ± 20	161 ± 32	458 ± 113
Plant parasites	O	445 ± 96	2 ± 2	14 ± 14	62 ± 42
	A	450 ± 81	3 ± 3	7 ± 3	25 ± 16
Omnivores-carnivores	O	368 ± 48	90 ± 14	155 ± 72	592 ± 121
	A	63 ± 15	47 ± 16	83 ± 16	115 ± 27

to be the dominant trophic group and comprised approximately 45%-63% of the total nematode abundance. No significant difference in the proportion of fungivores was found among forest types or between horizons.

In total, 62 nematode taxa were identified among the 4 forest types (Table 2). The total number of genera significantly varied among forest types, with 51 genera in the MCB, 28 in the DCSF, 37 in the DCS, and 33 in the EB. The relative abundances of all genera identified were not affected by the horizon ($p < 0.05$) with the exception of *Epidorylaimus*, the proportion of which was significantly higher in the A horizon (4.11%) than in the O horizon (1.69%) ($p < 0.05$). *Tylenchus*, *Filenchus*, and *Plectus* were dominant genera (with relative abundances of > 5%) in all forest types. *Malenchus* was the dominant nematode genus in all observed types of soil, except in the EB.

Nematode community indices

The horizon effect was not significant on any community indices, and therefore results are not shown according to the O or A horizon. Significant differences in λ, H', J', SR, ΣMI, and NCR were observed among the different forest types ($p < 0.05$) (Table 3). The decreasing trends in H', ΣMI, and SR, and an increasing trend in λ were found from the MCB through the DCS and EB to the DCSF. Values of the NCR were higher in the DCSF and DCS than in the MCB and EB. Nematode community indices, including λ, H', J', ΣMI, and SR, were significantly correlated with the C:N ratio (Table 3).

Relationships among nematode abundances, forest types, and soil environmental parameters

The observed soil properties, except pH, significantly differed among the forest types in the 2 soil layers ($p < 0.01$). Soil pH was found to decrease with increasing elevation (from the MCB to EB) but did not differ between the 2 soil layers. There were similar trends in variations of soil properties in both horizons. Higher values of TOC, TN, microbial biomass carbon, and soil moisture were observed in the O horizon in the MCB and EB.

The CCA diagram revealed that elevation, MBC, the C:N ratio, and pH were relatively more important variables than the others in explaining variations in the nematode community composition in different forest types at Changbai Mt. (Fig. 2). Among these variables, elevation explained 34.7% of the variations in soil nematode compositions. For the 1st and 2nd axes, eigenvalues were 0.281 and 0.143, and genera-environment correlations were 0.967 and 0.862, respectively.

Most of the nematode genera were positioned in the center of the diagram, such as *Anaplectus*, *Epidorylaimus*, *Filenchus*, *Plectus*, and *Tylenchus*. The DCSF and DCS were located closer to the lower left-hand side of the diagram and showed similar nematode assemblages, such as *Aporcelaimellus*, *Microdorylaimus*, *Plectonchus*, *Thonus*, and *Wilsonema*. In the EB, nematode

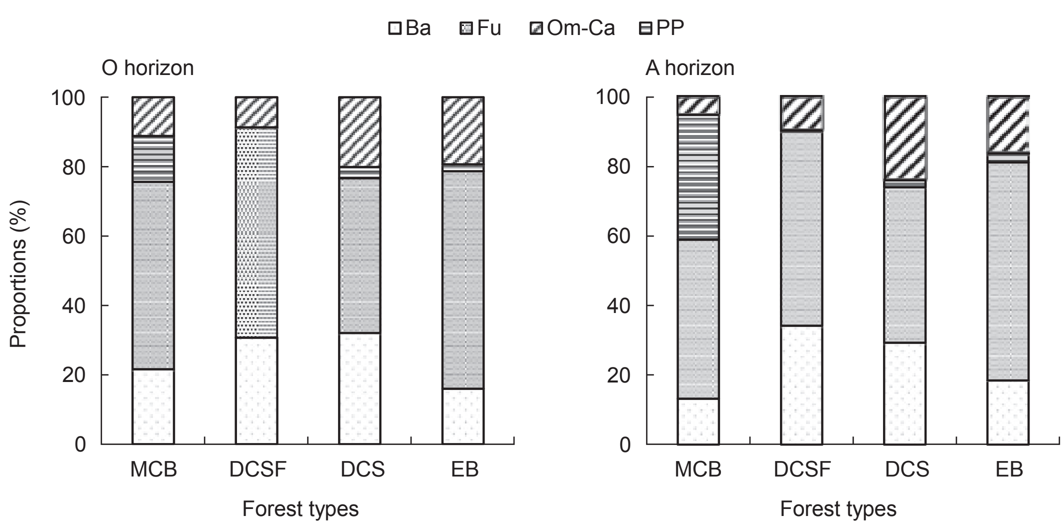

Fig. 1. Proportions of nematode trophic groups in the O and A horizons under different forest types at Changbai Mountain. Ba, bacterivores; Fu, fungivores; Om-Ca, omnivores-carnivores; PP, plant parasites.

genera such as *Aglenchus*, *Boleodorus*, *Lelenchus*, and *Tripyla* were negatively correlated with pH and positively correlated with elevation. In the MCB, *Mylonchulus*, *Rotylenchus*, *Rotylenchulus*, and *Paratylenchulus* were negatively correlated with elevation and positively correlated with pH.

DISCUSSION

Our study mainly focused on soil nematode assemblages in the Changbai Mountain Natural Reserve. With increasing elevation, there are diverse climates and various plant species. Beneficial protection of Changbai Mt. has ensured that little human disturbance has occurred. These all provide the various natural living environments for soil nematodes, allowing them to diversify.

Forest-type and horizon effects on abundances of soil nematodes

The MCB had the greatest nematode abundance, while the DCS had the lowest. A great abundance of soil nematodes may be related to the highest net primary production and soil fertility, and richest nutrients under the mixed stand (Zhang et al. 2003). Compared to coniferous needles (such as in the DCSF and DCS), deciduous birch leaves (such as in the EB) provide a higher quality of

Table 2. Proportional contributions (%) of various genera to the nematode assemblages in different forest types at Changbai Mountain

Genus	MCB	DCSF	DCS	EB	Genus	MCB	DCSF	DCS	EB
Plant parasites					*Cobbonchus*	0.6	0	0.1	0
Axonchium	0.2	0	0	0	*Comiconchus*	0	0	0.2	0
Cephalenchus	0	0.3	0.1	0.4	*Epidorylaimus*	0.5	2.6	3.8	4.7
Criconemoides	1.1	0	0	0	*Eudorylaimus*	0.5	1.5	3.6	1.5
Helicotylenchus	1.9	0.1	0.1	1.3	*Labronema*	0.1	0.3	0.2	0.3
Macroposthonia	2.5	0	0	0	*Laimydorus*	0.2	0	0	0
Nagelus	0	0	2.3	0	*Longidorella*	0.5	0	0.2	0
Ogma	0.1	0	0.1	0	*Mesodorylaimus*	0.3	0	0	0
Pararotylenchus	4.1	0	0	0	*Microdorylaimus*	0.7	1.4	8.7	2.5
Paratrichodorus	0	0	0	0.1	*Mylonchulus*	0.2	0	0	0
Paratylenchus	0.6	0	0	0.1	*Nygolaimus*	0.4	0	0	0
Rotylenchulus	6.3	0	0	0	*Paraxonchium*	0	0.3	0	0
Rotylenchus	6.7	0	0	0.5	*Parkellus*	0.2	0.1	1.2	0.4
Trichodorus	1.1	0	0	0	*Thonus*	0.7	2.0	1.6	0.7
Bacterivores					*Torumanawa*	0	0	0.1	0
Acrobeloides	1.2	7.6	3.0	1.7	*Tripyla*	1.7	0	0.1	6.8
Alaimus	1.7	2.0	1.6	0.8	*Trischistoma*	0.6	0	0	0
Anaplectus	1.3	0.8	1.4	2.2	Fungivores				
Bastiania	0.4	0	0	0	*Aglenchus*	0	0	0	2.6
Cephalobus	0.4	0.5	0.6	0	*Aphelenchoides*	1.3	2.7	1.0	0.9
Chronogaster	0.1	0.3	0.1	1.8	*Aphelenchus*	0.7	0	0	0
Euteratocephalus	1.8	2.3	2.6	2.3	*Boleodorus*	0.5	0	0	3.9
Monhystera	0.5	0	0	0.3	*Coslenchus*	0	0	0.8	0.4
Odontolaimus	0.1	0	0	0	*Diphtheropora*	3.5	0	0.7	1.4
Panagrolaimus	1.2	0	0	0	*Ditylenchus*	0	0.1	0.6	0.9
Plectonchus	0.3	1.1	3.3	0	*Ecphyadophora*	0.4	0.1	0	0
Plectus	7.4	15.7	11.3	5.9	*Filenchus*	13.5	33.6	11.4	35.5
Prismatolaimus	1.0	0.8	5.4	0.1	*Lelenchus*	0.2	0	0.9	5.7
Teratocephalus	0	0	1.0	2.1	*Malenchus*	16.8	6.4	11.3	0
Wilsonema	0	1.3	0.5	0	*Proleptonchus*	0.9	0	0	0
Omnivores-carnivores					*Tenunemellus*	0.2	0	0	0
Aporcelaimellus	0.5	0.4	0.5	0.3	*Tylencholaimellus*	6.6	9.4	1.2	3.9
Clarkus	0.4	0.5	1.6	0.5	*Tylenchus*	5.0	5.6	16.8	7.4

MCB, mixed coniferous-broadleaf forest; DCSF, dark-coniferous spruce-fir forest; DCS, dark-coniferous spruce forest; EB, Ermans birch forest.

water-soluble nutrients which are beneficial to soil nematodes (Keith et al. 2009). Coniferous needles are unfavorable resources for soil microorganisms due to the accumulation of high concentrations of polyphenols, which lower the conversion of needle litter carbon into microbial biomass carbon (Scheu et al. 2003). Thus, higher nematode population densities under the EB compared to the DCSF and DCS perhaps indicate higher decomposition rates under deciduous trees.

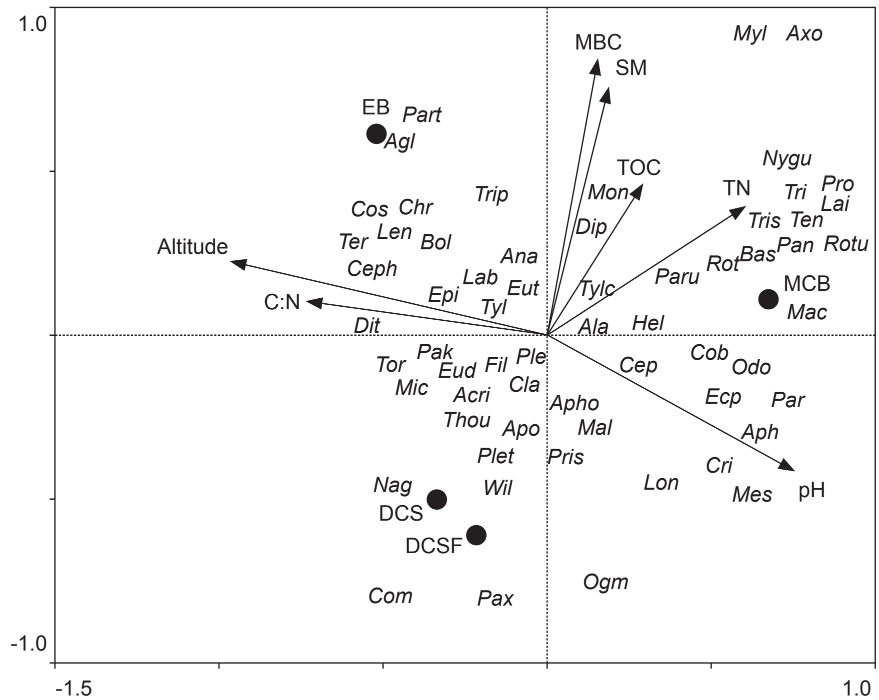

Fig. 2. Canonical correspondence analysis (CCA) diagram of soil nematode communities under different forest types at Changbai Mountain. *Acri*, *Acrobeloides*; *Apho*, *Aphelenchoides*; *Ceph*, *Cephalenchus*; *Part*, *Paratrichodorus*; *Paru*, *Paratylenchus*; *Plet*, *Plectonchus*; *Pris*, *Prismatolaimus*; *Rotu*, *Rotylenchulus*; *Trip*, *Tripyla*; *Tris*, *Trischistoma*; *Tylc*, *Tylencholaimellus*; the remaining genera were abbreviated with the 1st 3 letters of their full name (see Table 2).

Table 3. Nematode community indices (mean ± S.E.) and their correlations with soil environmental parameters under different forest types at Changbai Mountain

	λ	H'	ΣMI	J'	SR	NCR
MCB	0.11 ± 0.01b	2.63 ± 0.05a	2.62 ± 0.04a	0.83 ± 0.01a	3.12 ± 0.21a	0.27 ± 0.04ab
DCSF	0.21 ± 0.02a	2.02 ± 0.06b	2.36 ± 0.03b	0.73 ± 0.01b	2.26 ± 0.09b	0.36 ± 0.04ab
DCS	0.12 ± 0.01b	2.39 ± 0.04b	2.53 ± 0.05a	0.84 ± 0.01a	2.68 ± 0.18ab	0.41 ± 0.05a
EB	0.18 ± 0.02ab	2.27 ± 0.10b	2.50 ± 0.04a	0.78 ± 0.02ab	2.46 ± 0.20b	0.21 ± 0.03b
Correlation						
SOC	ns	**	ns	ns	ns	ns
TN	*	**	ns	ns	ns	ns
C:N	**	**	*	*	*	ns
MBC	ns	ns	ns	ns	ns	*
SM	ns	*	ns	ns	ns	*
pH	ns	ns	ns	ns	*	ns

Forest types are defined in the legend to figure 1. λ, Simpson's index for dominance; H', Shannon-Weaver diversity index; ΣMI, maturity index; J', evenness; SR, richness; NCR, nematode channel ratio. MBC, microbial biomass carbon; SM, soil moisture; TN, total nitrogen; TOC, total soil organic carbon. Different lowercase letters within a row indicate a significant difference ($p < 0.05$) among forest types in each horizon. * $p < 0.05$ and ** $p < 0.01$ indicate significant differences; ns, not significant.

In this study, abundances of total nematodes and tropic groups, except plant parasites, were higher in the O horizon than in the A horizon. Our results are consistent with those reported by Yeates (2007) in forest ecosystems. Fungivores were a dominant group in both the O and A horizons in the 4 forest types. Soil pH fluctuated between 4.12 and 5.82. A lower soil pH is favorable for fungi due to their greater tolerance of acidity and thus reduced competition from other microorganisms (Yeates 1996). Compared to the MCB and EB, there were smaller populations, but greater proportional contributions of bacterivores in the DCSF and DCS (32.4% and 30.6%, respectively). Keith et al. (2009) reported that pine roots promote bacterivores compared to birch roots, which shows that root inputs of different species may be important in determining trophic compositions of soil food webs. This result was also mirrored by the channel index, NCR, which also indicated higher bacterial decomposition in the DCSF and DCS compared to the MCB and EB.

Forest-type and horizon effects on soil nematode diversity

All nematode community indices significantly responded to the effect of forest types at different elevations, but not to a horizon effect. Higher values of nematode diversity, maturity, and generic richness were observed at a relatively low elevation in the MCB among the different forest types. Similarly, Yeates (2007) proved that higher biodiversity and species richness occurred in forest soils at lower elevations, which were associated with more-sustainable and -resilient ecosystems. It can be concluded that the soil ecosystem in the MCB was more favorable for maintaining ecosystem stability and biodiversity. Similar results on the nematode fauna were also observed in spruce forests of the Beskedy Mountains, Czech Republic (Háněl 1996) and in deciduous forests of the Vihorlat Mountains, Slovakia (Háněl and Čerevková 2010). However, the diversity of soil nematodes in the DCSF did not follow this pattern with elevation. In the DCSF at a lower elevation than the DCS and EB, the diversity and maturity indices (as indicated by the H', ΣMI, J', and SR) were the lowest. Popovici and Ciobanu (2000) reported that nematode richness did not appear to be affected by elevation under most conditions. This complex phenomenon indicates that elevation is not the only limiting factor, and the forest type is also very important to soil nematode diversity.

Effects of soil environmental parameters on nematode communities in the different forest types

Forest types were divided into 3 groups with the coniferous DCSF and DCS as 1 group according to the CCA. Similar habitats were classified by nematode genera which validated the bioindication of soil nematode communities into different forest types. Wall et al. (2010) and Li et al. (2010) concluded that the distribution of soil organisms (such as microbes and ciliates) can be explained to a great extent by simple soil properties such as soil moisture, pH, and the C:N ratio. Among soil environmental variables, the elevation, C:N ratio, pH, and microbial biomass carbon played key roles in explaining variations in the nematode community composition. The nematode communities in different forest types differed not only due to the resources provided for the decomposer community, i.e., needles vs. leaves, but also due to the their habitat characteristics such as soil pH (Scheu et al. 2003). The grazing of soil nematodes on microbes increased the turnover of microbial populations, which may be the reason why microbial biomass carbon was one of the main determining factors of the distribution of nematode genera. Microbial biomass is crucial for microbivores such as bacterivores and fungivores, and also omnivorous nematodes. The top-down control of microbes by soil nematodes was the principle mechanism by which soil nematodes make positive contributions to soil processes (Yeates 2007).

In conclusion, significant differences in soil nematode abundance and diversity were observed among different forest types along an elevational gradient at Changbai Mt. Both forest type and elevation were crucial for the distribution of soil nematode communities. The soil C:N ratio, microbial biomass carbon, and pH were important factors that affected the soil nematode fauna in the present study.

Acknowledgments: This research was conducted at the Research Station of Changbai Mountain Forest Ecosystems, Chinese Academy of Sciences. We thank Prof. S. Han, Dr. Q. Li, and Mr. G. Dai for assistance with sampling. This study was financially supported by the National Natural Science Foundation of China (31170577 and 31170484) and the Youth Fund for Creative Research Groups, Institute of Applied Ecology, Chinese Academy of Sciences.

REFERENCES

Bakonyi G, P Nagy, E Kovács-Láng, E Kovács, S Barabás, V Répási, A Seres. 2007. Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. Appl. Soil Ecol. **37:** 31-40.

Gong ZT, GL Zhang, ZC Chen. 2007. Pedogenesis and soil taxonomy. Beijing: Science Press, 626 pp. (in Chinese)

Háněl L. 1996. Soil nematodes in five spruce forests of the Beskydy Mountains, Czech Republic. Fundament. Appl. Nematol. **19:** 15-24.

Háněl L. 2008. Nematode assemblages indicate soil restoration on colliery spoils afforested by planting different tree species and by natural succession. Appl. Soil Ecol. **40:** 86-99.

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

Keith AM, RW Brooker, GHR Osler, SJ Chapman, DFRP Burslem, R van der Wal. 2009. Strong impacts of below ground tree inputs on soil nematode trophic composition. Soil Biol. Biochem. **41:** 1060-1065.

Körner C. 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. **22:** 569-574.

Li J, MG Li, J Yang, Y Ai, RL Xu. 2010. Community characters of soil ciliates at Baiyun Mountain, Guangzhou, China. Zool. Stud. **49:** 713-723.

Liang WJ, YL Lou, Q Li, S Zhong, XK Zhang, JK Wang. 2009. Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in Northeast China. Soil Biol. Biochem. **41:** 883-890.

McGill WB, CT Figueiredo. 1993. Total nitrogen. *In* MR Carter, ed. Soil sampling and methods of analysis. Boca Raton, FL: Lewis Publishers, pp. 201-211.

Neher DA, J Wu, ME Barbercheck, O Anas. 2005. Ecosystem type affects interpretation of soil nematode community measures. Appl. Soil Ecol. **30:** 47-64.

Okada H, H Harada, I Kadota. 2005. Fungal feeding habits of six nematode isolates in the genus. Soil Biol. Biochem. **37:** 1113-1120.

Pen-Mouratov S, N Shukurov, Y Steinberger. 2010. Soil free-living nematodes as indicators of both industrial pollution and livestock activity in Central Asia. Ecol. Indic. **10:** 955-967.

Popovici I, M Ciobanu. 2000. Diversity and distribution of nematode communities in grasslands from Romania in relation to vegetation and soil characteristics. Appl. Soil Ecol. **14:** 27-36.

Rowell DL. 1994. Soil science: methods and applications. London: Longman, 350 pp.

Scheu S, D Albers, J Alphei, R Buryn, U Klages, S Migge et al. 2003. The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forests. Oikos **101:** 225-238.

ter Braak CJF, P Šmilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (vers. 4.5). Ithaca, NY: Microcomputer Power, 500 pp.

Tomar VVS, W Ahmad. 2009. Food web diagnostics and functional diversity of soil inhabiting nematodes in a natural woodland. Helminthologia **46:** 183-189.

Tong FC, YH Xiao, QL Wang. 2010. Soil nematode community structure on the northern slope of Changbai Mountain, Northeast China. J. For. Res. **21:** 93-98.

Vance ED, PC Brookes, DS Jenkinson. 1987. An extraction method for measuring soil microbial biomass carbon. Soil Biol. Biochem. **19:** 703-707.

Wall DH, RD Bardgett, EF Kelly. 2010. Biodiversity in the dark. Nat. Geosci. **3:** 297-298.

Wang K-H, R McSorley, RN Gallaher. 2009. Can nematode community indices elucidate plant health conditions? J. Nematol. **41:** 392.

Yeates GW. 1996. Diversity of nematode faunae under three vegetation types on a pallic soil in Otago, New Zealand. NZ J. Zool. **23:** 401-407.

Yeates GW. 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils **37:** 199-210.

Yeates GW. 2007. Abundance, diversity, and resilience of nematode assemblage in forest soils. Can. J. For. Res. **37:** 216-225.

Yeates GW, T Bongers. 1999. Nematode diversity in agro-ecosystems. Agric. Ecosyst. Environ. **74:** 113-135.

Yeates GW, T Bongers, RGM de Goede, DW Freckmen, SS Georgieva. 1993. Feeding-habits in soil nematode families and genera: an outline for ecologists. J. Nematol. **25:** 315-331.

Zhang M, XK Zhang, WJ Liang, Y Jiang, GH Dai, XG Wang, SJ Han. 2011. Distribution of soil organic carbon fractions along the altitudinal gradient in Changbai Mountain, China. Pedosphere **21:** 615-620.

Zhang N, GR Yu, ZL Yu, SD Zhao. 2003. Analysis on factors affecting net primary productivity in Changbai Mountain based on process model for landscape scale. Chin. J. Appl. Ecol. **14:** 659-664. (in Chinese with English abstract)

Zhao SQ, JY Fang, ZJ Zong, B Zhu, MH Shen. 2004. Composition, structure and species diversity of plant communities along a gradient on the northern slope of Mt. Changbai, Northeast China. Biodivers. Sci. **12:** 164-173. (in Chinese with English abstract)

Zhu B, XP Wang, JY Fang, SL Piao, HH Shen, SQ Zhao, CH Peng. 2010. Altitudinal changes in carbon storage of temperate forests on Mt Changbai, Northeast China. J. Plant Res. **123:** 439-452.