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Community structure and diversity of soil nematodes around Lake Paiku in Tibet, China

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Abstract

The diversity and community structure of soil nematodes around Lake Paiku in Mount Qomolangma (Mt. Everst) National Nature Reserve were investigated, to obtain soil ecosystem information, assess local soil quality, and provide the basis for environmental protection. Twelve plots were selected for typical vegetation communities around the lake. Within each plot, soil samples were collected from depths of 0 to 25 cm. The Baermann tray method was used to extract nematodes. Overall, we acquired 2,272 nematodes belonging to 2 classes, 5 orders, 32 families and 48 genera. The nematode density was 0–413 individuals per 100 g dry soil (average 109). Bacterivores, predators and omnivores were the dominant trophic groups. The individual density and genus numbers of soil nematodes were highest in the northeast and southeast corners of the lake. For most of the area studied, soil nutrients were at a medium level and there was no human disturbance. The energy flow of the soil food web tends to be via fungus decomposition channels. The redundancy analysis shows that soil-available P, pH, alkali-hydrolytic N, and soil-available K have strong effects on the soil nematode community, whereas the soil's total N, organic matter and water content have only minor effects. Soil-available P and pH were negatively correlated with nematode diversity. Soil nematodes showed surface aggregation; the soil food webs tend to have complex structures because of the presence of K-strategist organisms; the lakeshore ecosystem is in the late stage of succession and relatively stable. The increasing amount of soil-available P and increasing pH value corresponded to reduced biodiversity and unstable soil nematode communities. A greater diversity of nematodes were found in the Lake Paiku region in comparison to studies carried out in alpine meadows of the Chang Tang (or Northern Tibet) Grasslands.

Profile

Protected area

Mount Qomolangma (Mt. Everst) National Nature Reserve

Mountain range

Himalaya

Country

China

Introduction

Mount Qomolangma National Nature Reserve (QNNR) is located in the northern ranges of the Himalayas in Tibet, China. Together with the Nepalese Sagamada National Park in the south, it forms a complete and rare alpine forest ecosystem, with an average altitude of 4,200 m, making it the highest nature reserve in the world (Cidanlunzhu et al. 1997). The reserve is characterized by its polar alpine ecosystem, includes the highest peak on earth, and serves as an important model for studying global climate change and biological succession (Olson et al. 1998; Sun et al. 2012). Among seven core reserve zones in QNNR, Qomolangma-Shishapangma is the largest and is typical of the semi-arid plateau shrub and grassland ecosystem in the northern ranges of the Himalayas (Ministry of Ecology and Environment PRC 2018). The core zones of a nature reserve not only typify the natural zones, but are also the *background* that determines the ecological quality of the reserve and its adjacent areas, and their development. They are also a source of species resources in a region, providing the research base for saving and protecting rare and endangered species, and for exploring the sustainable use of biological resources.

In the zoogeographical regionalization of the world, QNNR is located on the dividing line between the palearctic and Oriental regions. The great range of its vertical elevation gradients and the diversity of unique species in the region have attracted the attention of scholars from home and abroad. Since QNNR was established nearly 30 years ago, ecological investigation and research have focused predominantly on aboveground ecosystems such as glaciers (Immerzeel et al. 2013; Nie et al. 2017; Nie et al. 2012), climate (Wang et al. 2018; Dunzhu 2009), vegetation (Shi et al. 2012; Shi et al. 2012; Nie et al. 2012; Zhang et al. 2006), and megafauna (Chen et al. 2017; Li et al. 2013; Pan et al. 2013; Qian et al. 1974). Less research has been done on underground ecosystems and in the lake region (Wang et al. 2018; Wang et al. 2006). So far, no research has looked at soil nematodes.

As global climate change continues to intensify and population growth puts pressure on sustainable development, the Qomolangma region is facing urgent ecological challenges. Due to the region's high altitude,

Figure1 – Location of each sample plot (see Table 1) and the surrounding terrain. © 2022 Maxar Tecnologies, 2022 CNES / Airbus. 28°57'45.20" N, 85°28'47.43' E, elev. 4.872m.

cold dry climate, and slow plant growth, it is difficult for the ecosystem to recover if it is degraded. From 2016 to 2018, field investigations were carried out in the Lake Paiku area (in the Qomolangma-Shishapangma core zone of the QNNR) with a focus on fauna and flora resources and environmental quality. Lake Paiku is the largest lake in the core reserve; its surrounding area consists mainly of sensitive semi-arid shrubs and grasslands, which need to be protected urgently. The investigations involved both above-ground ecosystems and soil-dwelling nematodes, aiming to provide scientific support for biodiversity and environmental conservation, and resource exploitation in QNNR and its adjacent areas.

Nematodes are abundant and their assemblages diverse. Their species composition is a bio-indicator of substrate texture, climate, biogeography, organic inputs, and both natural and anthropic disturbances (Yeates 1984). Nematodes interact with other organisms in the soil food web, contributing to the stability of the soil ecosystem, and promoting energy flow and material circulation.

Climate change is one of the most serious threats to lake ecosystems generally, and Lake Paiku specifically has attracted remarkable scientific interest in recent decades. Dekey et al. (2016) and Dai et al. (2013) pointed out that the area and water level of Lake Paiku have fluctuated greatly, with a general decreasing trend, in the last 40 years. These retreating water tables occurred mainly in the northeast, southeast and southwest corners. An earlier study (Zhao 2019) showed that the plant communities in the lake area vary significantly in composition and quantity; species diversity has decreased from the middle of the lake shore towards the south and north sides.

The present study focuses on the structure and diversity of the soil nematode community in QNNR, aiming to answer the following questions: (1) Is the soil nematode diversity in line with that of plant species in the lake area? (2) What is the condition of the soil ecosystem under minor disturbance, as measured by the functional index of the soil nematode community? (3) Is the rate of the biotransformation of soil nutrients increasing or decreasing under protected conditions?

Materials and method

Study site

Lake Paiku is a brackish lake located in Qomolangma-Shishapangma core zone, QNNR, at the northern

Table 1 – Geographical location and plant community composition of each sample plot.

Plots	Survey method	Longitude (E)	Latitude (N)	Altitude (m)	Edificators of plant community	Cover degree (%)	Species quantity
1	50 m line transect	85°38'25.86''	29°1'5.77''	4,631	*Iris loczyi* Kanitz+ *Achnatherum splendens* (Trin.) Nevski	60	5
2	50 m line transect	85°37'1.73''	29°2'13''	4,665	*Festuca ovina* + *Artemisia younghusbandii*	70	11
3	50 m line transect	85°40'58.92''	28°45'47.26''	4,621	*Astragalus strictus* + *Elymus tangutorum*	75	11
4	10 m×10 m quadrat	85°41'7.05''	28°50'10.29''	4,645	*Caragana versicolor* Benth. + *Artemisia wellbyi*	30	4
5	10 m×10 m quadrat	85°41'7.06''	28°50'11.45''	4,645	*Caragana versicolor* Benth. + *Artemisia wellbyi*	40	6
6	50 m line transect	85°41'59.84''	28°48'18.47''	4,659	*Thermopsis lanceolata* + *Artemisia younghusbandii*	75	4
7	50 m line transect	85°41'59.59''	28°48'18.47''	4,659	*Poa tibetica* + *Carex moorcroftii*	90	11
8	50 m line transect	85°47'20.79''	28°44'19.47''	4,676	*Astragalus strictus* + *Carex angustifructus* + *Stipa purpurea*	35	11
9	50 m line transect	85°39'48.55''	28°45'22.43''	4,647	*Astragalus tibetanus* + *Roegneria aristiglumis*	70	6
10	10 m×10 m quadrat	85°32'34.37''	28°45'44.39''	4,614	*Caragana* Fabr. + *Orinus* Hitchc.	65	8
11	1 m×10 m quadrat	85°34'15.49''	28°46'20.56''	4,589	*Carex moorcroftii*	95	10
12	10 m×10 m quadrat	85°31'25.89''	28°51'7.73''	4,633	*Ceratocarpus latens* + *Artemisia younghusbandii*	35	5

foot of Mt. Shishapangma, in Nyalam County, Xigaze City, Tibet Autonomous Region, PR China. The geographical coordinates of the lake are N 28° 20' to N 26° 65', and E 85° 20' to E 86° 50' (see Figure 1). The lake surface is 4,594 m above sea level; the area of the watershed that falls within the reserve covers approximately 2,397 km^2, of which glaciers and Lake Paiku account for 5.6% and 11.3%, respectively. Precipitation and glacial meltwater are the main replenishment sources of Lake Paiku (Chinese Academy of Sciences 1983; Lei et al. 2014).

The Lake Paiku region is a plateau with a temperate monsoon and semi-arid climate; it has typical cold and continental climate characteristics, sufficient sunshine (2,723.5 hours annually), and an obvious distinction between wet and dry seasons (The Meteorological Bureau of the Tibet Climate Center 2013). The area is located in the shrubby sub-region of alpine steppe in southern Tibet, according to the Vegetation Regionalization of China. The local grasslands are characterized by *Stipa purpurea*; grasslands dominated by *Artemisia*, *Carex* spp. and *Caragana versicolor* Benth were also observed in this region.

Soil sampling and testing

At the end of August 2017, 12 sample plots measuring 50 m×50 m were selected to include representative plant communities and different topography (different slope directions in an area that is relatively flat) around Lake Paiku's riparian zone. (See Table 1 for details.) Bulk soil samples were obtained by pooling 5 subsamples from depths of 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, and 20–25 cm; soil cores measured 7 cm in diameter.

Soil samples were taken from at least 5 points, randomly, in each plot, giving a total of 60 bulk soil samples. These were packed in polyethylene bags, labelled, refrigerated, and stored in an insulated box with ice bags. The oven-drying method was used to calculate soil moisture content. Approximately 10 grams of fresh soil with a scale of 1/10,000 were weighed, and dried to a constant weight at 105°C (about 4 hours). The water content was then calculated (as a %), using the following formula:
(Fresh soil sample weight – dried soil sample weight) ×100 / fresh soil sample weight = soil moisture content (%)

Soil chemical properties were examined:
- the pH value was measured using the glass electrode method, in a 1:2.5 (soil:water) suspension;
- organic matter was measured using the potassium dichromate oxidation titration-external heating method;
- total phosphorus content was measured using the NaOH fusion-Molybdenum blue colorimetric method;
- total potassium was measured by NaOH fusion-flame photometer;
- available phosphorus was measured by the NaHCO_3–Molybdenum blue colorimetric method;
- alkali hydrolysis nitrogen was measured using diffusion.

Identification of soil nematodes

Nematodes were extracted from 30 g soil samples using a Baermann tray, kept at room temperature for 48 h (Oostenbrink 1960), and subsequently sieved using a 45 μm mesh. There can be up to several thousand nematodes in 100 g soil, especially soil samples with high humus content. For the sake of uniformity and for accurate counting, the sample weight was set at 30.0 g. The nematodes collected were fixed in 5% formaldehyde solution and mounted as temporary slides under a dissecting microscope. The nematode density was converted into number of individuals per 100 g of dry soil. Genus-level identifications were made using Olympus CX23 (Japan) according to available references (Bongers 1988; Yin 1998; Xie 2005). Dominant genera are those which represent more than 10% of the total; those accounting for 1% to 10%, and less than 1% were considered common and rare genera respectively.

Analyses of the diversity of the soil nematode communities

Shannon-Weiner diversity index:
$H' = -n_i / N \times \ln (n_i / N)$
Pielou evenness index: $J' = H' / \ln S$
Simpson dominance index: $\lambda = \Sigma(n_i / N)^2$
Margelef abundance index: $SR = (S - 1) / \ln N$

S ... number of groups
n_i ... number of individuals in group i
N ... total number of individuals of all groups in the community

Analyses of the functional groups of soil nematodes

Maturity Index, herbivore nematodes excluded (Bongers 1990): $MI = \Sigma c(i) \times p_i$
Plant Parasite Index (Bongers 1990): $PPI = \Sigma c(i) \times p_i$
Nematode Channel Ratio: $NCR = Ba / (Ba + Fu)$

p_i ... ratio of the non-plant parasitic soil nematode group i to the total number of individuals in the community (MI), or the ratio of the plant parasitic nematode group i to the total number of individuals in the community (PPI)
Ba and Fu ... the number of bacterivores and fungivores respectively
c(i) ... colonizer-persister value of the group i of non-plant-parasitic (or plant-parasitic) soil nematodes

Enrichment Index and Structure Index (Ferris et al. 2001)

The Enrichment Index (EI), based on the abundance of enrichment-opportunistic nematodes, can

be used as an indicator of the bacteria-mediated rapid decomposition of organic matter:
$EI = 100 \times (e / (e + b + s))$

The Structure index (SI), a weighted measure of the proportion of sensitive predator and omnivore nematodes, can be used as a sensitive indicator of soil food-web complexity:
$SI = 100 \times (s / (e + b + s))$

e, b and s ... enriched, basic and structural components respectively
$e = 3.2 \times Ba_1 + 0.8 \times Fu_2$
$b = 0.8 \times (Ba_2 + Fu_2)$
$s = Ba_n \times W_n + Fu_n \times W_n + Om_n \times W_n + Ca_n \times W_n$
$n = 3–5$
$W_3 = 1.8$
$W_4 = 3.2$
$W_5 = 5.0$

W ... weight coefficient
Om ... abundance of omnivorous nematodes
Ca ... abundance of predatory nematodes, and the subscript number
n ... c-p value of a nematode
c-p value ... colonizer-persister value

The higher the SI value is, plus the longer the food chain and the stronger the connectivity, plus the higher the EI value on the one hand, the more nutrients were input to the soil on the other. The particular distribution of the EI and SI results combined in the four quadrants (A, B, C, D) reflects the different succession states of the soil food webs.

When organic matter in soil is abundant and easily decomposed, the energy flow of the soil food web is more inclined to the bacterial decomposition channel; when organic matter in soil is scarce and difficult to decompose, the energy flow is more inclined to the fungal decomposition channel (Ingwersen et al. 2008).

Statistical analysis

A normality test was performed on the results of the soil's physical and chemical properties, and for nematode abundance. The data are normally distributed. Duncan's multiple comparative one-way ANOVA ($p < .05$) and Pearson's relevance analysis between multi-factors were conducted using IBM SPSS statistical 22.0 software to test the effects of different soil layers and soil physical and chemical properties on the structure of the soil nematode community. Redundancy analysis (RDA) and the visualization as graphs of correlations between soil traits and the structure of soil nematode communities were carried out using CANOCO 4.5.

Results

Plant community and soil properties

Twelve representative sample plots were selected covering various plant communities around Lake Paiku. The coordinates of each plot and its basic plant community are shown in Table 1.

Plots 1 and 2 were located in the northeast corner, 3–9 in the southeast corner, 10–12 near the southwest corner, and plot 12 near the central part of the lake's west bank. Sample plot 8 is the farthest from the lake.

Soil properties (pH, water content, total nitrogen, total potassium, available potassium and alkali-hydrolyzed nitrogen) were similar along the vertical profiles of the soil samples, while significant differences were observed among sample plots (Table 2). In terms of element content level, the soil along the bank of Lake Paiku has generally low fertility.

Structure of soil nematode communities

In total, 2,272 nematodes were acquired from soil samples taken from the 12 plots. The nematodes were identified as belonging to 48 genera, 32 families, 5 orders and 2 classes. The soil nematode density ranged from 0 to 413 individuals per 100 g dry soil (average 109 individuals); variations among plots were found to be significant ($F = 6.246$, $p < .001$). Specifically, the density of plots 5, 6 and 12 was lower than average while plots 2, 3, 7, 8 and 9 had relatively higher density. Soil nematode density in the 0–10 cm soil layer was significantly higher than that in the 10–25 cm layer ($F = 3.951$, $p = .008$). *Helicotylenchus* and *Cephalobus* were the two dominant genera in the soil nematode community.

The number of genera recovered ranged from 6 to 30 genera per plot, and inter-plot variations were found to be significant ($F = 14.189$, $p < .001$). Further variance analysis (Duncan) suggested that the 12 sam-

Table 2 – Physical and chemical properties of soil along the shore of Lake Paiku (mean values ± SD), and comparisons for them between sample plots and soil layers (ANOVA).

		pH	Soil		Total			Soil available		Alkali-hydrolyzable nitrogen (mg/kg)
			water content (g/kg)	organic matter (g/kg)	nitrogen (g/kg)	phosphorus (mg/kg)	potassium (%)	phosphorus (mg/kg)	potassium (mg/kg)	
		8.86±0.51	112.4±86.7	131.5±85.2	0.70±0.45	6.38±1.14	0.19±0.02	2.67±2.63	59.64±32.89	40.03±21.80
Plot	F	16.430	30.305	4.703	9.068	19.82	55.441	1.045	3.238	4.298
	Sig.	.000	.000	.003	.000	<.001	.000	.445	.016	.004
Clay	F	1.747	0.136	0.551	0.964	0.109	0.028	3.150	2.529	0.178
	Sig.	.203	.873	.586	.400	.979	.998	.067	.108	.838

Table 3 – Mean relative abundance (%) and c-p value of nematode genera in the sample plots.

Genus	c-p value	Sample plots											
		1	2	3	4	5	6	7	8	9	10	11	12
Fungivores													
Aphelenchus	2	0.5	10.2	3.1	2.2	0.0	15.3	0.6	5.1	2.5	0.8	1.0	0.0
Aphelenchoides	2	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0
Diphtherophora	3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ditylenchus	2	3.8	2.3	1.9	9.9	3.1	4.2	4.9	0.7	6.8	3.0	11.2	0.0
Filenchus	2	4.9	0.2	3.1	2.2	3.1	0.0	0.9	6.4	7.2	0.0	6.1	17.4
Leptonchus	4	0.5	0.2	2.5	4.4	6.3	0.0	0.3	1.7	1.7	1.5	0.0	0.0
Paraphelenchus	2	0.0	1.6	0.3	0.0	0.0	0.0	0.9	0.3	0.0	0.8	0.0	0.0
Tylencholaimellus	4	0.0	0.2	0.0	2.2	0.0	0.0	0.0	1.4	1.3	6.1	0.0	0.0
Tylencholaimus	4	6.5	4.3	4.4	3.3	0.0	0.0	0.9	5.4	14.8	12.1	0.0	0.0
Plant-parasites													
Coslenchus	2	0.0	0.0	15.9	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Dorylaimellus	5	12.5	18.6	10.6	2.2	3.1	0.0	0.3	2.4	5.9	18.9	14.3	0.0
Helicotylenchus	3	0.5	8.6	7.5	0.0	6.3	0.0	38.5	4.7	17.8	0.8	0.0	0.0
Hemicriconemoides	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Longidorella	4	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Malenchus	2	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Merlinius	2	10.9	0.0	1.9	1.1	0.0	0.0	2.0	0.0	0.4	0.0	0.0	0.0
Meloidogyne	3	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Miculenchus	2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Neothoda	2	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Paratylenchus	2	0.0	2.1	7.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tylenchorhynchus	3	0.5	5.9	7.5	0.0	0.0	0.0	0.0	22.9	0.0	0.0	1.0	0.0
Xiphinema	5	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bacterivores													
Acrobeles	2	1.6	2.5	3.8	6.6	0.0	2.8	0.6	9.8	6.4	0.0	0.0	0.0
Acrobeloides	2	0.0	2.7	5.0	5.5	0.0	12.5	0.0	2.7	0.9	0.8	0.0	4.3
Alaimus	4	1.1	0.0	0.0	0.0	0.0	4.2	0.0	1.0	0.0	0.0	0.0	0.0
Cephalobus	2	4.9	13.2	2.8	2.2	0.0	31.9	21.6	5.1	1.3	4.6	11.2	8.7
Cervidellus	2	4.4	7.7	7.2	1.1	6.3	5.6	10.1	5.1	6.4	20.5	5.1	0.0
Chiloplacus	2	4.4	0.0	0.0	0.0	0.0	4.2	1.4	0.0	0.0	0.0	0.0	0.0
Cylindrolaimus	3	6.0	0.5	2.2	2.2	0.0	0.0	0.0	3.0	3.0	0.0	0.0	0.0
Eucephalobus	2	0.0	0.0	0.0	0.0	6.3	13.9	8.1	0.0	0.0	0.0	0.0	4.3
Eumonhystera	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Mesorhabditis	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.4	0.0	0.0	0.0	60.9
Plectus	2	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1	0.0
Prismatolainus	3	1.1	0.0	0.3	2.2	6.3	0.0	0.0	0.3	0.0	0.0	0.0	4.3
Rhabdolaimus	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0
Wilsonema	2	0.5	0.0	0.6	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0
Omnivores – predators													
Aetholaimus	5	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Aporcelaimellus	5	5.4	0.2	4.7	12.1	15.6	4.2	0.3	3.4	3.0	3.0	0.0	0.0
Aporcelaimus	5	0.0	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.4	5.3	2.0	0.0
Campydora	4	6.5	2.7	0.6	1.1	0.0	0.0	0.0	1.0	1.7	0.0	0.0	0.0
Carcharolaimus	5	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clavicaudoides	5	0.0	0.2	0.0	1.1	0.0	0.0	0.0	0.0	0.4	3.0	0.0	0.0
Discolaimus	5	6.0	0.9	1.6	5.5	0.0	0.0	0.0	1.4	8.5	3.0	1.0	0.0
Dorydorella	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Ecumenicus	4	9.2	5.5	1.6	29.7	31.3	1.4	8.6	1.0	6.8	14.4	31.6	0.0
Enchodelus	4	6.0	2.5	0.6	0.0	6.3	0.0	0.0	2.0	0.9	0.8	8.2	0.0
Microdorylaimus	4	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
Paravulvus	5	1.6	1.4	0.3	3.3	6.3	0.0	0.0	1.4	0.4	0.0	0.0	0.0
Total	ΣG		24	28	30	20	12	11	17	30	24	18	14

ple plots could be divided into 4 groups according to the differences in the number of genera (group 1: 12, 5, 6, 4, 11, 10, 1; group 2: 4, 11, 10, 1, 9; group 3: 11, 10, 1, 9, 8; group 4: 9, 2, 3, 7). Sample plots 1, 11, 10, 9 and 4 appeared more frequently in the four groups; the number of genera found in these plots (14–24) was representative in the region.

The composition of the nematode communities in different plots is shown in Table 3. Bacterivores dominated most plots, accounting for 30.27% of indi-

*Table 4 – Ecological indices of each sample plot (Means± SD), and comparisons between sample plots and soil layers to understand the spatial variation indicated by the ecological indices of nematode communities. *: p < .05, **: p < .01. H' = Shannon-Weiner diversity index; J' = Pielou evenness index; λ = Simpson dominance index; SR = Margelef abundance index; MI = Maturity Index; PPI = Plant Parasite Index; NCR = Nematode Channel Ratio.*

Plots		Ecological indices						
		H'	*J'*	*λ*	SR	MI	PPI	NCR
1		2.27±0.13a	0.93±0.02a	0.12±0.02a	3.07±0.33ab**	3.63±0.25a	2.13±0.22ab	0.61±0.10ab
2		2.19±0.18ab	0.88±0.05a	0.14±0.02a	3.03±0.39ab**	3.09±0.45abc	2.68±0.09a	0.60±0.15ab
3		2.55±0.17a	0.88±0.04a	0.10±0.02a	4.17±0.59c	3.22±0.41ab	2.46±0.33ab	0.56±0.11ab
4		1.63±0.82bc*	0.90±0.08a	0.29±0.20ab	2.45±1.18bd**	3.47±0.35ab	0.40±0.89c**	0.62±0.28ab
5		1.14±0.68c**	0.94±0.02a	0.41±0.33b**	1.86±0.28de**	3.42±0.90ab	1.20±1.64bc	0.70±0.27bc
6		1.21±0.72c**	0.93±0.07a	0.40±0.34b*	1.86±0.38de**	2.21±0.27de**	0.00±0.00c**	0.83±0.18bc
7		1.59±0.30c*	0.78±0.10a	0.27±0.11ab	1.61±0.36def**	2.44±0.0.27cde**	2.96±0.06a	0.86±0.11bc
8		2.44±0.17a	0.88±0.08a	0.12±0.03a	4.13±0.50c	2.79±0.54bcd*	2.97±0.06a	0.64±0.13ab
9		2.35±0.31a	0.89±0.07a	0.13±0.06a	3.49±0.60ac	3.40±0.20ab	2.34±1.31ab	0.32±0.10a*
10		1.58±0.57c*	0.86±0.06a	0.28±0.16ab	2.05±0.69de**	3.70±0.55a	0.60±1.34c*	0.52±0.38ab
11		1.32±0.61c**	0.85±0.13a	0.36±0.22ab*	1.55±0.75ef**	3.45±0.39ab	1.20±1.64bc	0.60±0.39ab
12		0.44±0.44d**	0.30±0.38b**	0.76±0.25c**	0.92±0.28f**	2.04±0.94e**	0.00±0.00c**	1.00±0.00c*
Plot	F	9.626	7.828	4.758	15.612	5.504	7.543	2.475
	P	0.000	0.000	0.000	0.000	0.000	0.000	0.017
Clay	F	4.197	0.396	3.104	2.795	0.157	1.662	0.526
	P	0.006	0.811	0.025	0.039	0.959	0.177	0.717

viduals; predators / omnivores accounted for 28.46%; plant-parasites were less abundant (just 19.09%). More specifically, plots 6, 7, 8 and 12 were dominated by bacterivores; plot 3 was associated with plant-parasites; plots 1, 2, 4, 5, 10 and 11 had more predators / omnivores (the percentage is the largest in the community). Plot 9 stands out as the only one dominated by fungivores.

Ecological indices of the soil nematode community

The *H'*, *J'*, *λ* and SR indices were calculated to characterize the diversity of the nematode communities around Lake Paiku.

According to the results of the Duncan test, the H' values of sample plots 1, 2, 3, 8 and 9 were significantly higher than those of other plots (p 4,7,10 < .05; p 5,6,11,12 < .01; $n = 5$). The SR value was generally consistent with that of *H'*. The values of plots 1, 2, 3, 8 and 9 (especially 3, 8 and 9) were significantly higher than those of the other plots (p 1,2 < .01; p 4,5,6,7,10,11,12 < .01; $n = 5$). The *J'* index for plot 12 was significantly lower than for the other plots ($p < .01$). The *λ* index for plots 5, 6, 11 and 12 was significantly higher than for the other plots (p 6,11 < .05; p 5,12 < .01).

The maturity index MI, plant-parasitic nematode index PPI, and nematode channel index NCR were calculated to describe the functional and structural characteristics of the soil nematode community. MI and PPI values of the 12 sample plots were 1.13–4.42 and 2.00–3.02 respectively. It should be noted that plant-parasites were absent from 40% (24 out of 60) of the soil samples. The PPI values of less than 2 (see Table 4) are the result of including PPI values of 0 (plant-parasites were absent).

According to the Duncan test results, the MI values of plots 6, 7, 8 and 12 were significantly lower than those of other plots (p 6,7,12 < .01, p 8 < .05). The PPI values of plots 4, 6, 10 and 12 were significantly lower than those of other samples (p 10 < .05, p 4,6,12 < .01). For the NCR values, only plot 9 was less than 0.5.

The *H'*, *λ* and SR values differed significantly for different soil layers. Notably, *H'* reached an extremely significant level ($p < .01$).

EI and SI give indications of the structure and function of the soil food web. Figure 2 shows the distribution of the 12 sample plots in the four quadrants. The order of plots along the EI axis is 12 > 8 > 11 > 9 > 4 > 1 > 2 > 5 > 3 > 6 > 10 > 7. The order of plots along the SI axis is 5 > 1 >10 > 4 > 9 > 11 > 2 > 3 > 8 > 7 > 6 > 12.

Relationship between soil nematode communities and soil properties

The RDA analysis results (see Figure 3 and Table 5) showed that the chemical properties of the soil were related to the soil nematode community. Seven environmental variables (soil pH, total N, available P, alkali-hydrolytic N, available K, organic matter, water content) accounted for 77.7% of the total data difference. The contributions to the variance of the first and second axes are 24.1% and 0.0% respectively. The correlation coefficients of the species-environment fac-

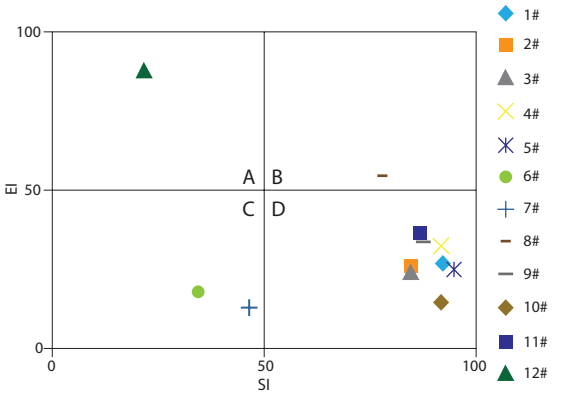

Figure 2 – Enrichment index (EI) and structure index (SI) of soil nematode community. The combination of EI and SI can be used to indicate the succession status of soil food web: A quadrant, high disturbance degree, good nutrient enrichment, organic matter degradation channel is dominated by bacteria, low C/N, food web is disturbed to A certain extent. B quadrant, low to medium disturbance, good nutrient enrichment, relatively balanced organic matter degradation channels, low C/N, mature food web. C quadrant, no disturbance, medium nutrient enrichment, fungal degradation channels, medium to high C/N, structured food web. D quadrant, the highest disturbance, poor nutrient enrichment, degradation channels mainly fungi, high C/N, food web degradation.

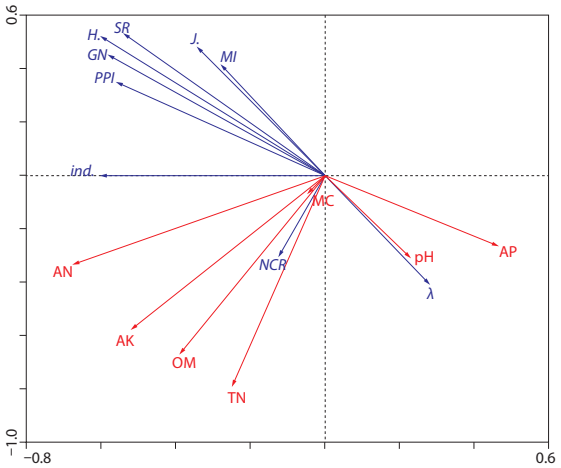

Figure 3 – Redundancy analysis (RDA) summary of the soil nematode community with soil properties. The blue lines represent ecological indicators; the red lines represent soil properties. The soil property and ecological indicators are as follows: MC: moisture content; TN: total nitrogen; AK: available potassium; AN: alkali-hydrolyzed nitrogen; OM: organic matter; AP: available phosphorus; GN: number of genera; ind.: nematode individual density.

Table 5 – Redundancy analysis (RDA) summary.

Ordination Summary	Axis 1	Axis 2	Axis 3
Eigenvalue	0.38	0.366	0.031
Species-environment correlation coefficient	0.616	0.606	0.672
Cumulative percentage variance of species data (%)	38.0	38.0	38.0

tor sequencing axis were 0.616 and 0.606 for the first and second axes respectively. The cumulative percentage of species-environment relationships was 100%, indicating that the species-environment correlation coefficient for the first ordination axis was high, and 100% of the total variance of species and environment was explained. The two-dimensional distribution figure (Figure 3) reflects well the relationship between the soil's nematode community and its physical and chemical properties.

Based on the RDA ranking results, soil-available P, pH, alkali-hydrolytic N and available K are key factors that have strong effects on the soil nematode community, whereas the total soil N, organic matter and water content have minor effects.

Various community characteristics correlate differently with soil properties. The density of nematodes (as opposed to the number of genera present) was more affected by the soil's physical and chemical properties. There was a strong correlation between nematode density and alkali-hydrolytic N content. Available P correlated negatively with several community characteristics. pH had a significant effect on α diversity of the nematode community. The redundancy analysis results (above) and the results of the Pearson correlation test (below) illustrate the consistency of the statistical results obtained by the two methods.

The Pearson results were as follows:
$r_{ins/AN} = 0.420^*, p = .021, N = 30$; [1]
$r_{GN/AP} = -0.401^*, p = .028$;
$r_{NCR/AK} = 0.394^*, p = .074$;
$r_{H'/AP} = -0.454^*, p = .012$;
$r_{J'/TN} = -0.529^{**}, p = .003$;
$r_{J'/AP} = -0.495^{**}, p = .005$;
$r_{SR/AP} = -0.458^*, p = .011$;
$r_{MI/AP} = -0.565^{**}, p = .001$;
$r_{PPI/pH} = -0.498^{**}, p = .005$.

Discussion

Structure of nematode communities

Our study in the Lake Paiku region recovered greater nematode diversity in comparison to studies carried out in the alpine meadows of the Northern Tibet Grasslands. For the years 2013, 2014 and 2015, at a similar altitude (4,596 m), we found 34, 42 and 39 genera respectively (Xue et al. 2017).

In a lower altitude zone in the eastern Qinghai-Tibet Plateau grasslands, Hu et al. (2016) found 42 gen-

[1] $r_{ins/AN}$ ... correlation coefficient between the individual number of nematodes and the amount of alkali-hydrolyzed nitrogen in the soil.

era. Furthermore, our figures exceeded the 31 genera reported by Vinciguerra (1988) from grasslands in the Alps, and the 33 genera reported by Gerber in Austria (Gerber 1991). With respect to nematode density, our study found a less abundant community (0–413 individuals per 100 g dry soil) in this region compared to other available studies: >500 individuals per 100 g^{-1} dry soil (Xue et al. 2017), and 1,033 individuals per 100 g dry soil (Hu et al. 2016).

In our study, the density of individuals and species diversity of the soil nematode community increased from the middle of the lake shore towards the south and north banks, which contrasted with the results of Zhao et al. (2019). According to RDA testing, total soil N, organic matter, available K and alkali-hydrolytic N contents were all at low levels, which would limit the numbers of nematodes and result in a low density. At the same time, the study showed that higher above-ground plant diversity may promote higher underground biodiversity (Zhang et al. 2006); lower density of nematodes may be related to the species composition and coverage of plant communities (see Table 1). Plants provide soil organic matter, and the distribution and quantity of roots affect the species diversity and total numbers of the soil nematode community through the presence of rhizosphere microorganisms and plant-parasite nematodes (Wardle et al. 2004).

Although the nematode density in plot 7 was the highest, its species diversity (genus number and the *H'*, SR, etc. indices) was significantly lower than for plots 1, 2, 3, 8 and 9. Genus Helicotylenchus was far more abundant in plot 7, accounting for 38.51% of the total nematodes and contributing to the high population density. This shows that the positive correlation between species diversity and individual density is not inevitable.

Nutritional structure of soil nematode communities

Our study reports a rare occurrence: only 2 of the 12 plots were dominated by plant-parasitic nematodes, and their percentage was relatively low (0–41%) in comparison to 69%–81% in the *Stipa grandis* steppe soil of Inner Mongolia (Ruan et al. 2007), 62%–66% in the Romanian steppe (Popovici et al. 2000), and 32%–42% in the alpine meadows of northern Tibet (Xue et al. 2013).

This might be related to sparse vegetation cover around the lake. The species present and number of plant-parasitic nematodes relate closely to plant biomass, including above-ground biomass and underground root biomass (Wardle et al. 2004).

Omnivores and predators are key trophic groups in determining the complexity of the soil food web (Polis et al. 1996). In the present study, half of the sample plots (plots 1, 2, 4, 5, 10 and 11) were dominated by these two trophic groups. As they are extremely sensitive to environmental disturbance, the prevalence of the omnivores and predators indicates that the region studied is in the stable later stage of succession, and the ecosystem has remained undisturbed. Soil environmental factors under the influence of plant communities, such as soil temperature and humidity, as well as pH, form and content of nutrient elements, organic matter content and soil type, explain the differences in nematode community composition between different sites, but no one of these factors can be said to be more important than the others (Zhan et al. 2019; Háněl 2017; Siemann et al. 1998).

Ecological function of soil nematode communities

MI and PPI values reflect the stability of the ecosystem and the degree of human disturbance. The higher the MI value and the higher the maturity of the ecosystem, the better the stability (Liu 2010); ecosystems are degraded by disturbance (Shao et al. 2007). The PPI value is positively correlated with the frequency of disturbance (Liu 2010). However, the MI values of plots 6, 7 and 12 in this investigation are lower, indicating that the stability of these three plots is lower than for other plots. The PPI value of plot 7 is the highest, indicating that this plot was most affected by disturbance.

Functional group-based EI indicates the outside-in nutrient inputs; SI indicates connectivity and the length of the food chains found within the soil food web (Ferris et al. 2001).

The results of the EI and SI showed that the soil nutrients were at a medium level without human disturbance, and the energy flow of the soil food web in most areas around the lake tended to be via fungus decomposition channels. The soil food webs were structured: the results of this study showed that most of the areas along the lake shore were more inclined to the fungal decomposition channel (the exceptions were plots 12 and 8, whose soil food webs were dominated by the bacteria decomposition channel); the food webs dominated by fungi channels, in comparison to bacterial decomposition channels, were more conducive to the preservation of soil nutrients.

Examples of degraded underground food webs also exist in the regions investigated. Plot 12 (the only plot in quadrant A) had the largest input of nutrients, but the connectivity was weak, the length of the food chain was very short, and environmental disturbance has led to serious degradation of the food chain. Plot 8 (in quadrant B) is similar. In plots 6 and 7, the nutrient input was lower, resulting in poor nutrient accumulation, and the high intensity of environmental disturbance resulted in significant degradation of the food web.

The NCR value also reflects the energy flow of the soil food web (Ingwersen et al. 2008). According to the NCR value, plot 9 was characterized by a fungal degradation channel, while the other sample plots all had bacterial degradation channels. This result is quite different from that indicated by the combination of

EI and SI, which use different calculation methods. The NCR value is calculated for all bacterial- and fungal-feeding nematodes combined, while EI and SI give different weights to different functional groups. They are therefore more sensitive to the energy flow of the soil food web.

Relationship between soil nematode community and soil properties

The RDA results showed the relationships between soil nematode communities and soil properties. Soil-available phosphorus (AP), pH and alkali solution nitrogen (AN) influence the soil nematode community significantly. An increase of the AN content and of the AP will increase the density of nematodes. In particular, increased AN caused an increase in the relative number of bacterivores (NCR increases), which was consistent with the conclusions of both EI and SI.

AP was negatively correlated with several community characteristics; the increase of AP would reduce the biodiversity and stability of the soil nematode community. Soil total nutrients, organic matter and water content were relatively unimportant, and Pearson correlation analysis also showed that there was no significant correlation between soil water content and any characteristic factors of the soil nematode community.

What deserves special attention is the AP, which has a significant negative correlation with some community characteristics, such as the number of genera, diversity index *H'*, richness index SR, and maturity index MI. Studies in other regions and under different environmental conditions also showed that the number of fauna species in soil and the density of individuals were significantly negatively correlated with soil P content (Li et al. 2017; Wang 2015).

However, each soil property factor (except water content) is at a poor or extremely poor level for fertility, so why does available phosphorus show a stronger correlation than other factors? This remains to be further studied.

Conclusion

Soil nematodes showed surface aggregation (mainly distributed in the 0–10 cm soil layer) for both individual density and biodiversity. The soil nematode community around Lake Paiku was rich in diversity but low in population density. The individual density of nematodes was more affected by the soil's physical and chemical properties than was the number of genera. Soil-available phosphorus, pH and alkali-hydrolytic nitrogen (AN) had significant effects on the soil nematode community. Total nutrients, organic matter and soil moisture content are less important. The soil AP content around Lake Paiku is at a low level (mean 2.67 mg / kg); low soil AP content is a limiting factor for plant growth, and affects nematode communities via plant biomass.

The soil food web in the Lake Paiku area was more complex, less disturbed by human activities, in the late stage of succession, and relatively stable. The results of the EI and SI based on functional groups showed that in most areas around the lake, the soil nutrients were at a medium level without human disturbance, the soil food web was structured, and the energy flow was dominated by the fungus energy channel. The energy flow of the soil food web given by the EI and SI is more sensitive and reliable than that of the NCR.

The individual density of soil nematodes was highest in the northeast and southeast corners of the lake; the genus numbers had the same distribution. The results of the diversity index *H'* support this distribution pattern.

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