Ecological Indicators 132 (2021) 108338

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Nematode communities indicate anthropogenic alterations to soil dynamics across diverse grasslands

Li Liu[a,1], Shuiyan Li[b,1], Gail W.T. Wilson[c], Adam B. Cobb[c], Chengyang Zhou[a], Jinsheng Li[a], Jiahuan Li[a], Lizhu Guo[a], Ding Huang[a,*]

[a] College of Grassland Science and Technology, China Agricultural University, Beijing 100093, China
[b] Xinhua Indices (Beijing) Co.Ltd., Beijing 100052, China
[c] Oklahoma State University, 008C AGH, Stillwater, OK 74078, USA

ARTICLE INFO

Keywords:
Alpine meadow
Community structure
Management practices
Meadow steppe
Typical steppe

ABSTRACT

Nematode communities are meaningful biological indicators of soil health and soil processes across different grassland types and management practices and analyses of nematode communities provide insight into structure, function, and sensitivity or resilience across multiple ecosystems. In three model grasslands: meadow steppe (MS), typical steppe (TS), and alpine meadow (AM), this current research examined responses of soil nematode communities and related edaphic characteristics to grazing, mowing, and crop cultivation at two soil depths. The research fills a critical knowledge gap by resolving multidirectional influences between local conditions, grassland management practices, and nematode communities. Across grassland types, nematode abundance in AM was greater than MS and TS grasslands, and nematodes were more abundant near the soil surface. Cultivation resulted in greater nematode abundance compared to all other management practices, and generally, bacterivores were the most dominant nematode trophic group. The TS and MS grasslands had relatively more bacterivores, exhibiting substantial influences on soil mineralization and organic matter decomposition pathways. The AM grassland showed relatively more plant feeding nematodes, driving soil mineralization pathways. Among the three management practices, crop cultivation had the greatest impact on nematode community structure and the soil environment, especially in relatively sensitive AM grasslands. In fact, AM soil environments responded most dramatically to cultivation, with nematode abundance, soil quality, and food web complexity increasing. However, soil ecosystem stability, food web reliance, and food web response to resources decreased in cultivated AM soils. Results indicate that unique environmental characteristics in the Qinghai-Tibet plateau drive substantially different AM grassland nematode community structure and soil conditions compared to TS or MS grasslands. As anthropogenic pressures on these ecosystems mount, it is critical to understand how different management practices influence grassland nematode communities, with cascading effects through soil environments.

1. Introduction

Grasslands are important terrestrial ecosystems, covering approximately 40% of the ice-free land area of the earth and providing many essential ecosystem services (Ren et al., 2018). Previous studies indicate grassland plant communities are directly connected to the functional composition of soil microbial communities (Zhou et al., 2019a). However, different grassland systems have distinctive soil environments due to inherent factors such as geography and climate, and human utilization of grasslands influences productivity, stability, and biodiversity. For example, management practices can alter surface vegetation characteristics with cascading effects on soil nutrient content, soil metabolic processes, microbial community assemblages, ultimately resulting in landscape-scale ecosystem modifications (Zhou et al., 2019b). Consequently, it is critical to assess different grassland management practices across grassland types to evaluate the influence of land management on soil microbial community dynamics, functional biodiversity conservation, and sustainable use of grassland ecosystems

* Corresponding author at: West campus of China Agricultural University, Haidian District, Beijing 100193, China.
E-mail address: huangding@263.net (D. Huang).

[1] These authors contributed equally to this work and should be considered co-first authors.

https://doi.org/10.1016/j.ecolind.2021.108338
Received 2 November 2020; Received in revised form 20 October 2021; Accepted 26 October 2021
Available online 30 October 2021

across the globe.

Soil fauna are key consumers and decomposers in terrestrial ecosystems, influencing soil microenvironments (Ma et al., 2018). Soil nematodes are one of the most abundant groups of soil fauna, playing critical roles in controlling organic matter decomposition, nutrient cycling, and resource availability (Yeates, 2003; Shao et al., 2008; Zhao et al., 2014; Li et al., 2016; Wu et al., 2017). The immense functional diversity of nematodes combined with their abundance, low motility, and sensitivity to environmental conditions make this group an ideal bioindicator of soil ecosystem health (Griffiths et al., 2001; Coffey and Otfinowski, 2019; Gao et al., 2019; Ney et al., 2019). Ecological indices calculated from nematode community parameters, including tools to assess diversity and functionality, can be used to measure how edaphic and environmental conditions, combined with grassland management, mediate soil and microbial dynamics (Bongers and Ferris, 1999; Ferris et al., 2001; Neher, 2001). Assessing soil nematode communities is an active and progressive field of ecology (Cesarz et al., 2017; Andriuzzi and Wall, 2018), as analyses of nematode communities provide insight into structure, function, and sensitivity or resilience of grasslands (Ferris et al., 1999; Ritz and Trudgill, 1999). However, previous grassland nematode studies have yielded few consistent conclusions, especially at different spatial scales, making it critical to elucidate consequences of grassland management on nematode community structure and diversity across grassland types. Researchers and land managers can apply this information at broad geographical scales to inform grassland management and conservation strategies.

While nematode communities are clearly meaningful biological indicators of soil health and soil processes across different grassland types and management practices, previous studies on the community structure of grassland nematodes have generally focused on an individual grassland (Hu et al.,2017; Wu et al.,2017; Han et al.,2020; Wu et al.,2021). In addition, previous studies on grassland management practices focus on grazing (Hu et al.,2015; Andriuzzi and Wall, 2018), with few studies examining effects of multiple grassland management practices on nematode community structure. Therefore, multiple grasslands were included in this study as model grasslands: meadow steppe, typical steppe, and alpine meadow. Each of these grasslands has unique biodiversity and environmental features, resulting in a range of ecological relationships. Further, multiple management practices were selected, with grazing, mowing, and crop cultivation as model management practices. Grazing, mowing, or crop cultivation are the main management practices of grasslands globally and likely differentially influence soil and ecosystem productivity, stability, and biodiversity. In addition, similarities and differences were explored in soil environmental conditions across these grassland types and management practices, aimed at resolving multidirectional influences between local conditions, grassland management, and nematode communities. The main research questions of this study are: (1) Do soil nematode communities differ across grassland types and management practices? and (2) What are the effects of grassland types and management practices on soil environments, local food webs, and nematode community stability? To disentangle context-dependent influences, structure, composition, diversity, and ecological indices of nematode communities were quantified in three model grasslands. Linking nematode community parameters with soil microenvironments can provide relevant strategies to encourage grassland management practices that simultaneously support sustainable production and biodiversity.

2. Materials and methods

2.1. Study region

The field work was conducted in northern China, covering three major grassland types: meadow steppe (MS), typical steppe (TS), and alpine meadow (AM) (Fig. 1). Sites extend from northeast to southwest, across Inner Mongolia, Hebei, and Qinghai provinces, from latitudes

Fig. 1. Locations of three model grasslands assessed in this study. Meadow steppe (MS) research was conducted at National Field Scientific Observation and Research Station of Hulunbuir Grassland Ecosystem, Inner Mongolia, China (119.92°E, 49.32°N). Typical steppe (TS) research was conducted at the National Grassland Ecosystem Field Scientific Observation and Research Station of Guyuan County, Hebei Province, China (116.23°E, 41.62°N). Alpine meadow (AM) research was conducted at Modern Ecological Animal Husbandry Science and Technology Experimental Demonstration Park on Haibei Plateau, Qinghai Province, China (100.85°E, 36.85°N).

36.7 to 49.4°N, longitudes from 100.4 to 119.9°E, and elevation ranges from 672 to 3200 m. Three research sites were located at the National Field Scientific Observation and Research Station of Hulunbuir Grassland Ecosystem of Inner Mongolia (MS), National Grassland Ecosystem Field Scientific Observation and Research Station of Guyuan County of Hebei Province (TS), and Modern Ecological Animal Husbandry Science and Technology Experimental Demonstration Park on Haibei Plateau of Haibei Tibetan Autonomous Prefecture in Northeast Qinghai Province (AM). Characteristics of study sites (climatic conditions, soil and vegetation types) varied substantially (Table 1).

2.2. Experimental design

The experiment was conducted as a double factor block design, the first factor being grassland type: MS; TS; or AM, with three replications of each management practice at each location. The second factor was grassland management practice: grazed areas; mowed areas; cultivated areas; or control areas. Grassland management practices (including control areas) were established at all plots for > 6 years. Grazed areas of

Table 1
Characteristics of study sites.

	Meadow steppe	Typical steppe	Alpine meadow
Coordinates	119.92°E, 49.32°N	116.23 °E, 41.62 °N	100.85 °E, 36.85 °N
Elevation (m)	680 *m*	1430 *m*	3200 *m*
Mean annual precipitation (mm)	370 mm	430 mm	580 mm
Mean annual temperature (°C)	-2.4 °C	1.4 °C	−1.7 °C
Growing season	July to September	June to September	May to September
Soil type	Dark chestnut	Typical chestnut	Alpine meadow soil
Dominate plant species	*Leymus chinensis, Stipa baicalensi, Carex duriuscula, Vicia amoena*	*Leymus chinensis, Stipa krylovii, Agropyron cristatum, Cleistogenes squarrosa*	*Kobresia pygmaea, Kobresia capillifolia, Poa crymophila.*

MS grassland and TS grassland were subject to herbivory by cattle (4 cattle per ha continuously grazed all year), while the AM grassland was grazed by sheep (7.5 sheep per ha continuously grazed throughout the growing season), and AM. Control plots were fenced to prevent livestock herbivory. Mowed areas (cut once a year to a height of 5–8 cm) were dominated by Gramineae; *Leymus chinensis* was the dominant species at MS and TS while *Elymus nutans* was dominant at AM. Cultivated areas were planted to cereal grains, with wheat in MS and TS and oats in AM.

2.3. Field sampling and measurements

Sampling was conducted between July-September 2016. At each grassland site, three separate plots for each management practice were selected, with an interval of 500 m or greater between plots with similar soil parent material and topography. Soil was sampled using three separate quadrats, with randomized locations within each of the three plots representing each management practice. Three 7-cm-diameter soil cores were collected from 0 to 15 cm and 15–30 cm depths in each quadrat. These three cores were mixed *in situ* to form one composite sample per quadrat, reducing variance associated with soil nematode spatial patterns. Thus, a total of 72 soil samples were collected. Composite soil samples were divided into two sub-samples and placed in sealed plastic bags. One sub-sample was stored at 4 °C for measurements of soil moisture and identification of soil nematodes. Another portion was air-dried and sieved through 2 mm-mesh for determination of soil pH, EC, total N and organic carbon (Bremner, 1996; Nelson and Sommers, 1996) (results shown in Table 2). The pH was measured in a 1:2.5 (soil: water) suspension; SOC was determined using the potassium dichromate volumetric method in conjunction with external heating. Total N was measured using the semi-micro-Kjeldahl method.

2.4. Soil nematode communities

Soil nematodes were extracted from 100 g moist soil samples using the improved Baermann shallow dish method for 48 h (Ingham et al., 1985). Extracted nematodes were killed at 60 °C and fixed in 5% Formalin solution to be identified and counted microscopically (OLYMPUS CX21), allowing identification to genus (Siddiqi, 1986; Jairajpuri and Ahmad, 1992). Based on feeding habits and esophageal structure, nematodes were assigned to one of four trophic groups: plant feeder (PF), bacterivores (BF), fungivores (FF), and omnivores / predators (OP) (Yeates et al., 1993, Ferris et al., 2001). Because predator nematodes were found infrequently, predator nematodes were included with omnivores (Ou et al., 2005).

2.5. Data analyses

All statistical analyses were conducted with SPSS Version 22.0 (IBM Company, Armonk, NY, USA) and figures were plotted with Sigma Plot 12.5. (Systat Software, Inc.) and program R 3.6.3(R Core Team, 2020). Prior to analyses, all data were checked for normality and homoscedasticity using Shapiro-Wilk test. Two-way ANOVA was utilized for comparisons of all response variables across grassland types and management practices, followed by Duncan's multiple range tests. When grassland type and management practice interactions occurred, one-way ANOVA was utilized to separate the influence of management practices within each grassland type, followed by Duncan's multiple range tests. Differences were considered statistically significant at $P < 0.05$.

Several ecological indices for nematodes were calculated. These included diversity indices: Shannon-Weaver diversity (H') (Shannon and Weaver, 1949), Evenness Index (J') (Pielou, 1975), and Species Richness Index (SR) (Yeates and Newton, 2009), which were used to evaluate the structure and distribution of soil nematodes. These also included

Table 2

Soil parameters (soil water content [SWC]; soil pH; soil electric conductivity [EC]; soil total nitrogen [TN]; and soil organic carbon [SOC]) of different grassland types (meadow steppe, typical steppe, alpine meadow) and management (grazed, mowed, cultivated, or control) from 0 to 15 cm and 15–30 cm depths, expressed as mean ± SE. Management practices within a grassland type that do not share a lowercase letter are significantly different, also indicated in bold ($P < 0.05$).

Environmental Parameter	Grassland type	0–15 cm Grazing	Mowing	Crop	CK	F-value	P-value	15–30 cm Grazing	Mowing	Crop	CK	F-value	P-value
Soil Water Content (%)	Meadow steppe	7.2 ± 0.3b	7.8 ± 0.1b	6.9 ± 0.4b	13.3 ± 1.2a	19.64	0.000	6.8 ± 0.3b	8.3 ± 0.8b	7.0 ± 0.4b	10.5 ± 0.3a	10.95	0.003
	Typical steppe	21.5 ± 3.5a	13.3 ± 1.4b	14.4 ± 0.5b	15.2 ± 0.5b	3.75	0.060	16.4 ± 0.9a	7.4 ± 0.8b	15.8 ± 1.0a	14.5 ± 0.8a	22.34	0.000
	Alpine meadow	17.6 ± 0.4b	21.2 ± 0.6a	15.4 ± 0.6c	18.1 ± 0.6b	20.39	0.000	15.3 ± 0.5ab	17.3 ± 1.3a	13.6 ± 0.3b	17.1 ± 0.7a	4.83	0.033
PH	Meadow steppe	6.4 ± 0.1	6.3 ± 0.1	6.2 ± 0.0	6.5 ± 0.1	1.65	0.254	6.9 ± 0.5	7.4 ± 0.3	6.4 ± 0.1	6.5 ± 0.1	2.33	0.151
	Typical steppe	8.4 ± 0.2a	8.2 ± 0.0ab	8.4 ± 0.0a	7.9 ± 0.1b	3.76	0.060	9.4 ± 0.2a	8.4 ± 0.0b	8.4 ± 0.0b	8.7 ± 0.2b	14.80	0.001
	Alpine meadow	8.2 ± 0.0b	8.4 ± 0.0a	8.5 ± 0.1a	8.1 ± 0.0b	13.95	0.002	8.5 ± 0.0	8.6 ± 0.1	8.6 ± 0.1	8.4 ± 0.1	1.00	0.440
EC (us/cm)	Meadow steppe	2139.0 ± 310.8	2355.7 ± 648.9	2823.3 ± 8.8	2062.3 ± 368.0	0.72	0.569	1754.5 ± 62.7c	8610.0 ± 531.2a	3170.0 ± 468.8b	1908.3 ± 236.6c	74.24	0.000
	Typical steppe	575.7 ± 76.5a	168.3 ± 7.9b	202.1 ± 11.7b	194.0 ± 5.2b	24.83	0.000	576.7 ± 75.7a	202.0 ± 15.6b	273.7 ± 17.4b	329.7 ± 62.9b	9.29	0.006
	Alpine meadow	195.9 ± 11.2	225.3 ± 5.4	207.0 ± 30.0	208.18 ± 8.3	0.53	0.676	340.7 ± 35.8a	215.3 ± 1.3b	227.7 ± 37.1b	196.0 ± 9.9b	6.15	0.018
TN(g/kg)	Meadow steppe	2.9 ± 0.3ab	2.6 ± 0.4b	2.1 ± 0.1b	3.7 ± 0.1a	7.30	0.011	1.8 ± 0.2	2.1 ± 0.1	1.9 ± 0.1	2.0 ± 0.2	1.23	0.361
	Typical steppe	2.3 ± 0.3a	1.9 ± 0.1ab	2.0 ± 0.1ab	1.6 ± 0.1b	3.57	0.067	1.7 ± 0.1ab	1.6 ± 0.1b	2.0 ± 0.1a	1.5 ± 0.1b	4.83	0.033
	Alpine meadow	3.6 ± 0.1a	1.9 ± 0.1b	1.8 ± 0.3b	3.6 ± 0.2a	24.39	0.000	2.5 ± 0.1a	1.5 ± 0.2b	1.7 ± 0.2bc	2.2 ± 0.1a	10.99	0.003
Soil Organic Carbon (g/kg)	Meadow steppe	27.0 ± 2.6b	35.8 ± 1.9a	19.7 ± 0.6c	39.4 ± 01.0a	26.77	0.000	16.4 ± 0.8ba	22.0 ± 0.9a	18.8 ± 0.7ab	20.2 ± 1.8ab	4.33	0.043
	Typical steppe	18.2 ± 4.6	13.9 ± 2.4	16.6 ± 2.4	12.2 ± 0.6	0.88	0.490	11.2 ± 1.2	12.6 ± 3.2	15.9 ± 2.5	12.1 ± 2.7	0.67	0.595
	Alpine meadow	30.0 ± 0.7a	16.2 ± 0.4b	17.8 ± 2.7b	29.6 ± 4.2a	8.53	0.007	21.9 ± 2.29a	13.4 ± 1.9b	15.6 ± 1.9ab	18.3 ± 1.9ab	3.42	0.073

functional indices: Wasilewska Index (WI) (Wasilewska and Bienkowski, 1985; Yeates, 2003), Nematode Channel Ratio (NCR) (Neher, 2001; Yeates, 2003), Maturity Index (MI) (Bongers, 1990), Basal Index (BI), Enrichment Index (EI), and Structure Index (SI) (Ferris et al. 2001, Ferris and Bongers, 2006). The NCR indirectly evaluates the dominant decomposition pathway of soil organic carbon. The WI indirectly describes whether the main drivers of soil mineralization are free-living nematodes (bacterivores or fungivores) or plant-feeder nematodes. The MI reflects soil ecosystem stability. The BI, SI, and EI assess soil food web status, where BI indicates soil food web resilience, SI indicates changes in food web structure following disturbance or restoration, and EI evaluates the response of the soil food web to available resources.

Redundancy analysis (RDA) was performed using “Vegan” package (Oksanen, 2013) in program R 3.6.3(R Core Team, 2020) to determine relationships between nematode trophic groups and environmental parameters. Correlation analysis was performed using “corrplot” package (Wei and Wei, 2017) with Pearson correlation coefficient in program R3.6.3(R Core Team, 2020) to analyze relationships between soil nematode communities and soil physiochemical characteristics, across grassland type and management practices at two soil depths.

3. Results

3.1. Composition and structure of nematode communities

Nematode abundance was significantly affected by different grassland types ($P < 0.001$), different management ($P < 0.01$), and interactions between grassland type and management ($P < 0.05$) (see Table S1). At all three sites, the number of nematodes was greater at 0–15 cm depth (Fig. 2), compared to 15–30 cm depth. Nematode abundance was significantly lower in TS, compared to MS or AM sites ($P < 0.001$). In addition, cultivated areas in MS sites led to significantly greater nematode abundance from 0 to 15 cm, compared to control or other management practices ($P < 0.05$). At a depth of 15–30 cm, cultivated areas were significantly associated with greater nematode abundance in AM sites, compared to control or other management practices, while in MS and TS, abundances in cultivated areas were significantly different from controls but not from other management practices ($P < 0.05$) (Fig. 2).

A total of 117 nematode genera were identified across all samples, including 28 PF, 47 BF, 7 FF, and 35 OP genera (Table S2). Among grassland types, at both depths, BF nematodes were the dominant trophic group in MS and TS sites, while PF nematodes were dominant in AM sites (Fig. 3). In AM sites, there were significant differences between management practices, with BF nematodes more abundant than any

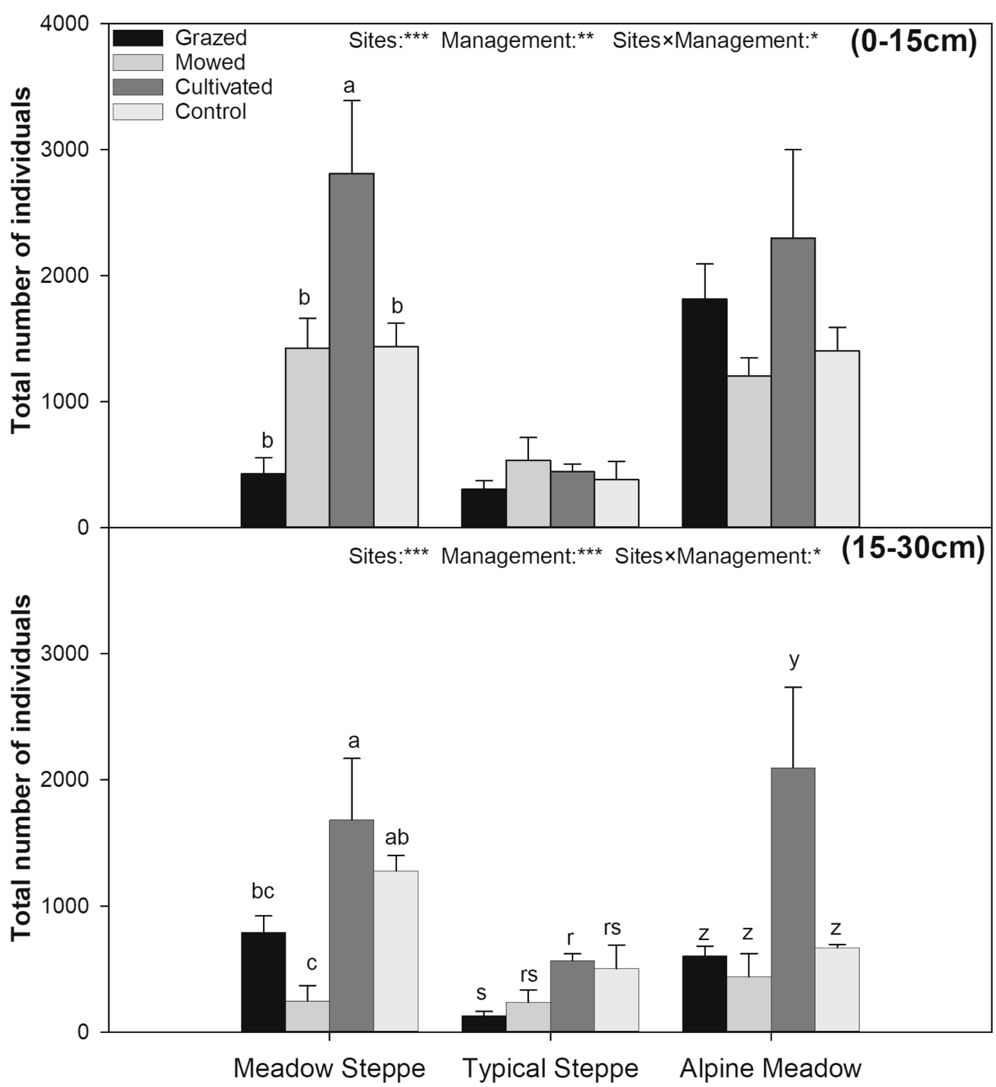

Fig. 2. Total number of individual nematodes associated with different grassland types and management practices (mean ± SE). Asterisks represent significant results of two-way ANOVA: different grassland types [sites]; different management practices [management]; and interactions. * indicates $P < 0.05$; ** indicates $P < 0.01$; *** indicates $P < 0.001$. Different letters represent significant differences in management (grazed, mowed, cultivated, or control) within a grassland type (meadow steppe, typical steppe, or alpine meadow) (ANOVA; Duncan test; $P < 0.05$). Lowercase letters [a-c] represent meadow steppe (MS); [r-s] represent typical steppe (TS); [y-z] represent alpine meadow (AM).

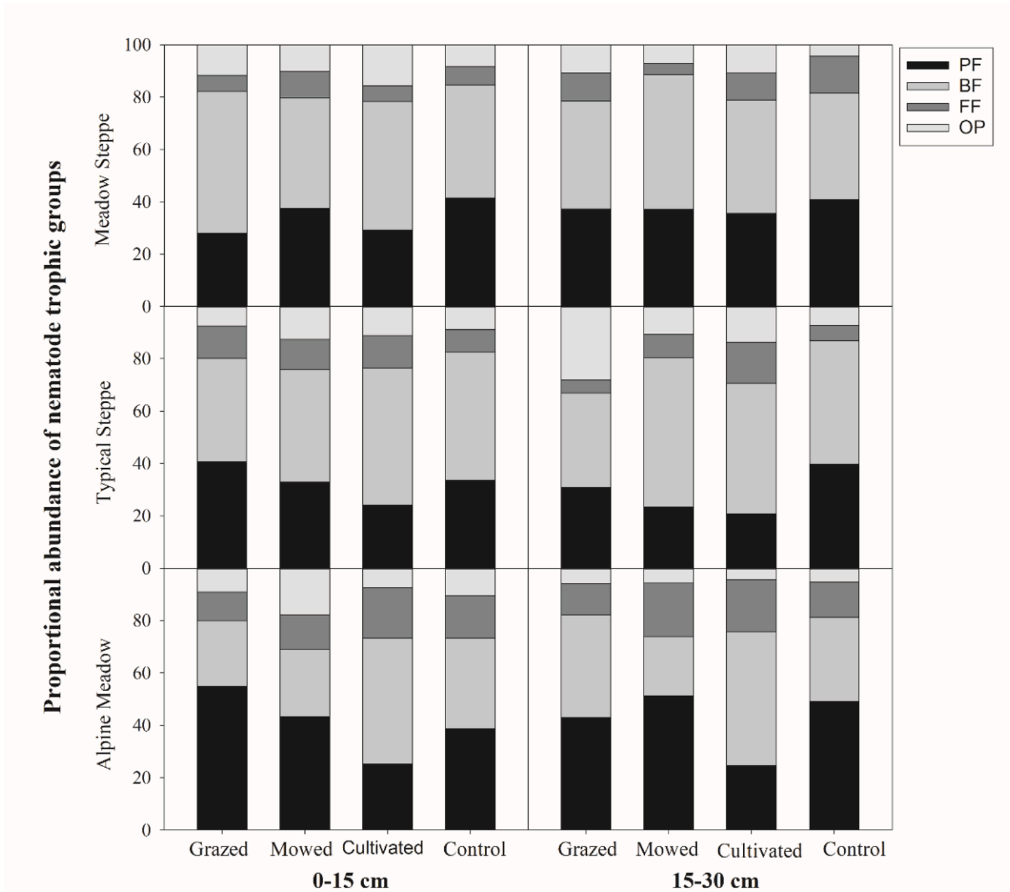

Fig. 3. Proportional abundances of soil nematode trophic groups (plant feeder [PF]; bacterivore [BF]; fungivore [FF]; or omnivore / predator [OP]) associated with different grassland types (meadow steppe, typical steppe, or alpine meadow), and management (grazed, mowed, cultivated, or control) at two soil depths (0–15 cm; 15–30 cm).

other tropic group in cultivated areas, while PF nematodes were more abundant than any other tropic group in all other management practices at either depth ($P < 0.05$) (Fig. 3).

3.2. Nematode diversity indices

Both grassland type and management had significant effects on nematode species richness (SR) at 0–15 cm ($P < 0.05$), but there was no significant interaction (Table S1). At a soil depth of 0–15 cm, SR was

Table 3
Diversity indices of soil nematodes across grassland type and management practices (mean ± SE). Shannon-Weaver diversity [H']; evenness [J']; species richness [SR]. Management practices within a grassland type that do not share a lowercase letter are significantly different, also indicated in bold ($P < 0.05$).

		0–15 cm						15–30 cm					
		MG	AMG	Crop	CK	F-value	P-value	MG	AMG	Crop	CK	F-value	P-value
H'	Meadow steppe	2.51 ± 0.18	2.91 ± 0.06	2.33 ± 0.62	2.67 ± 0.02	0.594	0.636	**2.76 ± 0.03a**	**2.17 ± 0.23b**	**2.58 ± 0.15ab**	**2.53 ± 0.06ab**	2.971	0.097
	Typical steppe	2.29 ± 0.06	2.61 ± 0.09	2.39 ± 0.20	2.42 ± 0.17	0.86	0.5	2.11 ± 0.07	2.23 ± 0.20	2.22 ± 0.15	2.39 ± 0.12	0.674	0.592
	Alpine meadow	2.49 ± 0.07	2.50 ± 0.04	2.42 ± 0.13	2.62 ± 0.06	1.1	0.404	2.47 ± 0.02	2.41 ± 0.09	2.40 ± 0.11	2.63 ± 0.03	2.054	0.185
SR	Meadow steppe	**3.70 ± 0.32b**	**5.20 ± 0.20a**	**5.28 ± 0.08a**	**4.64 ± 0.17a**	**12.009**	**0.002**	4.07 ± 0.20	3.04 ± 0.60	3.60 ± 0.19	3.97 ± 0.23	**7.308**	**0.011**
	Typical steppe	3.16 ± 0.26	4.09 ± 0.26	3.27 ± 0.77	3.54 ± 0.45	0.748	0.553	2.15 ± 0.18	2.60 ± 0.68	2.69 ± 0.40	3.18 ± 0.48	0.8	0.528
	Alpine meadow	3.78 ± 0.33	3.78 ± 0.34	4.21 ± 0.23	3.60 ± 0.14	0.913	0.477	**3.24 ± 0.06b**	**3.13 ± 0.41b**	**4.28 ± 0.11a**	**4.00 ± 0.09a**	**6.851**	**0.013**
J'	Meadow steppe	0.80 ± 0.03	0.80 ± 0.03	0.85 ± 0.08	0.75 ± 0.01	0.816	0.52	**0.83 ± 0.01a**	**0.82 ± 0.02a**	**0.80 ± 0.02a**	**0.75 ± 0.01b**	**7.308**	**0.011**
	Typical steppe	0.78 ± 0.02	0.81 ± 0.05	0.80 ± 0.01	0.79 ± 0.03	0.117	0.948	**0.87 ± 0.03a**	**0.85 ± 0.02ab**	**0.77 ± 0.01c**	**0.80 ± 0.01bc**	**6.326**	**0.017**
	Alpine meadow	**0.74 ± 0.00ab**	**0.76 ± 0.03ab**	**0.69 ± 0.03b**	**0.80 ± 0.02a**	3.411	0.073	**0.80 ± 0.01a**	**0.83 ± 0.05a**	**0.69 ± 0.03b**	**0.80 ± 0.01a**	**4.236**	**0.046**

significantly lower in grazed plots, compared to all other management practices or control in MS grasslands ($P < 0.05$); J' for cultivated areas was generally lower than grazed, mowed, or control in AM grasslands ($P < 0.05$); and management practices did not significantly effect H', J', and SR in TS grasslands ($P < 0.05$) (Table 3).

At 15–30 cm, grassland type had a significant impact on H' and SR ($P < 0.01$), while type, management, and their interaction had a significant impact on J' ($P < 0.05$) (Table S1). The H' and J' were significantly different by management in MS grasslands ($P < 0.05$). The J' for cultivated areas was lower than grazed or mowed areas in TS grasslands ($P < 0.05$). However, SR was significantly greater in cultivated areas, and J' for cultivated areas was generally lower than grazed, mowed, or control in AM grasslands ($P < 0.05$) (Table 3).

3.3. Ecological indices of nematode communities

At 0–15 cm, grassland type had a significant impact on NCR, BI, EI, and SI of nematodes ($P < 0.001$), while management only significantly influenced WI and SI ($P < 0.05$) (Table S1). There was also a significant interaction between grassland type and utilization pattern for EI ($P < 0.05$). At 15–30 cm, grassland type had a significant effect on WI, NCR, MI, BI, EI, and SI, while management significantly influenced WI, MI and SI, with significant interactions between grassland type and management for WI, BI, EI, and SI ($P < 0.05$) (Table S1).

Ecological indices (WI, NCR, MI, and BI) were applied to further understand relationships between soil nematode communities, local environments, and edaphic conditions across grassland types and management practices (Fig. 4). The WI value of cultivated AM areas was significantly greater than all other management practices and control for

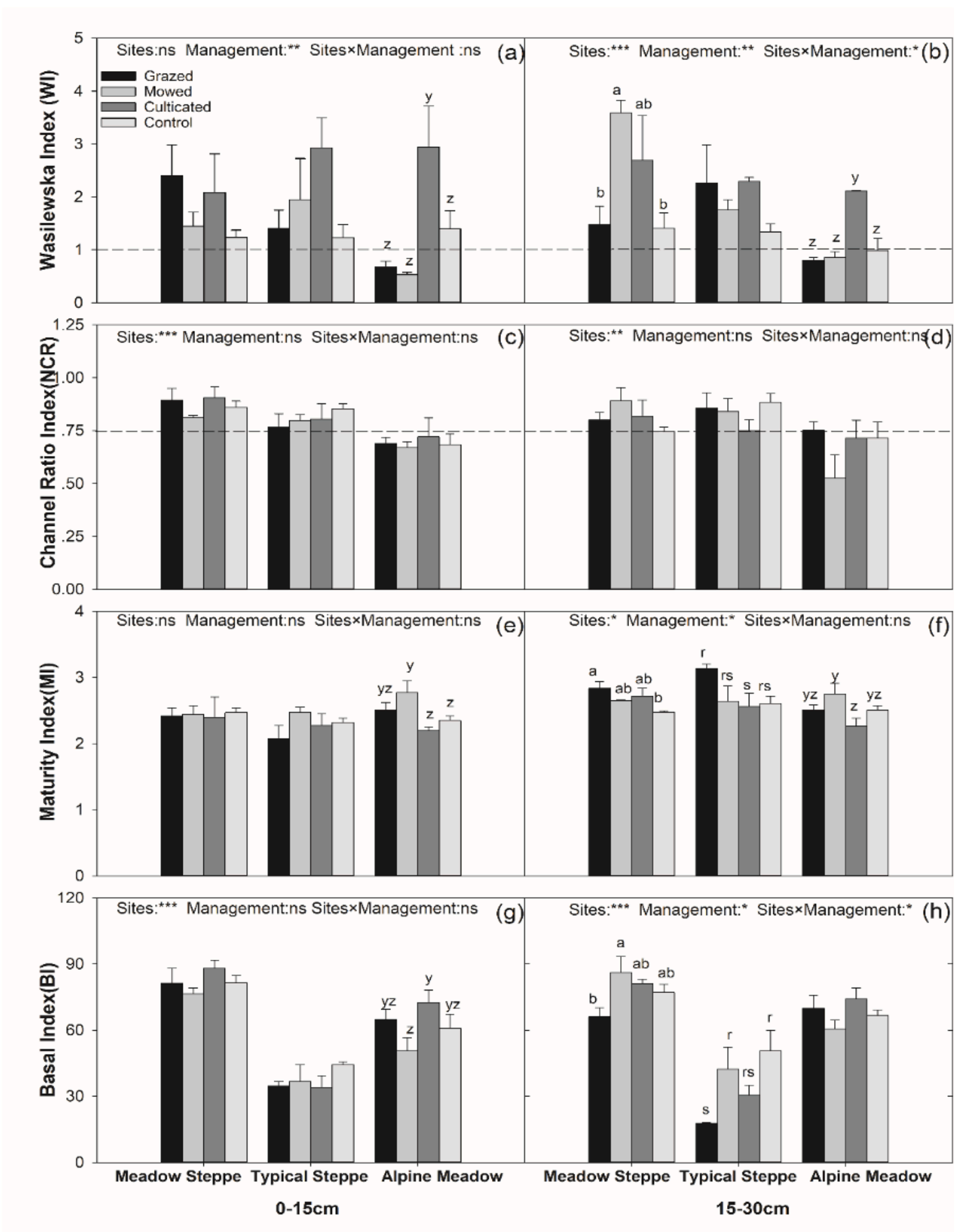

Fig. 4. Effects of grassland type (meadow steppe, typical steppe, or alpine meadow) and management practices (Grazed, Mowed, Cultivated, or Control) on function of soil nematode communities at two soil depths (0–15 cm, 15–30 cm) (means + SE). (a) (b): Wasilewska index (WI); the dotted line represents the WI value of 1; (c) (d): nematode channel ratio (NCR); the dotted line represents NCR value of 0.75; (e) (f): maturity index (MI) ;(g) (h): basal index (BI). Asterisks represent significant results of two-way ANOVA: different grassland types [sites]; different management practices [management]; and interactions. * indicates $P < 0.05$; ** indicates $P < 0.01$; *** indicates $P < 0.001$. Different letters represent significant differences in management (grazed, mowed, cultivated, or control) within a grassland type (meadow steppe, typical steppe, or alpine meadow) (ANOVA: Duncan test; $P < 0.05$). Lowercase letter [a-c] represent meadow steppe (MS); [r-s] represent typical steppe (TS); [y-z] represent alpine meadow (AM).

both soil depths ($P < 0.05$). There were no significant differences in NCR for any grassland type or management practices. Compared with other management practices in AM grasslands, the MI value of cultivated areas was lowest and mowed areas highest at both soil depths, while AM grassland BI values showed the opposite trend at 0–15 cm. For MS and TS grasslands, MI values in grazed areas were highest and BI values were lowest, particularly at 15–30 cm (Fig. 4).

EI and SI trajectories were plotted to assess soil food webs across grassland types and management (Fig. 5). For both depths, the EI/SI values of TS grasslands were greater than other grassland types regardless of management practices ($P < 0.05$). In addition, EI/SI values were lowest for cultivated areas (0–15 cm) and control areas (15–30 cm) at AM sites, compared to any other site or management practice ($P < 0.05$).

3.4. Relationship between soil nematode communities and environmental parameters

At 0–15 cm, the number of nematodes (N) positively correlated with electric conductivity (EC) but negatively correlated with pH ($P < 0.05$) (Figure S1). Species richness index (SR) and nematode channel ratio index (NCR) negatively correlated with soil water content (SWC) and pH but positively correlated with EC ($P < 0.001$); at 15–30 cm, NCR also negatively correlated with SWC, but was not as strong ($P < 0.05$). In addition, Wasilewska Index (WI) negatively correlated with SWC ($P < 0.05$) and positively correlated with EC ($P < 0.001$). At both soil depths, BI generally negatively correlated with EI and SI, but positively correlated with SR ($P < 0.001$). EI and SI were generally positively correlated with SWC and pH, and negatively correlated with EC, total nitrogen (TN), and soil organic carbon (SOC) ($P < 0.05$); BI generally negatively correlated with SWC and pH ($P < 0.001$), and positively correlated with EC, TN and SOC ($P < 0.05$) (Figure S1).

Direct ordination of sites (redundancy analyses; RDA) at 0–15 cm depth, resulted in eigen values of 0.1941 and 0.0644 for the first and second axes, respectively, and at 15–30 cm depth, resulted in 0.1476 and 0.0714 for the first and second axes, respectively (Fig. 6). All environmental factors passed the expansion test, and inflation factor (WIF) is < 10. RDA results suggest certain environmental parameters are either positively or negatively associated with nematode trophic groups across grassland types and management practices at 0–15 cm, with no significant correlation at 15–30 cm. There were substantial differences between grazed, mowed, and control plots in AM grasslands compared to MS and TS grasslands, with the most abundant nematode trophic groups being OP and BF. At 0–15 cm, nematode trophic groups were strongly influenced by soil pH and water content. Cultivated areas in AM grasslands, and grazed, mowed, and control areas in MS and TS sites were associated with BF nematodes, correlating with soil organic carbon, electric conductivity, and total nitrogen at 0–15 cm.

4. Discussion

This study of soil nematode communities is novel by relating ecological indices across three grassland types, enhancing definitions of soil quality by quantifying factors that drive microbial and plant community diversity in grassland ecosystems. Nematode community structure and context-dependent soil factors varied by geographic location of the model grasslands. Nematode communities of typical steppe (TS) and meadow steppe (MS) were composed largely of bacterivores, and this trophic group dominated soil organic matter decomposition pathways (NCR > 0.75), while soil mineralization pathways were dominated by free-living bacterivores and fungivores (WI > 1). However, nematode communities in alpine meadow (AM) were composed primarily of plant and fungal feeders (NCR < 0.75) and plant feeders dominated soil mineralization pathways (WI < 1). Globally, bacterivores are the most abundant group of nematodes, regardless of soil type or management (Van den Hoogen et al., 2019; 2020), and are tightly link to organic matter and nutrient cycling in the soil food web. Bacteria-based decomposition pathways are characteristic of high-input systems where labile substrates and bacterial-feeding faunas dominate. Fungal-based decomposition pathways typically occur in low-input systems characterized by more heterogeneous habitat and resources, leading to a dominance of more persistent fungal-feeding fauna (Bardgett et al.,1997; Chen et al., 2015; Hu et al.,2015). Plant feeding nematodes are primary consumers, directly damaging roots and potentially reducing nutrient uptake and plant production. Some of these nematodes also transmit plant viruses, affecting physiological functions. Results of the current study expand on this previous knowledge to highlight differences in environmental and nutritional status between grasslands across different geographic locations. These nematode community composition in TS and MS are likely due to abundant soil bacteria along with rapid decomposition of organic matter. However, abundant and fibrous plant organic residues in AM soils, along with slow decomposition of organic matter in this relatively cold and humid climate, likely drive the community dominance of plant feeding nematodes. Abundant bacterivores in MS and TS suggest a dynamic soil ecosystem, while abundant plant feeders in AM indicate lower resource availability.

The study found geographic location of grassland (grassland type), and management practice, as well as interactions between the two, had a significant impact on the number of nematodes at both soil depths, and vertical distribution of nematode populations also varied between different soil depths. Greater nematode abundance in soils collected from 0 to 15 cm, as compared to 15–30 cm, was observed in all three grasslands and across all management practices. These observations agree with previous studies that found soil fauna tends to gather on soil surfaces (Valocka and Sabova, 1997; Liang et al., 2007). Soil physical and chemical properties, as well as plant community composition, likely play an important role in the diversity and structure of nematode

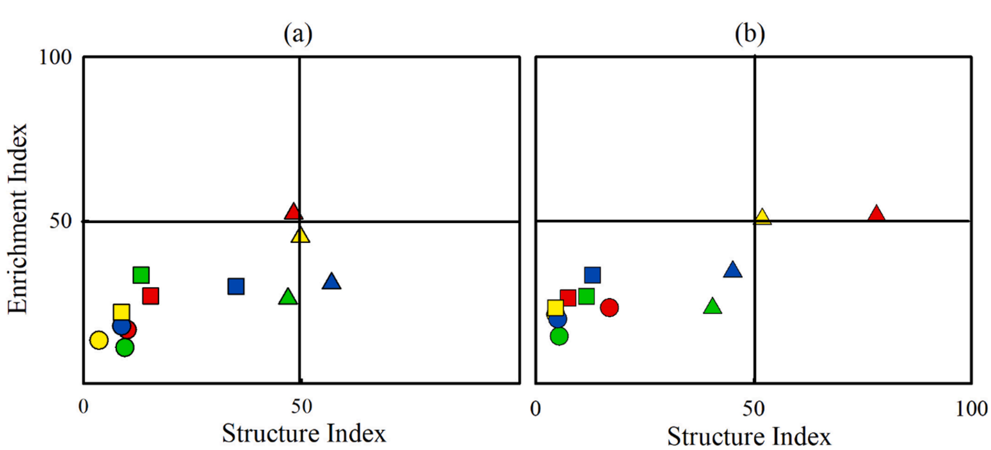

Fig. 5. Soil nematode analyses of grassland type (meadow steppe, typical steppe, or alpine meadow) and grassland management practices (grazed, mowed, cultivated, or control) at two soil depths (0–15 cm [a]; 15–30 cm [b]). EI/SI values vary from 0 to 100, and their combination indicates disturbance and soil food web status. Triangles represent typical steppe (TS), circles represent meadow steppe (MS), and squares represent alpine meadow (AM). Different colors represent grassland management: grazed areas [red]; mowed areas [blue]; cultivated areas [yellow]; and control areas [green]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

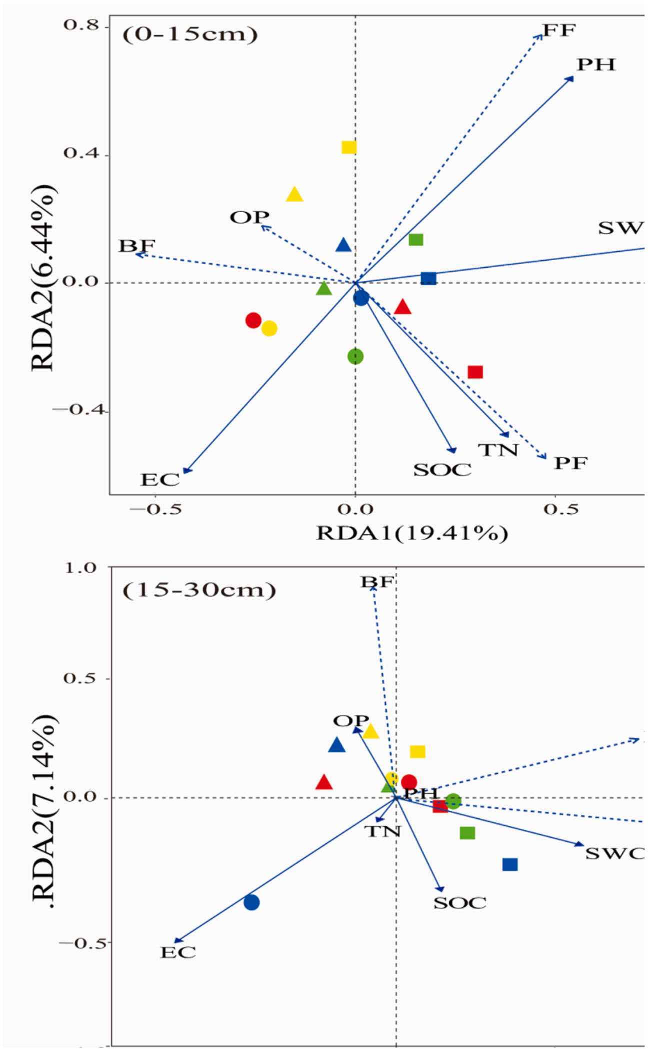

Fig. 6. Redundancy analysis (RDA) diagram of relationships between nematode trophic groups and environmental parameters. Environmental parameters: → Nematode trophic groups: ---------➔ soil pH; soil organic carbon [SOC]; soil total nitrogen [TN]; soil electric conductivity [EC]; soil water content [SWC]; plant feeders [PF], bacterivores [BF]; fungivores [FF]; omnivores and predators [OP]. Triangles represent typical steppe (TS), circles represent meadow steppe (MS), and squares represent alpine meadow (AM). Different colors represent grassland management: grazed areas [red]; mowed areas [blue]; cultivated areas [yellow]; and control areas [green]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

communities (Hu et al., 2015). Likewise, vertical distribution of nematodes may be driven by soil physical and chemical properties, such as soil nutrient availability. As soil depth increases, soil porosity, organic matter, and total nitrogen content decreased, while pH and salinity increased, thus reducing the number and diversity of nematodes. The major distribution of belowground components of most grassland plants occurs in the top 0–15 cm, and is therefore likely an important contribution for the greater number of nematodes in the top 15 cm in the study. Generally, spatial distribution of soil organisms is closely related to the spatial distribution of plants, due to the quantity and quality of plant litter returned to the soil, root turnover, and the amount of carbon exudated from roots into the soil. (Yeates 1999; Bardgett and Wardle, 2003; Jones et al., 2004).

Ecological indices were included to expand the understanding of nematode community structure in the context of local soil conditions, such as disturbance, ecosystem stability, and soil quality. Nematode communities were strongly influenced by soil quality, food web dynamics, and ecological functions that varied across grasslands and management practices. For example, food web complexity and food web response to soil resources were relatively higher in TS, while nematode abundance and food web resilience were relatively low in this grassland, regardless of management. In addition, all three management practices improved soil food web complexity and response to edaphic resources, reducing food web resilience compared with controls. In addition, EI and SI values of TS were higher, but the BI value was lower, compared to the same management practices of MS and AM grasslands. These differences were likely due to relatively high C: N ratios and greater nutrient availability in TS grasslands, compared to MS and AM grasslands.

While some trends were apparent across all grasslands, regardless of management, management practices often influenced nematode communities differentially by grassland type. For example, nematode abundance in cultivated areas was greater than all other management practices, and bacterivores were the dominate trophic group. Previous research reports an abundance of concurrent factors to explain this phenomenon, including fertilization, conventional tillage, alterations in soil water content, porosity, and permeability, all of which promote bacterial biomass and provide a rich source of nutrition for bacterivores (Liang et al, 2005; Huang and Cares, 2006; Meng et al., 2006; Hu et al., 2017). Additionally, the primary effect of these management practices is rapid organic matter decomposition, resulting in a dynamic soil ecosystem that supports abundant microorganisms and promotes bacterivores. Of three model grassland types, management practices in AM grasslands had the most significant impact on local soil environments. While cultivation of these humid and cold grasslands increased nematode abundance and food web complexity, there was a decrease in soil ecosystem stability, food web resilience, and soil biota response to resources. These outcomes were likely driven by a shift from plant-feeder to bacterivores following cultivation of AM grasslands, resulting in nematode community structure more similar to TS and MS grasslands. Furthermore, previous studies have found plant community composition and soil characteristics are important factors affecting soil nematode community structure, with resultant community shifts typically specific to particular trophic groups (Fu et al., 2000; Viketoft and Sohlenius, 2011; Cesarz et al.,2015). Future studies should further explore nematode community structure in combination with plant species composition and soil characteristics in grasslands across greater geographical distributions and additional management practices, ideally including multi-year investigations to determine stability and resilience of nematode communities across systems and time.

In conclusion, this study fills an important knowledge gap by elucidating how nematode community structure, soil food webs, and environmental factors are influenced by common grassland management practices across three diverse grassland systems. Unique environmental characteristics of the Qinghai-Tibet plateau led to substantial differences in AM grassland soil conditions that cascade through the ecosystem, and drives nematode community structure that is distinct from TS and MS grasslands. Among all management practices, cultivation had the greatest influence on nematode community structure, especially in the more sensitive AM grasslands. Results support the important role of soil nematodes as informative biological indicators of grassland quality.

CRediT authorship contribution statement

Li Liu: Conceptualization, Formal analysis, Visualization, Writing – original draft. **Shuiyan Li:** Conceptualization, Investigation, Methodology. **Gail W.T. Wilson:** Writing – review & editing. **Adam B. Cobb:** Writing – review & editing. **Chengyang Zhou:** . **Jinsheng Li:** . **Jiahuan Li:** . **Lizhu Guo:** . **Ding Huang:** Conceptualization, Resources, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Key Research and Development Program of China (grant No. 2018YFD0502402-5, No. 2016YFC05051902), and the Beijing Scientific Committee project of China (grant No. Z181100009618031). ABC was supported by National Institute of Food and Agriculture (NIFA) from the USDA (grant No. OKL03144 / project accession No. 1019172)

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108338.

References

Andriuzzi, W.S., Wall, D.H., Noelia Barrios-Garcia, M., 2018. Grazing and resource availability control soil nematode body size and abundance–mass relationship in semi-arid grassland. Journal Animal Ecology 87 (5), 1407–1417. https://doi.org/10.1111/jane.2018.87.issue-510.1111/1365-2656.12858.

Bardgett, R.D., Leemans, D.K., Cook, R., Hobbs, P.J., 1997. Seasonality of the soil biota of grazed and ungrazed hill grasslands. Soil Biol. Biochem. 29 (8), 1285–1294. https://doi.org/10.1016/S0038-0717(97)00019-9.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends in Ecology Evolution 14, 224–228. https://doi.org/10.1016/S0169- 5347(98)01583-3.

Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84 (9), 2258–2268. https://doi.org/10.1890/02-0274.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19. https://doi.org/10.2307/4219289.

Bremner, J.M., 1996. Nitrogen-total. In: Sparks, D.L. (Ed.), Methods of Soil Analysis Part 3: Chemical Methods, SSSA Book Series 5. Soil Science Society of America, Madison, Wisconsin, pp. 1085–1122.

Cesarz, S., Reich, P.B., Scheu, S., Ruess, L., Schaefer, M., Eisenhauer, N., 2015. Nematode functional guilds, not trophic groups, reflect shifts in soil food webs and processes in response to interacting global change factors. Pedobiologia 58 (1), 23–32. https://doi.org/10.1016/j.pedobi.2015.01.001.

Cesarz, S., Ciobanu, M., Wright, A.J., Ebeling, A., Vogel, A., Weisser, W.W., Eisenhauer, N., 2017. Plant species richness sustains higher trophic levels of soil nematode communities after consecutive environmental perturbations. Oecologia 184 (3), 715–728. https://doi.org/10.1007/s00442-017-3893-5.

Chen, D., Cheng, J., Chu, P., Hu, S., Xie, Y., Tuvshintogtokh, I., Bai, Y., 2015. Regional-scale patterns of soil microbes and nematodes across grasslands on the Mongolian plateau: relationships with climate, soil, and plants. Ecography 38 (6), 622–631. https://doi.org/10.1111/ecog.2015.v38.i610.1111/ecog.01226.

Coffey, V., Otfinowski, R., 2019. Legacies of afforestation on soil nematode community composition, structure, and diversity in a northern Canadian prairie. Plant Soil 435 (1-2), 437–447. https://doi.org/10.1007/s11104-018-03906-w.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. Journal of Nematology 38, 3–12.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18 (1), 13–29. https://doi.org/10.1016/S0929-1393(01)00152-4.

Ferris, H., Bongers, T., Goede, R.D.M., 1999. Nematode faunal indicators of soil food web condition. Journal of Nematology 31, 534–535.

Fu, S., Coleman, D.C., Hendrix, P.F., Crossley, D.A., 2000. Responses of trophic groups of soil nematodes to residue application under conventional tillage and no-till regimes. Soil Biol. Biochem. 32 (11-12), 1731–1741. https://doi.org/10.1016/S0038-0717(00)00091-2.

Gao, D., Wang, F., Li, J., Yu, S., Li, Z., Zhao, J., 2019. Soil nematode communities as indicators of soil health in different land use types in tropical area. Nematology 22 (6), 595–610. https://doi.org/10.1163/15685411-00003325.

Griffiths, B.S., Bonkowski, M., Roy, J., Ritz, K., 2001. Functional stability, substrate utilisation and biological indicators of soils following environmental impacts. Appl. Soil Ecol. 16 (1), 49–61. https://doi.org/10.1016/S0929-1393(00)00081-0.

Huang, S.P., Cares, J.E., 2006. In: Soil biodiversity in Amazonian and other Brazilian ecosystems. CABI, Wallingford, pp. 163–183. https://doi.org/10.1079/9781845930325.0163.

Han, X., Li, Y.H., Du, X.F., Li, Y.B., Wang, Z.W., Jiang, S.W., Li, Q., 2020. Effect of grassland degradation on soil quality and soil biotic community in a semi-arid temperate steppe. Ecological Processes 9, 63. http://creativecommons.org/licenses/by/4.0/.

Hu, J., Chen, G.R., Hassan, W.M., Chen, H., Li, J.Y., Du, G.Z., 2017. Fertilization influences the nematode community through changing the plant community in the Tibetan Plateau. Eur. J. Soil Biol. 78, 7–16. https://doi.org/10.1016/j.ejsobi.2016.11.001.

Hu, J., Wu, J., Ma, M., Nielsen, U.N., Wang, J., Du, G., 2015. Nematode communities response to long-term grazing disturbance on Tibetan plateau. Eur. J. Soil Biol. 69, 24–32. https://doi.org/10.1016/j.ejsobi.2015.04.003.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi and their nematode grazers: effects on nutrient cycling and plant growth. Ecol. Monogr. 55 (1), 119–140. https://doi.org/10.2307/1942528.

Jairajpuri, M.S., Ahmad, W., 1992. Dorylaimida-Free-living, predaceous and plant-parasitic nematodes. Brill Leiden, Netherlands.

Jones, D.L., Hodge, A., Kuzyakov, Y., 2004. Plant and mycorrhizal regulation of rhizodeposition. New Phytol. 163 (3), 459–480. https://doi.org/10.1111/nph.2004.163.issue-310.1111/j.1469-8137.2004.01130.x.

Li, X.Y., Lewis, E.E., Liu, Q.Z., Li, H.Q., Bai, C., Wang, Y.Z., 2016. Effects of long-term continuous cropping on soil nematode community and soil condition associated with replant problem in strawberry habitat. Sci. Rep. 6, 30466. https://doi.org/10.1038/srep30466.

Liang, W.J., Li, Q., Jiang, Y., Neher, D.A., 2005. Nematode faunal analysis in an aquic brown soil fertilized with slow-release urea, Northeast China. Appl. Soil Ecol. 29, 185–192. https://doi.org/10.1016/j.apsoil.2004.10.004.

LIANG, W.-J., ZHONG, S., HUA, J.-F., CAO, C.-Y., JIANG, Y., 2007. Nematode faunal response to grassland degradation in Horqin Sandy Land. Pedosphere 17 (5), 611–618. https://doi.org/10.1016/S1002-0160(07)60072-1.

Ma, Q., Yu, H., Liu, X., Xu, Z., Zhou, G., Shi, Y., 2018. Climatic warming shifts the soil nematode community in a desert steppe. Clim. Change 150 (3-4), 243–258. https://doi.org/10.1007/s10584-018-2277-0.

MENG, F.-X., OU, W., LI, Q.i., JIANG, Y., WEN, D.-Z., 2006. Vertical distribution and seasonal fluctuation of nematode trophic groups as affected by land use. Pedosphere 16 (2), 169–176. https://doi.org/10.1016/S1002-0160(06)60040-4.

Neher, D.A., 2001. Role of nematodes in soil health and their use as indicators. Journal of Nematology 33, 161–168. https://doi.org/10.1034/j.1600-0684.2001.300606.x.

Nelson, D.W., Sommers, L.E., 1996. Total C, organic C, and organic matter. In: Sparks, D. L. (Ed.), Methods of soil analysis: chemical methods. Soil Science Society of America, Madison, WI, pp. 961–1010.

Ney, L., Franklin, D., Mahmud, K., Cabrera, M., Hancock, D., Habteselassie, M., Newcomer, Q., Dahal, S., Subedi, A., 2019. Sensitivity of Nematode Community Analysis to Agricultural Management Practices and Inoculation with Local Effective Microorganisms in the Southeastern United States. Soil Systems 3, 41. https://doi.org/10.3390/soilsystems3020041.

Oksanen, J., 2013. Multivariate analysis of ecological communities in R: vegan tutorial. r package version.

Ou, W., Liang, W.J., Jiang, Y., Li, Q., Wen, D.Z., 2005. Vertical distribution of soil nematodes under different land use types in an aquatic brown soil. Pedobiologia 49, 139–148. https://doi.org/10.1016/j.pedobi.2004.10.001.

Pielou, E.C., 1975. Ecological diversity. Wiley, New York.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ren, H., Eviner, V.T., Gui, W., Wilson, G.W.T., Cobb, A.B., Yang, G., Zhang, Y., Hu, S., Bai, Y., Gallery, R., 2018. Livestock grazing regulates ecosystem multifunctionality in semi-arid grassland. Funct. Ecol. 32 (12), 2790–2800. https://doi.org/10.1111/fec.2018.32.issue-1210.1111/1365-2435.13215.

Ritz, K., Trudgill, D.L., 1999. Utility of nematode community analysis as an integrated measure of the functional state of soils: perspectives and challenges. Plant Soil 212, 1–11. https://doi.org/10.1023/a:1004673027625.

Shao, Y., Zhang, W., Shen, J., Zhou, L., Xia, H., Shu, W., Ferris, H., Fu, S., 2008. Nematodes as indicators of soil recovery in tailings of a lead/zinc mine. Soil Biol. Biochem. 40 (8), 2040–2046. https://doi.org/10.1016/j.soilbio.2008.04.014.

Shannon, C.E., Weaver, W., 1949. The mathematical theory of communication. University of Illinois, Urbana.

Siddiqi, M.R., 1986. Tylenchida: parasites of plants and insects. CAB International, Slough.

Valocka, B., Sabova, M., 1997. Communities of soil and plant nematodes in two types of grass land. Helminthologia 34, 97–103.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q.i., Liang, W., Magilton, M., Marais, M., Martín, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J.-i., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572 (7768), 194–198. https://doi.org/10.1038/s41586-019-1418-6.

van den Hoogen, J., Geisen, S., Wall, D.H., Wardle, D.A., Traunspurger, W., de Goede, R.G.M., Adams, B.J., Ahmad, W., Ferris, H., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., da Cunha e Castro, J.M., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q.i., Liang, W., Magilton, M., Marais, M., Martín, J. A.R., Matveeva, E., Mayad, E.H., Mzough, E., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., da Silva, J.C.P., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., Vestergård, M., Villenave, C., Waeyenberge, L., Wilschut, R.A., Wright, D.G., Keith, A.M., Yang, J.-i., Schmidt, O., Bouharroud, R., Ferji, Z., van der Putten, W.H., Routh, D., Crowther, T.W., 2020. A global database of soil nematode abundance and functional group composition. Sci. Data 7 (1). https://doi.org/10.1038/s41597-020-0437-3.

Viketoft, M., Sohlenius, B., 2011. Soil nematode populations in a grassland plant diversity experiment run for seven years. Appl. Soil Ecol. 48 (2), 174–184. https://doi.org/10.1016/j.apsoil.2011.03.008.

Wasilewska, L., Bienkowski, P., 1985. Experimental study on the occurrence and activity of soil nematodes in decomposition of plant material. Pedobiologia 28, 41–57. https://doi.org/10.2307/3565796.

Wei, T., Wei, M.T., 2017. Package 'corrplot'. Statistician 56, 316–324.

Wu, P.F., Zhang, H.Z., Cui, L.W., Wickings, K., Fu, S.L., Wang, C.T., 2017. Impacts of alpine wetland degradation on the composition, diversity and trophic structure of soil nematodes on the Qinghai-Tibetan Plateau. Sci. Rep. 7, 1–12. https://doi.org/10.1038/s41598-017-00805-5.

Wu, Y., Zhou, H., Chen, W., Zhang, Y., Wang, J., Liu, H., Zhao, Z., Li, Y., You, Q., Yang, B., Liu, G., Xue, S., 2021. Response of the soil food web to warming and litter removal in the Tibetan Plateau. China. Geoderma 401, 115318. https://doi.org/10.1016/j.geoderma.2021.115318.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. Journal of Nematology 25, 315–331. https://doi.org/10.0000/PMID19279775.

Yeates, G.W., 1999. Effects of plants on nematode community structure. Annu. Rev. Phytopathol. 37, 127–149. https://doi.org/10.1146/annurev.phyto.37.1.127.

Yeates, G.W., Newton, P.C.D., 2009. Long-term changes in topsoil nematode populations in grazed pasture under elevated atmospheric carbon dioxide. Biol. Fertil. Soils 45 (8), 799–808. https://doi.org/10.1007/s00374-009-0384-9.

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37 (4), 199–210. https://doi.org/10.1007/s00374-003-0586-5.

Zhao, J., Zhang, W., Wang, K., Song, T., Du, H., 2014. Responses of the soil nematode community to management of hybrid napiergrass: The trade-off between positive and negative effects. Appl. Soil Ecol. 75, 134–144. https://doi.org/10.1016/j.apsoil.2013.10.011.

Zhou, J., Wilson, G.W.T., Cobb, A.B., Yang, G., Zhang, Y., 2019a. Phosphorus and mowing improve native alfalfa establishment, facilitating restoration of grassland productivity and diversity. Land Degrad. Dev. 30 (6), 647–657. https://doi.org/10.1002/ldr.v30.610.1002/ldr.3251.

Zhou, J.Q., Zhang, F.G., Huo, Y.Q., Wilson, G.W.T., Cobb, A.B., Xu, X.X., Xiong, X., Liu, L., Zhang, Y.J., 2019b. Following legume establishment, microbial and chemical associations facilitate improved productivity in degraded grasslands. Plant and Soil 443, 273–292. https://doi.org/10.1007/s11104-019-04169-9.