



Effects of mowing frequency on abundance, genus diversity and community traits of soil nematodes in a meadow steppe in northeast China

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Abstract

Aims Soil nematodes, as key bioindicators, play crucial roles in soil ecological process. Management of grasslands, such as meadow steppes in northeast China, is often done by mowing, which has an impact on soil nematode communities. However, few studies have explored effects of mowing frequency on the community structure and biomass of soil nematodes.

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Highlights • Mowing had substantial effects on soil nematode communities.

- Intermediate mowing disturbance significantly enhanced the abundance and genus diversity of soil biota.
- Vegetation and soil physicochemical properties assumed major importance in the causation.

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Methods Routine field and laboratory methods concerning plant community, soil properties, and soil nematodes were applied in this study. Soil nematode community structure was analyzed by using nonmetric multidimensional scaling (NMDS) and principal component analysis (PCA). The relationships between nematode genus and biotic and abiotic factors were analyzed by redundancy analysis (RDA).

Results High mowing frequency significantly reduced abundance, biomass, and functional or metabolic regimes of soil nematodes in this ecosystem, whereas moderate mowing frequency enhanced those indices and regimes.

Conclusions Our findings showed that changing patterns in nematode indices across the mowing frequency conformed with the intermediate disturbance theory. Variations in soil nematode community were related to changes in belowground biomass, aboveground litter, soil available nitrogen and acidity, and the effects of edaphic and vegetal traits appeared to be trophic or genus-specific. This study has potential benefits for grassland restoration in northeast China.

Keywords Grassland · Vegetation · Biodiversity · Trophic group · Ecosystem function

Abbreviations

PP	Plant parasitic nematodes
Ba	Bacterivores
Fu	Fungivores
Op	Omnivores/predators
H'	Shannon–Weaver Index

WI	Wasilewska index
EI	Enrichment index
SI	Structure index
Ppf	Metabolic footprints of parasitic nematodes
Baf	Metabolic footprints of bacterivores
Fuf	Metabolic footprints of fungivores
Opf	Metabolic footprints of omnivores/predators
Ef	Enrichment footprint
Sf	Structure footprint
NMDS	Nonmetric Multidimensional Scaling
RDA	Redundancy analysis
PCA	Principal component analysis

Introduction

Grassland ecosystems occupy the largest part of global land area, being among the most important biomes of the global ecosphere. They assume crucial importance in the primary production, maintaining biodiversity, and soil and water conservation, and play an important role in mitigating the climate change effects and combating desertification (Li et al. 2020a).

Various studies have linked grassland ecosystem functions, such as nutrient cycling, with the abundance, species diversity, functional group composition and community structure of soil fauna (Hu et al. 2015; Wang et al. 2018, 2020). It has become an important research topic to deeply probe the response of soil animal community to anthropogenic activities. Such research is helpful to better understand, conserve, and restore the functions of grassland ecosystems around the world (Kardol and Wardle 2010; Wasof et al. 2019).

Soil nematodes are among the most important components of the soil food web in grassland ecosystems (Wang et al. 2020). Free-living soil nematodes have evolved diverse feeding habits, such as bacterivores, fungivores, plant parasitic nematodes, omnivores and predators (Yeates et al. 1993). They occupy different trophic levels and therefore carry on ecosystem functions at a node of the soil food web. For example, bacterial and fungal feeders may influence organic matter decomposition and nutrient mineralization through their interactions with the microbial community, while plant parasitic nematodes affect canopy and root biomass (Neher 2010) by direct feeding and organic matter decomposition by inducing root exudation and simulating microbial growth (Denton et al. 1998). By contrast,

omnivores and predatory nematodes can regulate soil fauna at lower trophic levels thereby reducing the grazing pressure on microorganisms (Laakso and Setälä 1999). Such trophic relations between soil nematodes and other soil organisms play a central role in delivering soil functions such as decomposition of plant litter and nutrient cycling (Zak et al. 1994; Ferris 2010).

The structure and function of the soil nematode community are closely related to edaphic properties (Neher et al. 1999; Ruan et al. 2012), climate (Wang et al. 2019; Xiong et al. 2020), and vegetation composition (Zhao et al. 2015; Wilschut et al. 2019). However, influences of these factors on nematode communities are multiple, interactive and specific to soil nematode groups. Ferris (2010) introduced the nematode metabolic footprint concept, which allows a functional quantification of the metabolic activity and magnitudes of carbon and energy flows in the soil food web of terrestrial ecosystems (Ferris et al. 2012; Zhang et al. 2015). The metabolic footprints of nematodes, based on carbon utilization in production and respiration, could provide information about the responses of the soil food web to resources and their relative contributions to ecosystem services (Ferris et al. 2012).

Soil nematodes are abundant in grasslands, which consist of species that vary in resource use efficiency (Hu et al. 2015). Root-feeding nematodes are the main group of root herbivores in temperate grasslands and they can consume as much as a quarter of the plant biomass in this biome (Stanton 1988). Their feeding activities affect plant abundance, biomass quality, and plant species composition (De Deyn et al. 2004; Viketoft et al. 2009). Bacterivores are the most important consumers of bacteria among soil invertebrates (Mesel et al. 2004) and they influence decomposition and nutrient mineralization processes in grassland soils (Stanton 1988). Furthermore, grassland soils also contain fungal feeding, omnivores and predators (Wang et al. 2018). Despite the potential role of soil nematodes in processes relating to vegetation dynamics and nutrient cycling, their metabolic and functional roles have been poorly documented via field studies of grassland.

Vegetation composition has substantial impacts on the abundance, species diversity and community composition of soil nematodes (De Deyn et al. 2004). This is mainly due to the fact that plant parasitic nematodes are highly plant-specific or life-form group-specific (Yeates and Bongers 1999; Diakhaté et al. 2013). It has been widely shown that vegetation canopy and plant detritus

cover have considerable effects on edaphic conditions (Zhang et al. 2012; Reese et al. 2018), especially soil moisture, temperature, soil acidity, and total or available nutrient levels, which all are important factors influencing the abundance and community traits of soil nematodes. Similarly, vegetation may also affect the microbial flora in terms of its abundance and species or functional composition, posing impacts on the bacterial feeding nematodes and fungivores to varying extents (Ferris and Matute 2003; Sánchez-Moreno et al. 2008; Briar et al. 2012). Several authors noted that plant diversity and plant root have particular influences on the abundance of rhizospheric microbes (Gastine et al. 2003; Tkacz et al. 2015; Revillini et al. 2019).

It is a matter of fact that such pasture utilization and management practices as grazing, shallow harrowing, and mowing have significant effects on the aforementioned vegetal and edaphic aspects of grasslands, and thus these grassland management practices inevitably would lead to changes in the soil nematode communities. Whereas several studies have examined the effects of stocking on the soil fauna (Ferris et al. 2012; Zhang et al. 2012; Pan et al. 2020), fewer studies have explicitly assessed the effects of mowing on soil nematodes of grassland ecosystems.

The meadow steppe is among the highest of Chinese temperate steppes in terms of net primary productivity, species richness and organic matter retention sequestration (Li et al. 2020a). While the bulk of this grassland type has been utilized as mowing pastures for harvesting hay in the relevant areas of northeast China. A number of studies showed that mowing may exert differing impacts on the vegetal traits of this meadow steppe ecosystem, depending substantially on the frequency and intensity of mowing practices (Huang et al. 2013; Yang et al. 2015). In contrast, the effects of mowing on the below-ground functions and processes, soil fauna-related aspects in particular, are poorly documented.

In this study, the effects of mowing frequency on the soil nematode communities of an Inner Mongolian meadow steppe were examined, the objectives of which were: (1) to examine the overall effects of mowing frequency on the abundance and biomass of the total soil nematodes and their major trophic groups; (2) to estimate major controlling factors and indices leading to the differences in soil nematode indices and the underpinning mechanisms; and (3) to determine the relations between nematode communities and vegetation and

edaphic factors in response to gradient mowing frequency.

Study site and methods

Site description

An experiment was conducted in Hulun Buir Grassland Ecosystem Observation and Research Station with a *Leymus chinensis* meadow steppe in Hulun Buir, Inner Mongolia Autonomous Region, China, where the grassland ecosystem research station has been run for two decades. The Station is located about 10 km east of the Shel Tara Ranch, roughly at 49°33'N and 120°05'E, with elevations mostly between 670 and 677 m. The climate in this region is cold temperate and semi-arid, with the average annual temperature varying between –5 and –2 °C, annual precipitation of 350 to 400 mm, and a frost-free period about 110 days. The vegetation is comprised predominantly of *Leymus chinensis*, *Filifolium sibiricum*, and *Stipa baicalensis*, with forbs, short bunchgrasses, and composites the commonly associated species. The dominant soil is the Mollisol with neutral to slightly alkaline and a sandy-loam texture (Tan 2015). The experimental plot was established in 2005 with four treatments: high mowing frequency (M1), with cutting taking place once a year; intermediate mowing frequency (M2), once every 2 years; low mowing frequency (M6), once every six years; and no mowing (CK), without cutting from the beginning. Each treatment was represented by five replicates, with a total area of 2 ha. Mowing was conducted in mid-August.

Soil and vegetation sampling and analysis

Soil samples were collected from the 0–20 cm soil profile with a 5 cm diameter auger in August, 2018. Ten soil samples were collected from each replicate in a treatment. At the same time, the canopy and litter biomass were measured using a 1 m² quadrat with five sites for each replication in a treatment, accompanied by relevant measurements of species composition and vegetal traits. Ten soil samples with an area of 30 cm x 30 cm and a depth of 0–20 cm were excavated for each treatment, whereby root biomass was measured. The collected soil and vegetal samples were taken back to the research station for extraction of soil nematodes,

measurement of soil physiochemical properties and canopy biomass.

Soil water was measured by the oven-drying method at 105 °C (Lu 2000). Soil organic carbon content was determined by the dichromate oxidation method with an ultraviolet spectrophotometer (at 589 nm wavelength) (Nelson and Sommers 1996); total soil nitrogen and available nitrogen was analyzed using Kjeldahl digestion method with an ultraviolet spectrophotometer (Bremner 1996); soil available phosphorus was determined by Olsen method using the 0.5 mol L⁻¹ sodium bicarbonate extraction method, and total phosphorus content was determined by the molybdenum antimony resistance-colorimetric method with an ultraviolet spectrophotometer (Kuo 1996); total soil K was determined using the NaOH molten flame photometer method, and the soil available potassium content was measured using NH₄OAc extraction and flame photometry (Lu 2000). The soil pH value was measured in water extracts using a digital pH meter.

Extraction and identification of soil nematodes

Soil nematodes were extracted from 100 g fresh soil per sampling spot by a modified Baermann funnel method (Barker 1985). All nematodes were killed in hot water at 60 °C for 10 min and preserved in a triethanolamine formaldehyde solution for nematode identification. The nematode suspension was taken out with a pipette for identification after it was shaken by hands. The first 100 nematode individuals were used to identify them to a genus level under a compound microscope at 400X or 1,000X magnification. The total abundance of soil nematodes was determined by counting the total number of individuals with the aid of anatomical lens at 25X to 60X. Soil nematodes were assigned to the following trophic groups according to their feeding habits: plant parasitic nematodes, bacterivores, fungivores and omnivores/predators (Yeates et al. 1993). Each nematode genus was also assigned a c-p value of 1–5 according to Bongers (1990). Soil water content was measured and finally the abundance of soil nematodes was converted to individuals per 100 g dry weight.

Calculations of ecological indices

Shannon–Weaver Index (H') (Shannon and Weaver 1949), nematode channel ratio (NCR) (Yeates 2003), and Wasilewska index (WI) (Wasilewska 1995) were

used to describe the genus diversity, decomposition pathways, and soil health regimes, respectively. Enrichment index (EI) and structure index (SI) were calculated to indicate conditions of soil food web (Ferris et al. 2001). Nematode body length (L) and maximum body width (D) were measured to estimate average fresh body weight (W, μg) of each nematode taxa. The fresh body weight was calculated as $W = (D^2 \times L) / (1.6 \times 10^6)$ (Ferris 2010). The fresh body weight was also used as biomass of soil nematodes. The nematode metabolic footprint (F) was used to assess the amount of carbon entering the soil food web, and it was calculated as $F = \sum (N_i (0.1 (W_i / m_i) + 0.273 (W_i^{0.75})))$, where W_i , m_i , and N_i represent the fresh weight (μg), c-p value of t taxa, and abundance, respectively. Metabolic footprints of plant parasitic nematodes, bacterivores, fungivores and omnivores/predators were used to characterize different ecosystem functions. Enrichment footprint (Ef) and structure footprint (Sf) were the sums of the metabolic footprint of soil nematodes with c-p values of 1 to 2 and 3 to 5, respectively (Ferris 2010).

Statistical analysis

All statistical analyses were performed using SPSS 17.0 (IBM Corp., Armonk, NY, USA). The effects of mowing treatments on the abundance, biomass, ecological index, and metabolic footprint were tested by Duncan test of Multiple Comparisons with One-Way ANOVA ($P < 0.05$). Nonmetric multidimensional scaling (NMDS) based on Bray curtis distance was applied to analyze composition changes at levels of genus and functional group of soil nematodes. The redundancy analysis (RDA) was conducted by using genus-level abundance data as the response variable, and vegetal and edaphic indices as explanatory variables to evaluate the relationships between nematode genus and the biotic and abiotic factors. Shifts in genus composition were analyzed by applying the principal component analysis (PCA).

Results

Differences in plant community conditions

Across the different mowing regimes, there were significant differences in the available K (195.0–345.0 mg kg⁻¹), soil moisture (20.8%–24.2%), plant species

evenness (0.5–0.7), species diversity (1.6–2.0), soil pH value (6.4–7.6), and root biomass (465.9–609.9 g·m⁻²). The difference in other edaphic properties and vegetal traits across treatments, however, were not significant (Table 1). These effects differed substantially with varying mowing frequency. For example, M1 (high mowing frequency) most substantially enhanced the soil pH value to 7.6, whereas it significantly decreased the available K content (195.0 mg kg⁻¹), root biomass (465.9 g m⁻²), and plant species diversity (1.6). M2 (intermediate mowing frequency) substantially reduced the plant species evenness (1.6), available P (6.5 mg kg⁻¹), soil moisture (20.8%) and pH value (6.4), while M6 (low mowing frequency) had the highest available N (25.3 mg kg⁻¹) and P (11.1 mg kg⁻¹) and litter biomass (57.7 g·m⁻²). By contrast, CK (no mowing) maintained the highest measures of soil available K (345.0), soil water (24.2%), root biomass (609.9 g m⁻²), and plant species diversity (2.0) and evenness (0.7).

Differences in abundance of soil nematodes

Significant differences in the abundance of soil nematodes among varying mowing frequency treatments in the meadow steppe ecosystem, which exhibited bump-shaped shifts for the total abundance and abundance of constituent trophic groups. It was observed that the total abundance of soil nematodes was more or less reduced in M1 treatment, whereas it was increased in the other mowing treatments compared to that of CK. The abundances of the four trophic nematode groups also showed similar trends (Fig. 1). More specifically, M2 most significantly increased the total abundance and the abundances of plant parasitic nematodes, fungivores, and omnivores/predators, while M6 most significantly increased the abundance of bacterivores. In contrast, M1 and CK were generally comparable in this regard, and there were no significant differences in both the total and group-specific abundances among the two treatments (Fig. 1).

Differences in biomass of soil nematodes

The biomass of the total soil nematodes ranged from 211.2 to 441.8 µg per 100 g dry soil among the various treatments (Table 2). Of the trophic groups, the

proportion of bacterivores ranged between 28.9% and 42.9% among treatments and had the highest proportion in all treatments except the proportion of bacterivores in the M2 treatment was lower than that of omnivores/predators. Correspondingly, fungivores had the lowest proportion, with a range between 8.4% and 17.8%.

The biomass of the total soil nematodes and four trophic groups responded differently to mowing frequency treatments. Just like the case for the total abundance and abundance of constituent trophic groups discussed above, all mowing treatments except M1 enhanced the biomass of the total soil nematodes, plant parasitic nematodes, fungivores, and omnivores/predators. Mowing treatments M2 and M6 increased the biomass of bacterivores compared to CK. To summarize, M1 had the highest proportion of biomass of bacterivores; M2 had higher biomass measures of plant parasitic nematodes and omnivores/predators; and M6 had the highest biomass values of the total soil nematodes (Table 2).

Further analysis of the data shown in Table 2 indicates that the proportional compositions in biomass of the trophic groups did not differ significantly among the treatments, meaning that with changes in mowing frequency, the trophic structure of the soil nematode communities did not change significantly, with the bacteria-feeding group being predominant throughout.

Shifts in community composition and structure of soil nematodes

Overall, a total of 56 nematode genera were identified in this meadow steppe ecosystem, with an average range of 33 to 43 genera in the various treatments (Table 3). Among them, *Paratylenchus* (CK), *Helicotylenchus* (M1, M2), and *Aglenchus* (M6) were the most abundant plant parasitic nematodes; *Acrobeles* (CK), *Eucephalobus* (M1), and *Acrobeloides* (M2, M6) were the most abundant bacterivores; *Ditylenchus* (CK), *Aphelenchoides* (M1), and *Filenchus* (M2, M6) were the most abundant fungivores; and *Microdorylaimus* (CK), *Longidorella* (M2) and *Microdorylaimus* (M1, M6) were the most abundant omnivores/predators.

The result of PCA showed that the effects of mowing frequency treatments on the nematode community structure were significant, which showed that the first axis of

Table 1 Soil physicochemical properties and vegetal traits under different mowing treatments

	SOC (g kg ⁻¹)	TN (g kg ⁻¹)	TP (g kg ⁻¹)	Available N (mg kg ⁻¹)	Olsen P (mg kg ⁻¹)	Available K (mg kg ⁻¹)	pH	Soil water (%)	Canopy biomass (g m ⁻²)	Litter biomass (g m ⁻²)	Belowground biomass (g m ⁻²)	Evenness index	Shannon- Weaver index
M1	23.1 ± 0.9	2.5 ± 0.2	0.5 ± 0.0	23.7 ± 1.7	7.9 ± 1.1b	195.0 ± 8.7c	7.6 ± 0.8a	21.2 ± 0.2bc	200.3 ± 16.6	27.8 ± 4.3	465.9 ± 6.3b	0.6 ± 0.0b	1.6 ± 0.1b
M2	24.3 ± 0.6	2.6 ± 0.2	0.5 ± 0.0	24.9 ± 1.4	6.5 ± 0.5b	235.0 ± 31.8b	6.4 ± 0.1b	20.8 ± 0.9c	195.3 ± 13.0	41.7 ± 4.8	562.1 ± 3.1b	0.5 ± 0.0bc	1.6 ± 0.1b
M6	24.0 ± 0.4	2.6 ± 0.0	0.5 ± 0.0	25.3 ± 1.7	11.1 ± 2.1a	280.0 ± 69.5b	7.0 ± 0.2b	21.7 ± 0.2b	242.9 ± 8.1	57.7 ± 6.6	592.2 ± 6.7a	0.5 ± 0.0b	2.0 ± 0.1a
CK	22.4 ± 1.6	2.3 ± 0.1	0.5 ± 0.0	24.9 ± 3.4	9.2 ± 0.5ab	345.0 ± 31.2a	6.8 ± 0.1b	24.2 ± 0.1a	195.1 ± 8.7	55.1 ± 16.7	609.9 ± 4.5a	0.7 ± 0.0a	2.0 ± 0.1a

SOC: soil organic carbon; TN: total soil nitrogen; TP: total soil phosphorus. M1: cutting grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing. Values are means ± standard errors (n = 5). Different letters in each column show significant differences at $P < 0.05$, while unmarked values throughout a column are not significantly different between one another

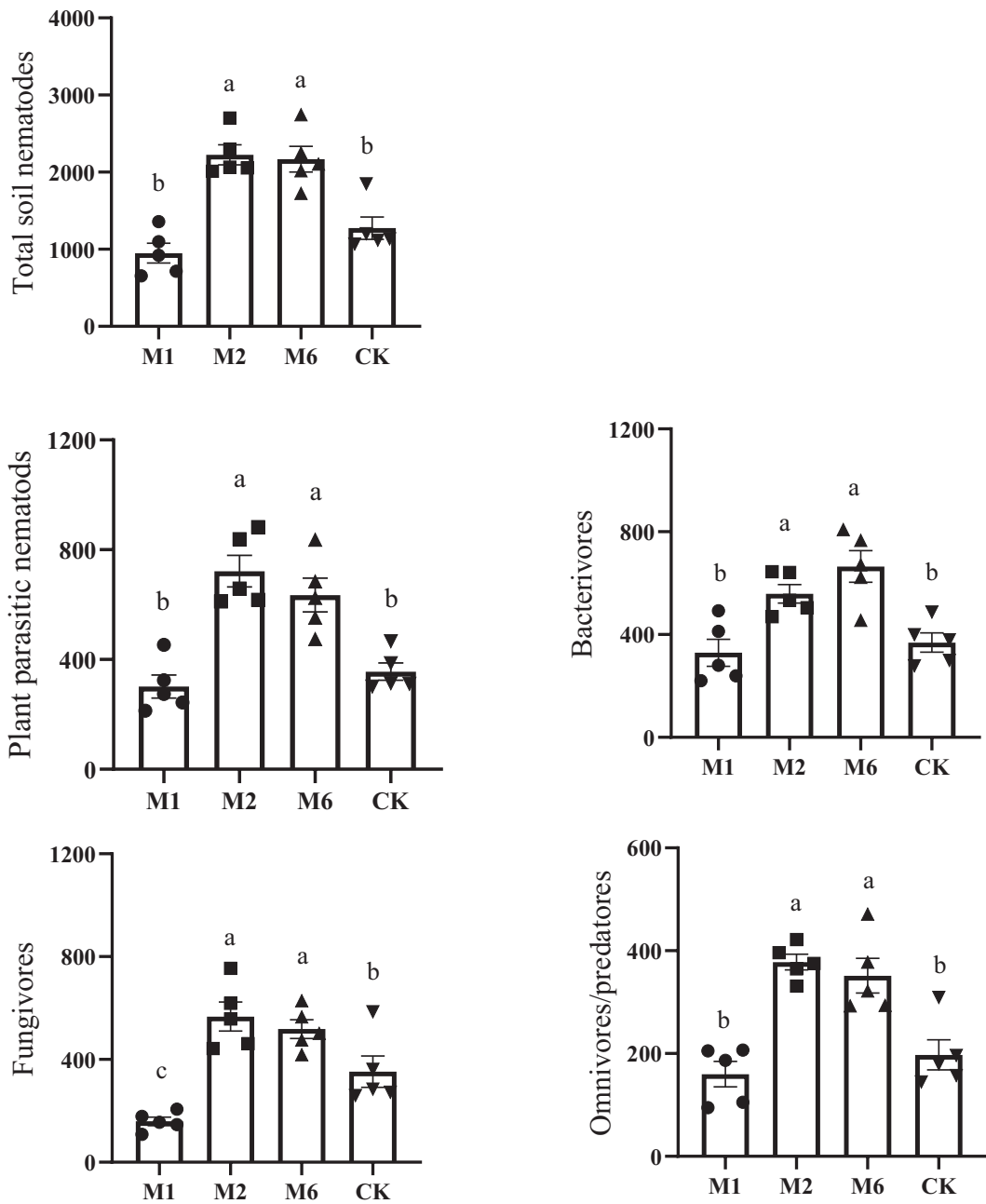


Fig. 1 Total and group-specific abundances of soil nematodes (individuals per 100 g dry soil) under different mowing treatments. M1: cutting grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing.

Values are means ± standard errors (n = 5). Different lowercase letters indicate significant differences among treatments at $P < 0.05$

the PCA explained 32.1% of the variance in generic composition, and the second axis explained 16.5% of the variance (Fig. 2). It can be seen that the four treatments were rather clearly divergent from one another in terms of generic composition.

Our nonmetric multidimensional scaling analysis also showed obvious shifts in community composition in terms of genus and trophic group of soil nematodes (Fig. 3a and b). In terms of genus composition, three aggregation zones was clearly defined, which represent

Table 2 Means of biomass of soil nematodes (μg per 100 g dry soil) under different mowing treatments

	M1	M2	M6	CK
Ppw	46.9 \pm 14.5b (22.2%)	108.1 \pm 16.8a (24.7%)	103.9 \pm 21.2a (23.5%)	52.3 \pm 12.7b (20.9%)
Baw	90.5 \pm 29.2bc (42.9%)	126.3 \pm 17.5ab (28.9%)	158.8 \pm 36.8a (35.9%)	87.4 \pm 21.0c (34.9%)
Fuw	17.8 \pm 5.5c (8.4%)	70.4 \pm 12.4a (16.1%)	61.4 \pm 15.0ab (13.9%)	44.6 \pm 21.9b (17.8%)
Opw	56.0 \pm 20.2b (26.5%)	132.3 \pm 13.2a (30.3%)	117.6 \pm 21.6a (26.7%)	66.2 \pm 28.3b (26.4%)
Tow	211.2 \pm 65.8b	437.1 \pm 28.0a	441.8 \pm 70.4a	250.5 \pm 79.2b

Ppw, Baw, Fuw, Opw and Tow are abbreviations for the biomass of plant parasitic nematodes, bacterivores, fungivores, omnivores/predators and total soil nematodes, respectively. M1: cutting grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing. Values are means \pm standard errors ($n = 5$). Values with different lowercase letters in each column are significantly different at $P < 0.05$

the cases for M1, CK, and M2 plus M6 (Fig. 3a). For the structure of nematode functional group, two sections were differentiated as shown in Fig. 3b, each including CK and M1 on the lower left part and the remainder on the top right part of the plot.

Ecological indices of nematode communities

The diversity of soil nematode genera displayed a single-peaked trend across the gradient of mowing frequency, with M6 having a significantly higher species richness and H' measure than those of the other treatments (Table 4). The NCR value was significantly higher for M1 than for the other treatments. The WI and EI values exhibited an increasing trend with decreasing mowing frequency, in which both values were significantly higher in CK than those of the other treatments with the exception of EI in M6 (Table 4). By contrast, MI and SI were the highest in the treatment M2, although differences for both indices were significant only between M1 and M2.

Differences in the metabolic activity of soil nematodes.

Variations in the metabolic footprint for each trophic group of soil nematodes among mowing frequency gradient treatments displayed relatively similar trends (Fig. 4). Of these, the gradient trend for bacterivores may be delineated by a parabolic curve with opening downward, with M6 having the maximal metabolic footprint measure; by contrast, those for the other trophic groups were single-peaked, the maximums of which consistently occurred at M2. In addition, the peak value for each trophic group was significantly higher

than the relevant values at the two ends across the mowing frequency gradient. The trend for Ef followed a top-down parabolic curve, with the peak value at M6, whereas the trend for Sf was single-peaked, with its maximal value at M2.

Relationships between the abundance of soil nematodes and vegetation-soil variables

RDA results showed strong relationships between soil-vegetation variables and the abundance of different soil nematode genera (Fig. 5). Of these, available nutrients, belowground biomass, litter biomass and soil pH were mostly related to the nematode community composition via axis 1. Soil organic carbon, total nitrogen, and soil water were more closely related to the nematode community composition via axis 2. Most nematode genera, with the exception of *Plectus*, *Criconemella*, *Prismatolaimus*, *Pratylenchus*, and *Dorylaimoides*, were negatively correlated to soil pH. *Xiphinema* positively correlated to belowground biomass. Bacterivores *Chiloplacus* and *Cephalobus* were positively correlated to canopy biomass. The available nutrients were mainly correlated to bacterivores and omnivores/predators.

Discussion

Effects of mowing on soil and vegetal conditions

Our findings indicate that various mowing treatments had significant impacts on soil water, pH value, root and litter biomass, and plant species diversity and evenness.

Table 3 Composition and abundance (individuals per 100 g dry soil) of nematode genera under different treatments of the meadow steppe ecosystem

	Trophic groups ^a	c-p value ^b	M1	M2	M6	CK	Abbreviations
<i>Aglencbus</i>	Pp	2	30 ± 5	67 ± 14	65 ± 18	35 ± 7	<i>Agle</i>
<i>Boleodorus</i>	Pp	2	-	19 ± 6	29 ± 6	14 ± 8	<i>Bole</i>
<i>Criconemella</i>	Pp	3	1 ± 1	5 ± 3	-	3 ± 3	<i>Cric</i>
<i>Helicotylenchus</i>	Pp	3	59 ± 9	81 ± 9	56 ± 8	39 ± 3	<i>Heli</i>
<i>Heterodera</i>	Pp	3	-	4 ± 2	5 ± 2	4 ± 2	<i>Hete</i>
Juveniles of Hoplolaimidae	Pp	3	40 ± 8	72 ± 18	58 ± 12	32 ± 6	<i>Juve</i>
<i>Lelenchus</i>	Pp	2	21 ± 5	32 ± 9	52 ± 3	31 ± 5	<i>Lele</i>
<i>Longidorus</i>	Pp	5	15 ± 4	35 ± 8	22 ± 3	7 ± 5	<i>Long</i>
<i>Malenchus</i>	Pp	2	2 ± 1	53 ± 21	47 ± 4	42 ± 8	<i>Male</i>
<i>Pararotylenchus</i>	Pp	3	34 ± 4	40 ± 10	46 ± 4	22 ± 5	<i>Para</i>
<i>Paratrichodorus</i>	Pp	4	-	8 ± 5	21 ± 5	8 ± 5	<i>Pari</i>
<i>Paratylenchus</i>	Pp	3	28 ±	66 ± 14	58 ± 11	44 ± 18	<i>Parl</i>
<i>Pratylenchus</i>	Pp	3	21 ± 4	45 ± 12	19 ± 5	6 ± 2	<i>Prat</i>
<i>Rotylenchus</i>	Pp	3	12 ± 5	57 ± 8	41 ± 8	19 ± 7	<i>Roty</i>
<i>Scutellonema</i>	Pp	3	-	-	7 ± 2	6 ± 3	<i>Scut</i>
<i>Trichodorus</i>	Pp	4	-	3 ± 3	14 ± 5	3 ± 2	<i>Tric</i>
<i>Tylenchorhynchus</i>	Pp	3	33 ± 3	80 ± 16	54 ± 8	25 ± 3	<i>Tylo</i>
<i>Tylenchus</i>	Pp	2	5 ± 2	52 ± 15	25 ± 6	9 ± 5	<i>Tyle</i>
<i>Xiphinema</i>	Pp	5	-	3 ± 3	15 ± 7	6 ± 2	<i>Xiph</i>
<i>Acrobeles</i>	Ba	2	48 ± 8	87 ± 4	119 ± 20	74 ± 19	<i>Acro</i>
<i>Acrobeloides</i>	Ba	2	75 ± 11	109 ± 9	127 ± 17	69 ± 6	<i>Acri</i>
<i>Alaimus</i>	Ba	4	13 ± 3	35 ± 7	57 ± 10	26 ± 2	<i>Alai</i>
<i>Anaplectus</i>	Ba	2	-	-	8 ± 4	7 ± 5	<i>Anap</i>
<i>Cephalobus</i>	Ba	2	-	43 ± 8	58 ± 10	25 ± 2	<i>Ceph</i>
<i>Cervidellus</i>	Ba	2	22 ± 5	106 ± 17	86 ± 12	47 ± 4	<i>Cerv</i>
<i>Chiloplacus</i>	Ba	2	-	-	3 ± 2	-	<i>Chil</i>
<i>Diplolaimeloides</i>	Ba	1	-	3 ± 3	34 ± 7	28 ± 4	<i>Dipl</i>
<i>Eucephalobus</i>	Ba	2	91 ± 17	47 ± 11	58 ± 20	39 ± 8	<i>Euce</i>
<i>Mesorhabditis</i>	Ba	1	8 ± 1	11 ± 3	45 ± 3	12 ± 6	<i>Meso</i>
<i>Monhystera</i>	Ba	1	-	-	6 ± 3	8 ± 5	<i>Monh</i>
<i>Plectus</i>	Ba	2	30 ± 6	12 ± 3	23 ± 4	12 ± 3	<i>Plec</i>
<i>Prismatolaimus</i>	Ba	3	32 ± 18	84 ± 11	26 ± 10	15 ± 11	<i>Pris</i>
<i>Wilsonema</i>	Ba	2	10 ± 2	22 ± 7	15 ± 5	6 ± 3	<i>Wils</i>
<i>Aphelenchooides</i>	Fu	2	54 ± 5	88 ± 11	83 ± 6	46 ± 11	<i>Aphe</i>
<i>Aphelenchus</i>	Fu	2	19 ± 2	73 ± 14	47 ± 4	21 ± 4	<i>Aphs</i>
<i>Diphtherophora</i>	Fu	3	15 ± 4	49 ± 9	36 ± 11	22 ± 8	<i>Diph</i>
<i>Ditylenchus</i>	Fu	2	20 ± 3	91 ± 14	84 ± 14	76 ± 18	<i>Dity</i>
<i>Doryllium</i>	Fu	4	-	-	-	3 ± 3	<i>Dorl</i>
<i>Filenchus</i>	Fu	2	25 ± 2	106 ± 12	121 ± 14	76 ± 14	<i>File</i>
<i>Tylencholaimellus</i>	Fu	4	15 ± 4	64 ± 19	85 ± 18	74 ± 16	<i>Tyll</i>
<i>Tylencholaimus</i>	Fu	4	12 ± 2	96 ± 14	61 ± 3	34 ± 8	<i>Tyls</i>
<i>Aporcelaimus</i>	Op	5	14 ± 3	31 ± 6	34 ± 2	15 ± 3	<i>Apor</i>
<i>Discolaimus</i>	Op	5	10 ± 3	14 ± 6	18 ± 6	8 ± 3	<i>Disc</i>
<i>Dorylaimoides</i>	Op	4	21 ± 3	20 ± 6	18 ± 2	5 ± 2	<i>Dory</i>

Table 3 (continued)

	Trophic groups ^a	c-p value ^b	M1	M2	M6	CK	Abbreviations
<i>Enchodelus</i>	Op	4	-	7 ± 3	6 ± 2	-	<i>Ench</i>
<i>Epidorylaimus</i>	Op	4	-	22 ± 8	31 ± 5	19 ± 5	<i>Epid</i>
<i>Eudorylaimus</i>	Op	4	19 ± 5	36 ± 9	30 ± 6	10 ± 6	<i>Eudo</i>
<i>Labronema</i>	Op	4	16 ± 5	43 ± 8	21 ± 6	16 ± 9	<i>Labr</i>
<i>Laimydorus</i>	Op	4	11 ± 3	34 ± 11	29 ± 6	25 ± 6	<i>Laim</i>
<i>Longidorella</i>	Op	4	15 ± 4	62 ± 18	46 ± 11	21 ± 7	<i>Loni</i>
<i>Mesodorylaimus</i>	Op	5	-	-	3 ± 3	2 ± 2	<i>Mesd</i>
<i>Microdorylaimus</i>	Op	4	36 ± 4	59 ± 14	67 ± 12	35 ± 9	<i>Micr</i>
<i>Mononchus</i>	Op	4	10 ± 3	-	13 ± 5	3 ± 2	<i>Mono</i>
<i>Nygolaimus</i>	Op	5	-	4 ± 4	6 ± 2	7 ± 7	<i>Nygo</i>
<i>Torumanawa</i>	Op	5	8 ± 3	20 ± 6	21 ± 4	22 ± 6	<i>Toru</i>
<i>Tripyla</i>	Op	3	-	26 ± 9	6 ± 4	6 ± 4	<i>Trip</i>
<i>Trischiostoma</i>	Op	3	-	-	4 ± 3	5 ± 3	<i>Tris</i>

^a Trophic groups of soil nematodes are divided according to Bongers and Bongers (1998) and Ferris et al. (2001), the abbreviations of which are the same as in Table 2. ^b c-p value is determined following the method of Bongers (1990). Pp: plant parasitic nematodes; Ba: bacterivores; Fu: fungivores; Op: omnivores/predators. M1: cutting grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing. Values are means ± standard errors (n = 5)

M1 and M2 had no significant effect on the canopy biomass in the meadow steppe ecosystem although they had a relatively minor influence on the total soil nutrient

stocks (Table 1). Similar results have been reported in an analogous study, in which, no difference was observed in total soil N between mowing and control treatments

Fig. 2 Principal component analysis of soil nematode abundances under different treatments including all sampling replicates. M1: cutting grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing. For the abbreviations of nematode genera, one can refer to Table 3. The eigenvalues of the first four axes are 32.1%, 16.5%, 10.5%, and 8.6%, respectively

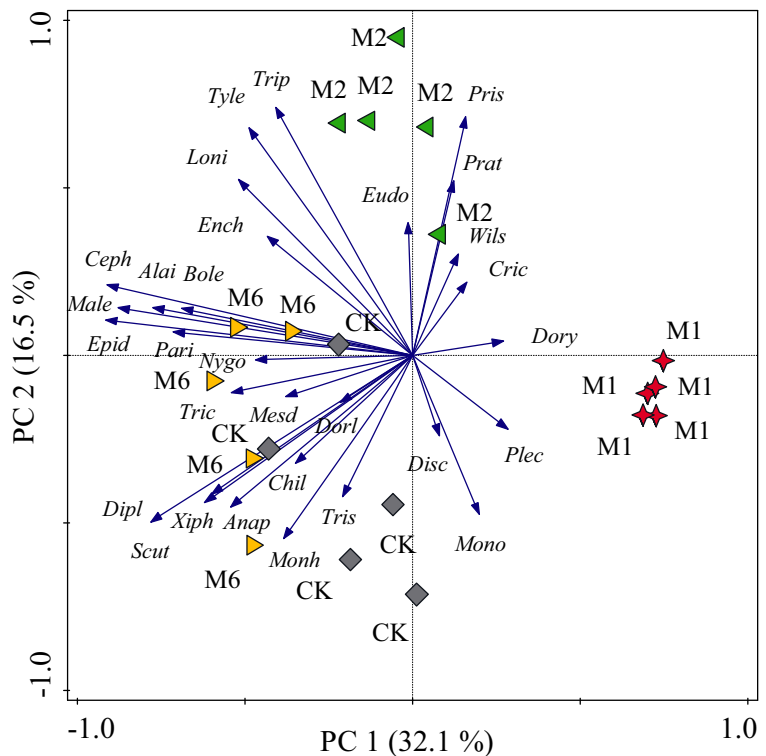


Fig. 3 Nonmetric multi-dimensional scaling (NMDS) plots in light of genera (a) and trophic groups (b) of soil nematodes among different treatments. M1, cutting grass once a year; M2, cutting grass once every two years; M6, cutting grass once every six years; CK, no mowing. The eigenvalues of the first three axes for (a) plot are 71.1%, 22.3%, and 6.6%, respectively. The eigenvalues of the first three axes for (b) plot are 64.3%, 25.7% and 10.0%

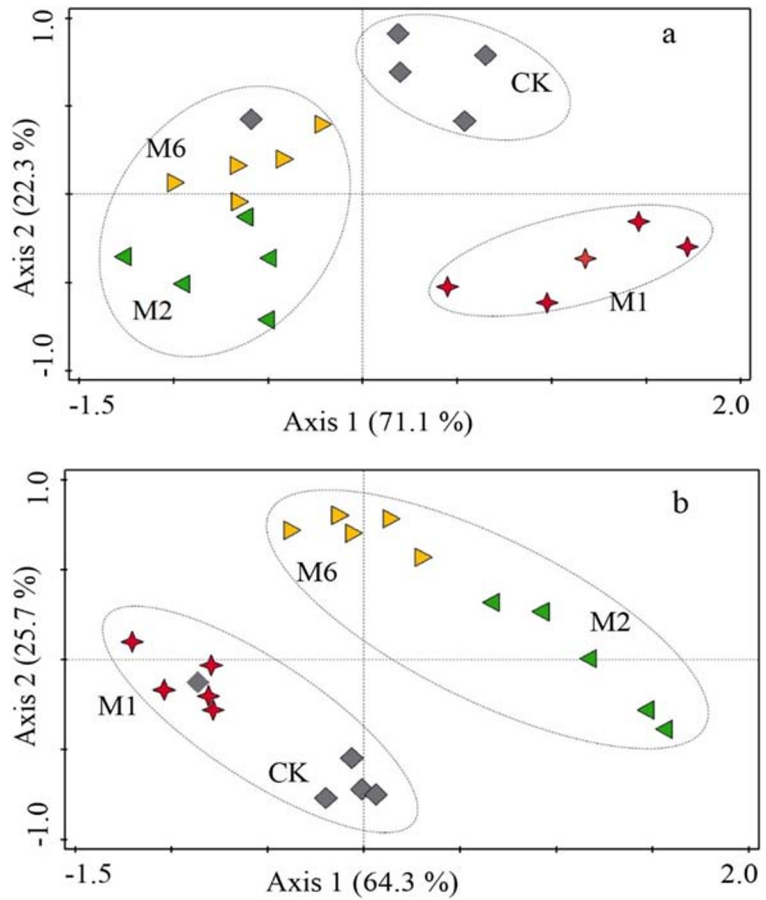


Table 4 Ecological indices of soil nematode communities under different treatments

	M1	M2	M6	CK
S	33 ± 2b	35 ± 2b	39 ± 1a	33 ± 3b
H'	3.3 ± 0.0c	3.4 ± 0.1b	3.6 ± 0.0a	3.3 ± 0.1c
MI	2.7 ± 0.1b	2.9 ± 0.1a	2.8 ± 0.1ab	2.8 ± 0.1ab
NCR	0.7 ± 0.1a	0.5 ± 0.1b	0.6 ± 0.1b	0.5 ± 0.1b
WI	1.6 ± 0.1c	1.6 ± 0.2c	1.9 ± 0.1b	2.1 ± 0.1a
EI	27.7 ± 3.3b	33.9 ± 5.0b	44.4 ± 4.3a	44.3 ± 6.3a
SI	70.0 ± 4.4b	77.2 ± 2.4a	75.3 ± 2.3a	75.0 ± 3.8a

S: species richness (presented as genus number); H': Shannon-Weaver index; MI: free living nematode maturity index; NCR: nematode channel ratio; WI: Wasilewska index; EI: enrichment index; and SI: structure index. M1: cutting grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing. Values are means ± standard errors (n = 5). Different lowercase letters indicate significant differences at the level of $P < 0.05$

(Maron and Jefferies 2001). Nevertheless, significant decreases stemming from mowing disturbance in canopy biomass and nutrient stocks has been shown before (Bao et al. 2004; Yang et al. 2012). These inconsistencies between different studies were likely due to different mowing heights and experimental sites. The mowing height in the study of Bao et al. (2004) was about 6 cm, but the height was more than 10 cm in the present study, which might result in differences in canopy biomass and nutrient left in the soil. The significant rise of pH value in M1 is consistent with the results of previous mowing studies (Nagata and Ushimaru 2016), which resulted principally from a reduction in plant detritus accumulation by the mowing harvest over the steppe ground. In our study, lower mowing frequency (M6) increased in canopy biomass, which is consistent with previous reports, the mechanism for which has been variously elaborated upon (Huhta et al. 2003; Gonzales and Clements 2010; Yang et al. 2020).

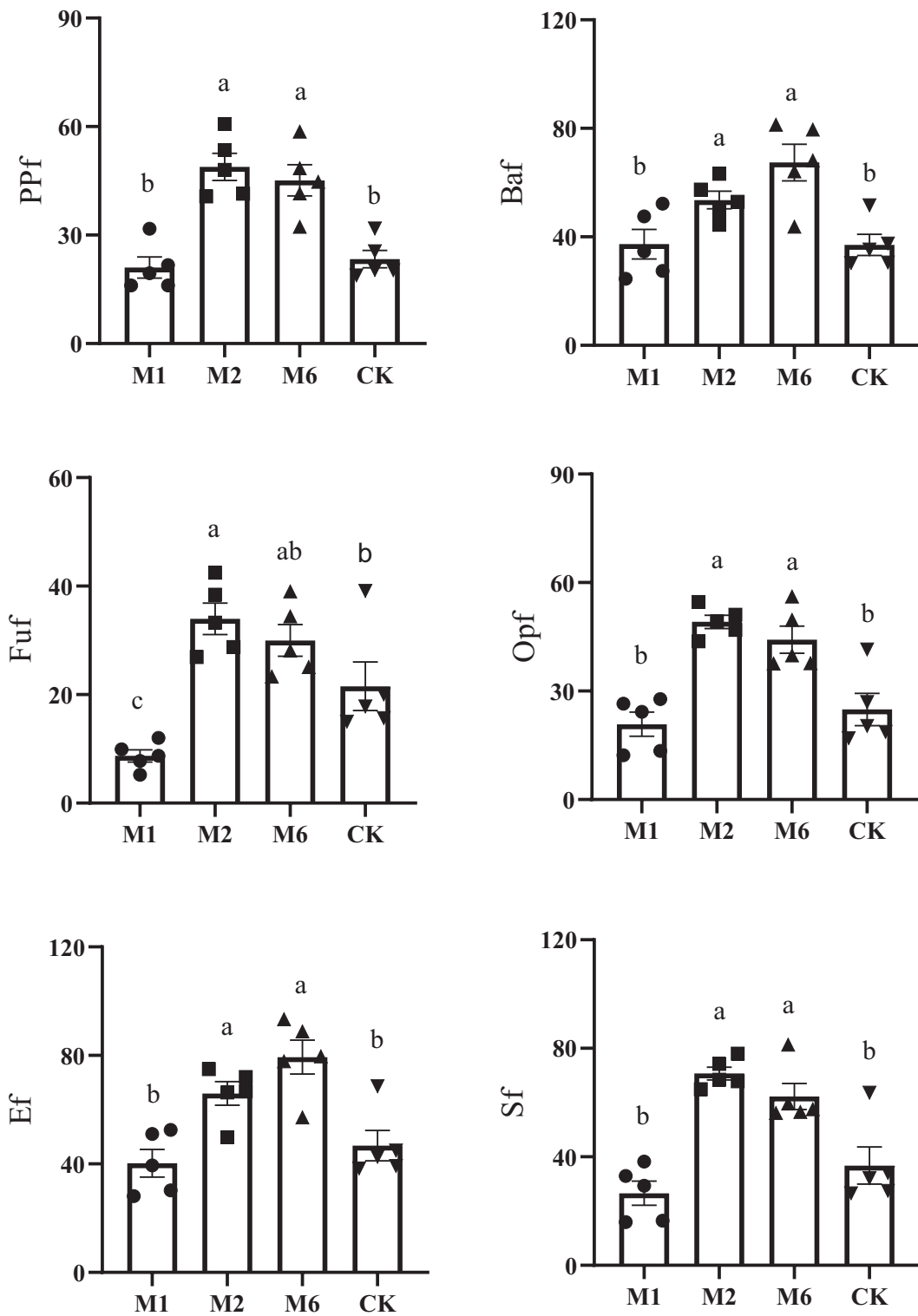
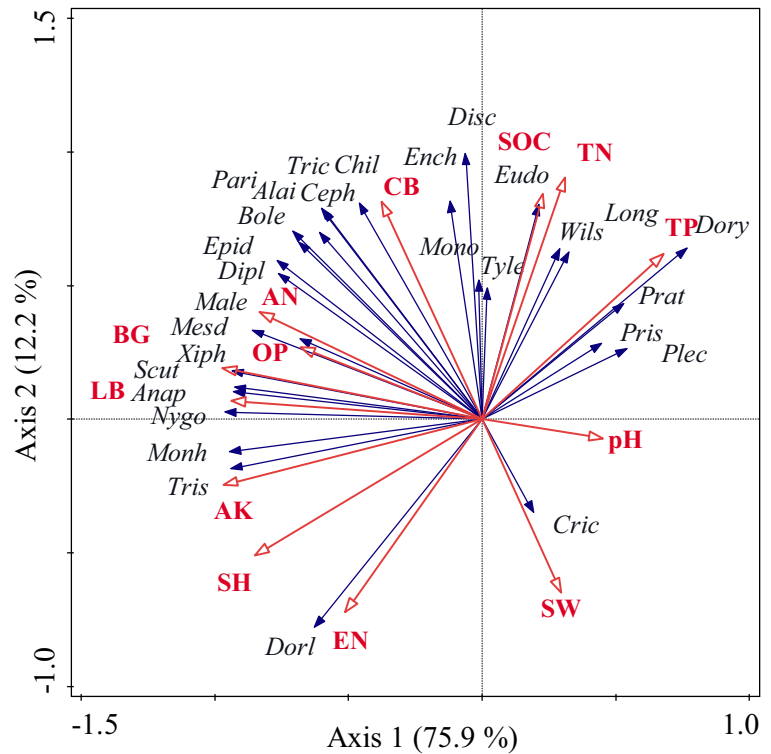


Fig. 4 Metabolic footprint of soil nematodes ($\mu\text{g}\cdot 100\text{ g}^{-1}$ dry soil) under different treatments. Ppf, Baf, Fuf and Opf each represent the metabolic footprint of plant parasitic nematodes, bacterivores, fungivores, and omnivores/predators, respectively. Ef and Sf indicate the enrichment footprint and structure footprint of total soil nematodes, respectively. M1: cutting

grass once a year; M2: cutting grass once every two years; M6: cutting grass once every six years; CK: no mowing. Values are means \pm standard errors ($n=5$). Different lowercase letters indicate significant differences among treatments at $P < 0.05$

Fig. 5 Results of RDA exhibiting the relationships between soil-vegetal variables and the abundances of different soil nematode genera with all treatments as a whole. Only the names of important nematode genera with a large contribution to first two axes are involved. SOC: soil organic carbon; TN: total soil nitrogen; TP: total soil phosphorus; AN: available N; BG: belowground biomass; LB: litter biomass; CB: canopy biomass; AK: available K; OP: Olsen P; SH: Shannon-Wiener index; EN: evenness index; SW: soil water. For the abbreviations of nematode genera, one can refer to Table 3



Significant decreases in belowground biomass in M1 and M2 were largely attributable to frequent harvesting of canopy biomass which may reduce the allocation of carbohydrates into live root biomass as reserve for their overwintering of perennial roots, shorten the root lifespan, or carry more available nutrients out of the soil (Wei et al. 2016; Jaramillo and Detling 1988). A slight increase in plant species diversity was observed in M6. This was supported by the findings of Antonsen and Olsson (2005) who showed that moderate mowing frequency may increase the plant species diversity and richness of pastures, especially those of non-grass species. Decreases in soil moisture with increasing mowing frequency were observed in the present study, which correspond rather well with the linear decreases in plant detritus accumulation, highlighting the role of litter cover in keeping soil moisture (Shao et al. 2012).

Effects of mowing on the abundance and biomass of soil nematodes

The results of the present study showed that the intermediate mowing disturbance (M2) and light mowing disturbance (M6) led to higher abundance (Fig. 1) and biomass (Table 2) of all trophic nematode groups. In the

same experiment site, Tan (2015) also reported the highest abundance of bacteria and fungi in the M2 treatment. All these results suggest that concerted responses occurred among soil biota in the steppe ecosystem by their responses to different mowing frequencies, which comply with the intermediate disturbance theory that is the intermediate grazing rate had highest species richness and canopy dominance (Yan et al. 2015). Similar responses have also been reported in several other analogous studies. For example, Hu et al. (2015) reported that an intermediately disturbed site had the highest abundance of fungivores in an alpine meadow grassland. Wall-Freckman and Huang (1998) found an identical response pattern of soil nematode communities to livestock grazing in a shortgrass steppe of North America.

In the present study, the highest abundance and biomass values of the total soil nematodes and/or different trophic groups in M2 correspond to the lowest values of both soil available P and soil pH in this treatment (Table 1). In contrast, the lowest measures of the abundance and biomass of soil nematodes occurring in M1 (heavy mowing disturbance) coincide with the lowest values of available K, soil moisture, litter and root biomass, and plant species diversity, whereas it was

inconsistent with the highest soil pH value. In addition, the highest abundance and biomass of bacterivores in M6 coincide with the highest value of soil available P. All the above observations point to the fact that the mowing-led differences in soil water, soil pH, and available nutrient content assume more substantial importance in explaining the relevant differences in the abundance and biomass of soil nematodes in this meadow steppe ecosystem. We assume that mowing first resulted in changes in the vegetal aspects, i.e. various plant biomass compartments such as canopy, root, and litter. In the present study, marginally positive and linear relations between plant biomass traits and certain soil parameters (soil moisture, available K, available P, soil acidity) were found across the mowing frequency gradients (Table 1). The differences in the abundance and biomass of soil nematodes were generally not linearly associated with those in the aforementioned edaphic traits, but instead were more consistent with differences in the canopy biomass and plant species diversity measures across the mowing frequency gradient (Tables 1 and 2; Fig. 1). It is possible that mowing-resultant shifts in plant species (functional or life-form) composition and diversity are likely a major mechanism underlying the changing patterns of soil nematode abundance and biomass in this ecosystem. We observed that rhizomatous herbs (*Leymus chinensis*, *Carex* spp.) had significantly increased in their dominance with increasing mowing frequency, whereas bunch grasses (*Stipa baicalensis*), broadleaved forbs (*Filifolium sibiricum*), and annuals decreased considerably in their abundances in our treated swards (Tan 2015). Yang et al. (2012) found that both plant species numbers and ecosystem stability increased in response to intermediate mowing disturbance in the Inner Mongolia typical steppe ecosystem. Similar results have also been reported by other authors (Baoyin et al. 2015). On the one hand, plant parasitic nematodes were shown to be rather host plant-specific, and differences in their abundances were thus highly related to plant species composition (van der Putten and van der Stoel 1998; De Deyn et al. 2004); on the other hand, a higher plant species or functional group richness may enhance the development of soil nematode communities via its effects on the rhizospheric bacterivores and fungivores (Li et al. 2020b).

It has been reported that excess plant detritus accumulating on the surface of soil, as occurring in the CK treatment of our study, would lower the soil surface

temperature and increase the humidity thereof (Shao et al. 2012), which is unfavorable to the survival soil nematodes. In contrast, heavy mowing could decrease soil moisture but increase soil pH value due to decreased litter accumulation and its decomposition into soils (Li et al. 2015), lowered canopy biomass and carbon allocation to the belowground (Shao et al. 2012; Fynn et al. 2004), and cause substantial impacts on the nutrient cycling in various grasslands. Our study suggested, in the pH range of 6.4 to 7.6, intermediately moist soil conditions are more favorable to the development of soil nematodes in terms of the species diversity and community structure in grassland ecosystems (Ruan et al. 2012). However, in more acidic soils, soil nematodes are more abundant in the soil with higher pH value of 6.3 (Pan et al. 2012). Soil available K has been shown to be closely related to soil microbes and hence the microbe-dependent soil nematodes, whereas available P has significant positive effects on the abundance of fungi (saprotrophic fungi and AMF in particular) (Tan 2015). It has been shown that the removal of aboveground biomass by mowing can decrease C deposits, reduce soil nutrient stocks belowground, and result in substrate limitation to soil microorganisms (Wan and Luo 2003).

Mowing has been one of the most important management practices in grassland ecosystems worldwide. Jungerius et al. (1995) found that frequent and/or intensive mowing drastically reduced the abundance and occurrence depth of belowground micro-arthropods. De Szalay and Resh (1997) reported that mowing decreased the density of invertebrates such as Oligochaete. Chen et al. (2014) found that mowing decreased the abundance of AOA in a temperate steppe of Inner Mongolia. Bacterivores and fungivores feed on bacteria and fungi, respectively, and their abundance and biomass are thus limited largely by the abundance of soil bacteria and fungi. Omnivores/predators occupy a higher position in the soil food web and feed on soil nematodes and/or soil microorganisms, so their abundance and biomass are also limited by the food abundance. All these results strongly corroborate the relevant findings of the present study.

Effect of mowing on the community composition and diversity of soil nematodes

In the present study, mowing frequency treatments resulted in substantial differences in both genus diversity (Table 4) and dominant genus composition (Table 3) of

each trophic group of soil nematodes, with increases in genus richness in both M6 and M2. This indicates that moderate mowing can promote biodiversity in meadow steppe. The relevant mechanisms are basically identical to those associated with the intermediate disturbance theory as discussed in the earlier section. Previous studies demonstrated that intermediate disturbances may lead to increases in nematode genus diversity to varying extents in different grassland ecosystems (Hu et al. 2015; Wang et al. 2018).

NMDS plots show that M2 and M6 were clearly separated from either M1 or CK in terms of genus composition (Fig. 2a), indicating that different mowing frequencies differed significantly in their impacts on the community composition of soil nematodes. These were very likely due to the differences in plant community traits and edaphic properties in response to different mowing frequencies. Of these, we argue that differences in soil pH value, plant species and/or functional group composition, and available nutrient contents assumed major importance, as these indices largely determine the presence or absence rather than the quantity and mass of nematode genera in a terrestrial ecosystem (Li et al. 2020b). As discussed previously, plant parasitic nematodes are mostly host-specific (De Deyn et al. 2004), in which, bacterivores are more microbial flora-dependent (Hooper et al. 2000; Steinauer et al. 2016) and fungivores are sensitive to soil acidity and available nutrients (Tan 2015), which would definitely regulate the community structure and composition of soil nematodes. In general, the higher plant diversity community would support a higher diversity of soil nematode community (Wasilewska 1995; Hu et al. 2015). In the functional group structure analysis, CK and M1 were clustered together and clearly separated from the combination of M2 and M6. The functional group assemblage of soil nematodes is more closely related to the ecological process of an entire soil food web, being substantially subject to soil physical and chemical properties (Ferris et al. 2001; Liang et al. 2009). Our data generally support this argument.

Ecological indices of soil nematodes can furnish a full understanding of the effects of disturbances on the soil food web and the associated ecological functions, nematode interactions in particular. The highest NCR value in M1 among all treatments in the present study (Table 4) suggests that bacteria-based decomposition was more predominant in the soil food web in M1, which was characterized by a faster relative rate of

mineral-N or C turnover in this treatment. This is consistent with previous findings showing that abandonment of mowing caused a reduction in N availability and drawdown in N transformation processes (Robson et al. 2007). This may reflect a strategy for a soil biotic system to self-regulate itself in order to balance the nutrient loss caused by excess export of plant materials due to mowing. The WI value was significantly higher in CK and M6 than in M1 and M2 (Table 4), suggesting that light mowing disturbance can increase the relative abundance of bacterivores and fungivores against plant parasitic nematodes, being conducive to the health of the soil subsystem.

Effect of mowing on metabolic footprints of soil nematodes

The metabolic footprints of soil nematodes are an important proxy characterizing the carbon or energy flow along a soil food web (Ferris 2010). The highest metabolic footprints of the different nematode trophic groups as well as the highest values of Ef and Sf occurred mostly in M2 and partially in M6, suggesting that moderate mowing can promote the overall metabolic activity and carbon flow in soil food web. Chen et al. (2014) noted that moderate mowing may cause rather differential impacts on soil microorganisms, which will correspondingly regulate the metabolic activity of their predators (bacterivores and fungivores) and the associated higher trophic guilds (omnivores/predators) constituting the soil food web. In this process, litter accumulation plays a rather important role in C and N cycling and soil acidity regime. For instance, Robson et al. (2007) showed that moderate mowing can increase the availability and transformation process of soil N, and Zak et al. (1994) reported that harvesting aboveground plant biomass may promote nitrogen cycling by limiting carbon input in the soil. In contrast, long-term accumulation of plant detritus on the ground, as occurring in our CK treatment, would lead to excessive nutrient stocks and consequently a drawdown of C and N cycling, in terms of both the metabolic strength of the soil trophic chain as well as the diversity of its cycling pathways.

Potential driving factors and relationships

Our RDA results showed that available nutrients, belowground biomass, litter biomass and soil pH were more commonly related to soil nematode community

composition via axis 1, whereas other edaphic and vegetal traits were more related to soil nematode community composition via axis 2 except Shannon-Wiener index and total soil phosphorus. The edaphic and vegetal traits are more genus-specific in their effects of this kind. Our relevant explanation is that the former group of variables is associated with the substrate or food providers determining the quantity of soil nematodes and the presence of different soil nematode genera. Similar relations indeed have been reported in a Tibetan Plateau meadow grassland ecosystem by Hu et al. (2015), which showed that the abundance of individual nematode genera were related to the canopy biomass of the total flora or individual life-form groups of plants. Wang et al. (2018) has reported that nematode community composition was significantly associated with soil pH in alpine meadow.

Different genera and trophic groups of soil nematodes always differ to varying degrees in their niches in a specific ecosystem or among different ecosystem types. Whereas certain genera are sensitive to changes in edaphic conditions, others may be more associated with changes in vegetal traits. However, edaphic variables (soil moisture, soil pH, nutrient contents) are more heterogeneous horizontally and vertically (Bo et al. 2014), whereas vegetal traits are rather heterogeneous both horizontally and vertically, especially in view of the diversity aspects of plant species, function, and life-form levels (Fan et al. 2016). As a result, the abundance or biomass of soil nematodes is related to soil physiochemical characteristics and plant biomass, whereas the richness and diversity of soil nematode taxa should be more dependent on the diversity regimes of plant communities.

Conclusions

Our findings demonstrated that mowing had substantial impacts on the abundance, biomass, community composition, and genus diversity of soil nematodes in the meadow steppe ecosystem of Inner Mongolia. The changing patterns in the above nematode indices across the mowing frequency abided by the intermediate disturbance theory rather rigorously. Our results suggest that differences in the abundance and community of the soil nematodes were largely related to soil available nitrogen, belowground biomass, litter biomass and soil pH, and partially associated with the composition of vegetation and other soil nutrients, as well as soil water.

The effects of edaphic and vegetal traits appeared to be trophic or genus-specific. Our study suggests that moderate mowing frequency indeed improve the biodiversity and carbon flue in the meadow steppe ecosystem, which is beneficial for exploring restoration practices in this grassland region. However, for a better understanding of relevant mechanisms, more specific studies remain to be carried out, especially those concerning the soil food web and interactions among plants, microbes, and soil animals within ecosystems in question.

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