Effects of grazing intensity on soil nematode community structure and function in different soil layers in a meadow steppe

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Abstract

Aims Grazing is a key driver of plant communities and soil functions in grassland ecosystems. Soil nematodes play a vital role in soil ecological functions. The aim of this study was to explore how grazing shapes soil nematode community in different soil layers.

Methods We investigated the composition, abundance, diversity, metabolic footprint, and food web metrics of soil nematodes over a gradient of grazing in the 0–10 cm and 10–20 cm soil layers in a meadow steppe. The relationships between nematode community structure and biotic and abiotic factors were analyzed by principal component analysis and structural equation model analysis.

Results Light grazing increased the abundance of total soil nematodes by 18.5%. Intensive grazing decreased the carbon used in production and metabolic footprints of plant parasites, fungivores, and total soil nematodes in 0–10 cm soils. There was no difference in the carbon used in production and metabolic footprints of soil nematodes among different grazing intensities in the 10–20 cm soil layer. Soil moisture, aboveground biomass, belowground biomass and Shannon diversity of grass contributed more to changes in soil nematode composition in both soil layers. In the 0–10 cm soil layer, grazing directly
and indirectly affected soil nematode diversity via soil moisture and aboveground biomass, while grazing directly affected soil nematode diversity in 10–20 cm soil layer.

**Conclusions** Our results indicate that increasing soil depth can weaken the effect of grazing intensities on soil nematode fauna. Grazing affected the soil nematode community structure via different paths in different soil layers.

**Keywords** Community structure · Grazing intensity · Metabolic footprints · Soil nematodes · Soil food web

**Abbreviations**

H′ Shannon–Wiener index  
PPI Maturity index of plant-parasitic nematodes  
MI Maturity index of free-living nematodes  
EI Enrichment index  
SI Structure index  
AGB Aboveground biomass  
BGB Belowground biomass  
TOC Soil organic carbon  
TP Total soil phosphorus  
SAN Soil available nitrogen  
SAP Soil available phosphorus  
SBD Soil bulk density  
NMDS Nonmetric multidimensional scaling  
PCA Principal component analysis  
SEM Structural equation model

**Introduction**

Grasslands are important ecosystems and occupy approximately one-fifth of the land surface in the world (Cao et al. 2019). They assume crucial importance in maintaining biodiversity and combating desertification (Li et al. 2020). Grazing is one of the most common and economical uses of grassland ecosystems. It is well known that herbivore grazing can influence the structure and composition of aboveground ecosystems and can induce potential consequences in belowground ecosystems (Bardgett et al. 1998), such as C and N allocation to roots (Hokka et al. 2004; Ilmarinen et al. 2005); additionally, faeces of herbivores can change the community structure and diversity of soil biota (Bardgett et al. 1998; Wardle et al. 2004). In general, herbivore grazing affects the soil fauna by decreasing or increasing the nutritional quality and quantity of plants or by nutrient return from animal wastes (Wang et al. 2006), but these nutrients have a heterogeneous spatial distribution (Chen et al. 2012). So far, we know little about the response of soil fauna to grazing in different soil layers.

Soil nematodes are important components of soil ecosystems and are widely used as bioindicators reflecting soil biodiversity and processes in underground ecosystems (Bongers and Bongers 1998). Soil nematodes are assigned to different trophic groups according to their feeding habits, such as plant parasites, bacterivores, fungivores, omnivores and predators (Yeates et al. 1993). They play critical roles in soil ecological processes such as organic matter decomposition and nutrient cycling (Yeates 2003), especially bacterivores and fungivores, which can affect soil ecological processes by regulating the structure and function of bacteria and fungi (Ingham et al. 1985). Plant parasites feeding on plant roots can affect the growth and productivity of plants, and omnivores and predators regulating soil fauna at lower trophic levels in the soil food web are sensitive to external disturbance.

Soil nematode indices can provide insight into the changes in community structure and functions of soil nematodes recovering from disturbance or comparisons among ecosystems (Korthals et al. 2001; Guan et al. 2018). These ecological indices of soil nematodes promote the application of soil nematodes as soil bioindicators. The maturity indices of free-living nematodes (MI) and plant parasites (PPI) are based on the life history traits of individual nematode taxa, and they can reflect changes in soil nematode community structure related to the disturbance of soil ecosystems (Bongers 1990). The enrichment index (EI) and structural index (SI) of the food web provide information about resource availability and the structure or complexity of the soil food web (Ferris et al. 2001). The metabolic footprints of nematodes provide different metrics of ecosystem functions by assessing C utilization in the soil food web (Ferris 2010). These ecological indices of soil nematodes have been widely used to estimate the soil conditions and structure and function of the soil food web under different ecosystems, such as forestry (Zhang et al. 2015), farmland (Griffiths et al. 2005), and grassland (Hu et al. 2017).
Previous studies have reported that grazing can induce effects on belowground ecosystems by changes in vegetation composition or soil properties (Andriuzzi and Wall 2017). For example, grazing can regulate the linkages between aboveground and belowground parts via direct and indirect shrub effects (shrubs protected grass communities from grazing when herbivores were present) on nematode abundance (Wang et al. 2018), and can increase the abundance of soil nematodes such as omnivores and predators in a humid grassland (Wang et al. 2006) and fungivores in an arid steppe (Wall-Freckman and Huang 1998). The effects of grazing intensity on community structure of soil nematodes are inconsistent. Hu et al. (2015) found that heavy grazing increased the species richness and abundance of total soil nematodes, but other studies have shown that soil nematodes are more abundant in ungrazed sites or have no response to grazing (Zolda 2006; Andriuzzi and Wall 2017). The contrasting results may be attributed to different grassland ecosystems, as soil nematode composition is known to be highly spatially variable (Rodrigues et al. 2010). More studies in grassland ecosystems are needed to quantify the grazing effect on the community structure of soil nematodes. Information on the response of soil nematode community to grazing intensity in semiarid grasslands can increase our understanding of linkages between aboveground and belowground ecosystems.

Soil nutrients affect soil nematode community structure (Pan et al. 2020). Therefore, for the heterogeneous spatial distribution of soil nutrients caused by grazing (Chen et al. 2012), soil nematodes may also have different spatial distribution patterns. In this study, we evaluated the effect of grazing intensity on soil nematode fauna in the 0–10 cm and 10–20 cm soil layers in a northeast China meadow steppe. We hypothesized that grazing intensity has different effects on the community structure and carbon utilization function of soil nematodes in the 0–10 cm and 10–20 cm soil layers and that grazing modifies the soil nematode community via different paths in the two soil layers. The specific objectives of the present study were to (1) determine the effects of grazing intensity on the community structure and metabolic footprint of soil nematodes; (2) evaluate the relationship between biotic and abiotic factors and soil nematode community composition in different soil layers; and (3) determine the paths by which grazing affects soil nematode fauna in different soil layers.

**Materials and methods**

Experimental site

The study was conducted at the Hulun Buir Grassland Ecosystem Research Station (HGERS) of the Chinese Academy of Agricultural Sciences (CAAS) (49°19′ N, 119°56′ E) in Hulun Buir, Inner Mongolia, China. The study site has a semiarid continental climate with a mean annual temperature of −3 °C and an annual precipitation range of 350 ~ 400 mm. The soil type is defined as kastanozems. The study site is a typical meadow steppe dominated by the natural plant species *Leymus chinensis*, *Stipa bailcalensis*, *Carex duriuscula*, *Galium verum*, *Bupleurum scorzonerifolium*, and *Filifolium sibiricum*.

Experimental design

The grazing experiment was established in 2009 and included six levels of cattle grazing intensity designed in a randomized complete block. All these blocks have been used as summer pastures, beginning in June and ending in September every year. The plots were not grazed from October to May of the following year. Details of the experimental design and management history have been described in a previous publication (Xun et al. 2018). Four of the six grazing intensities with 0, 2, 4 and 8 cattle per plot beginning in June, corresponding to 0.00, 0.23, 0.46 and 0.92 Animal Units (AU) ha⁻¹ (1 AU = 500 kg of adult cattle), were selected for the present study, and the grazing intensities were respectively designated G0 (no grazing), G1 (light grazing intensity), G2 (moderate grazing intensity) and G3 (intensive grazing). There were 3 replicate plots for each grazing intensity, and each plot was 5 ha in area. Soil samples were collected from 0–10 cm and 10–20 cm depths with a 10 cm diameter coring tube in each plot in August 2018. Checkboard sampling was used, the length and width of each plot were divided into 5 parts. A total of 25 samples were collected from each plot, and all soil samples were sieved and mixed well by hand. Soils
used to measure soil properties were air-dried, and soils used to determine soil nematode diversity were stored for less than 4 days in a refrigerator at 4 °C.

Nematode extraction and identification

Soil nematodes were extracted from 100 g of fresh soil for 48 h using the modified Baermann tray method (Barker 1985). Total nematodes in each sample were counted under an anatomical lens. One-quarter of the soil nematodes in each sample were identified to the genus level with an Olympus microscope (400× and 1000×). All soil nematodes were assigned to trophic groups (plant parasites, Pp; bacterivores, Ba; fungivores, F; and omnivores/predators, Op) (Yeates et al. 1993). The abundances of total nematodes and each taxonomic group were converted to the individuals per 100 g of dry soil. The nematode length (μm) and maximum body diameter were measured for metabolic function calculation with an ocular micrometre.

Calculation of community structure indices

For soil nematodes, the Shannon–Wiener index (H′) and maturity indices of plant-parasitic nematodes (PPI) and free-living nematodes (MI) were calculated to represent the soil nematode diversity and life-history characteristics (Shannon and Weaver 1949; Bongers 1990). The enrichment index (EI) and structure index (SI) were calculated to estimate the effect of grazing on the soil food web condition (Ferris et al. 2001). We also calculated the soil nematode metabolic footprint, including the footprints of plant parasites (Ppf), bacterivores (Baf), fungivores (Fuf), and omnivores/predators (Opf), and the enrichment footprint (ef) and the structure footprint (sf), based on nematode biomass (W) to estimate the contributions of soil nematodes to ecosystem functions of grassland. The nematode biomass (μg) was calculated as \[ W = \frac{(D^2 \times L)}{(1.6 \times 10^6)} \] (Ferris 2010). L and D were nematode body length (μm) and maximum body width (μm) of each nematode genus, respectively. The carbon used in production of soil nematodes was calculated as \[ C = 0.1 \left( \frac{W}{m} \right) + 0.273 \left( W^{0.75} \right) \], where W, m, and N represents the fresh weight (μg), c-p value, and abundance of t taxa, respectively (Ferris 2010). The carbon used in production of plant parasites, bacterivores, fungivores, omnivores/predators, and total soil nematodes are presented as PPC, Bac, Fuc, Op, and Toc, respectively. The nematode metabolic footprint was calculated as \[ F = \sum (N_i (0.1 (W/m_i) + 0.273 (W_i^{0.75}))) \]. The functional footprint is the total area of the structure and enrichment footprints as: (SI-0.5 sf/k, EI); (SI + 0.5 sf/k, EI); (SI, EI-0.5 ef/k); (SI, EI + 0.5 ef/k) (Ferris 2010). The adjusted k value is 4. The ef and sf are the nematode metabolic footprints of those nematodes which respond most rapidly to resource enrichment and those nematodes at higher trophic levels in soil food web, respectively. The plant community aboveground biomass (AGB), belowground biomass (BGB), and Margarlef and Shannon diversity indices were calculated to test whether grazing affects soil nematode community by affecting grass community.

Soil properties

Details of soil physical and chemical property measurements were provided by Yan et al. (2016) and are briefly described here. Soil moisture was measured by drying soil for 72 h at 105 °C; the dichromate oxidation method was used to determine soil organic carbon (TOC); the molybdenum antimony resistance colorimetric method was used to determine total soil phosphorus (TP); the alkali diffusion method was applied to determine the soil available nitrogen (SAN); sodium bicarbonate extraction was used to determine the soil available phosphorus (SAP); the electrode method was used to measure soil pH; and the ring knife method was used to measure soil bulk density (SBD).

Data analysis

The effects of grazing intensity on the abundance, biomass, ecological index, and metabolic footprint of soil nematodes were tested by Tukey’s test of multiple comparisons with one-way ANOVA (P < 0.05). Non-metric multidimensional scaling (NMDS) based on Bray Curtis distance was applied to analyse composition changes at the genus level. Principal component analysis (PCA) was conducted to assess the relationships between the community structure of soil nematodes and environmental factors. In the PCA, soil nematode abundance at the genus level was the response variable, and biotic (AGB and BGB) and abiotic factors (soil physical and chemical properties) were explanatory variables. A structural equation...
model (SEM) analysis was performed to explore the direct effect of grazing on soil nematode diversity and the indirect effects via changes in AGB, BGB, and soil physical and chemical properties. In the SEM analysis, the number of cattle was standardized and used as different grazing levels to analyze the influence path of grazing levels on soil nematode diversity in different soil depths. Nematode diversity was presented by the Shannon–Wiener index. The physical and chemical properties of the soil were assembled into many combinations for SEM, and only the model deemed most reasonable was reported. The maximum likelihood estimation method was used to parameterize the model in Amos version 17.0.2 (SPSS Inc.). The chi-square test, its associated p value, and the comparative fit index (CFI) were used to assess the model. PCA was performed in CANOCO version 5.0 software, and all other statistical tests were conducted using the SPSS version 16.0 software package (SPSS, Chicago, IL, USA).

### Results

**Effect of grazing intensity on abundance of soil nematodes**

Grazing affected the abundance of soil nematodes (Table 1). In the 0–10 cm soil layer, both G2 and G3 decreased the abundance of plant parasites compared to G0. The abundance of bacterivores and omnivores/predators was not affected by grazing compared to G0, but G3 decreased the abundance of bacterivores, and both G3 and G2 decreased the abundance of omnivores/predators compared to G1. Both G2 and G3 showed trends of decreased abundance of fungivores, but no difference was observed compared to G0. G3 (1702 ± 290 individuals per 100 g of dry soil) significantly decreased the total abundance of soil nematodes compared to G0 (2821 ± 500 individuals per 100 g of dry soil) and G1 (3344 ± 376 individuals per 100 g of dry soil). G1 showed a tendency to increase nematode abundance, but the difference was not significant compared to G0. In the 10–20 cm soil layer, G3 decreased the abundances of plant parasites, fungivores, omnivores/predators and total soil nematodes compared to G0 (Table 1). G2 decreased the abundance of fungivores compared to G0 and G1. Both G1 and G2 also decreased the abundance of omnivores/predators compared to G0. G3 decreased the abundance of bacterivores compared to G1. There was no difference in the abundance of plant parasites, bacterivores, or total soil nematodes among G0, G1 and G2. In 0–10 cm and 10–20 cm soil layers, plant parasites and bacterivores were dominant trophic groups over the range of grazing intensity, and their relative abundances were higher

| Grazing intensity | PP     | Ba     | Fu     | Op     | To     |
|-------------------|--------|--------|--------|--------|--------|
| **0–10 cm**       |        |        |        |        |        |
| G0                | 996 ± 114 (35.3%) | 786 ± 119 (27.9%) | 689 ± 174 (24.4%) | 350 ± 95 (12.4%) | 2821 ± 500 (ab) |
| G1                | 1118 ± 79 (33.4%) | 1023 ± 128 (30.6%) | 685 ± 98 (20.5%) | 518 ± 103 (15.5%) | 3344 ± 376 (a) |
| G2                | 574 ± 106 (26.0%) | 851 ± 133 (38.6%) | 465 ± 89 (21.1%) | 314 ± 27 (14.2%) | 2204 ± 306 (bc) |
| G3                | 467 ± 82 (27.4%) | 614 ± 115 (36.1%) | 443 ± 96 (26.0%) | 178 ± 17 (10.5%) | 1702 ± 290 (c) |
| **10–20 cm**      |        |        |        |        |        |
| G0                | 686 ± 69 (42.0%) | 401 ± 41 (24.5%) | 352 ± 52 (21.5%) | 196 ± 27 (12.0%) | 1635 ± 169 (a) |
| G1                | 431 ± 138 (30.9%) | 548 ± 75 (39.2%) | 351 ± 51 (25.1%) | 67 ± 20 (4.8%) | 1397 ± 271 (ab) |
| G2                | 441 ± 97 (39.1%) | 447 ± 153 (39.6%) | 191 ± 69 (16.9%) | 51 ± 15 (4.5%) | 1129 ± 327 (ab) |
| G3                | 247 ± 65 (31.9%) | 277 ± 58 (35.8%) | 185 ± 32 (23.9%) | 65 ± 10 (8.4%) | 774 ± 146 (b) |

PP, Ba, Fu, Op, and To represent plant parasites, bacterivores, fungivores, omnivores/predators, and total soil nematodes, respectively. Grazing intensities G0, G1, G2, and G3 indicate 0.00, 0.23, 0.46, and 0.92 AU ha⁻¹, respectively. The numbers in parentheses are the relative abundance of each nematode trophic group. Means with the same column, same depth and followed by the same lower case letter are not significantly different (p > 0.05)
than those of fungivores and omnivores/predators (Table 1). In both soil layers, grazing decreased the relative abundance of plant parasites, but increased the relative abundance of bacterivores.

Effect of grazing intensity on soil nematode community diversity

Grazing affected the community composition of soil nematodes. In total, 53 and 39 taxa were observed in the 0–10 cm and 10–20 cm soil layers, respectively (Table S1). Malenchus was dominant genus in plant parasites, and Acrobeles and Cervidellus were dominant genera under different grazing intensities. Grazing decreased the relative abundance of Filenchus but increased the relative abundance of Acrobeles (Table S1). NMDS analysis showed that G3 was clearly separated from G0, G1 and G2 in both 0–10 cm and 10–20 cm soil layers (Fig. 1). In 0–10 cm soil layers, soil nematode community structure developed along the direction from G1 to G0, G2 and G3, while in 10–20 cm soil layer, there was no clear development direction of soil nematode community structure among G0, G1 and G2. The ecological indices of soil nematodes changed over a range of grazing intensity (Table 2). In the 0–10 cm soil layer, both G2 and G3 decreased the H’ value, and the H’ value showed a decreasing trend with an increase in grazing intensity. G2 decreased the PPI value compared to G0, but no difference was observed between G3 and G0. The MI value was lowest in G3, and it also showed a decreasing trend with an increase in grazing intensity. In the 10–20 cm soil layer, all grazing treatments decreased the values of H’ and MI compared to G0. G3 increased the PPI value, while there was no difference in PPI values among G0, G1, and G2 (Table 2).

Effect of grazing intensity on soil nematode production carbon

In the 0–10 cm soil layer, G3 decreased the PPc, Fuc and Toc compared to G0 (Table 3). G2 decreased the PPc and Fuc compared to G0. Compared with G0, G1 increased the Opc but had no effect on the carbon used in production of other nematode trophic groups or total soil nematodes. The PPc, Opc and Toc were higher in G1 than in G3. In the 10–20 cm soil layer, G3 decreased the Bac, Fuc, Opc and Toc compared to G0 (Table 3), and G2 decreased the Fuc and Opc. There was no difference

| Table 2 Nematode ecological indices in the 0–10 cm and 10–20 cm soil layers across a grazing intensity gradient. Values are means ± standard errors (n = 3) |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Ecological index | 0–10 cm          | 10-20 cm         |                  |                  |                  |                  |                  |
|                  | G0              | G1              | G2              | G3              | G0              | G1              | G2              | G3              |
| H’               | 3.29 ± 0.06a    | 3.31 ± 0.12a    | 3.12 ± 0.02b    | 2.95 ± 0.04c    | 3.06 ± 0.04a    | 2.69 ± 0.07b    | 2.57 ± 0.03c    | 2.74 ± 0.11b    |
| PPI              | 2.56 ± 0.06ab   | 2.43 ± 0.02bc   | 2.29 ± 0.01c    | 2.65 ± 0.10a    | 2.38 ± 0.02b    | 2.47 ± 0.03b    | 2.41 ± 0.11b    | 2.79 ± 0.04a    |
| MI               | 2.56 ± 0.04ab   | 2.69 ± 0.05a    | 2.47 ± 0.10bc   | 2.38 ± 0.06c    | 2.52 ± 0.02a    | 2.15 ± 0.04c    | 2.18 ± 0.01bc   | 2.26 ± 0.05b    |

H’, PPI, and MI represent Shannon–Wiener index, maturity index of plant-parasitic nematodes, and maturity index of free-living nematodes, respectively. Grazing intensities G0, G1, G2, and G3 indicate 0.00, 0.23, 0.46, and 0.92 AU ha⁻¹ respectively. Means in the same row, same depth and followed by the same lower case letter are not significantly different (p > 0.05)
in the carbon used in production of soil nematodes between G1 and G0 except G1, which decreased the Opc. No difference was observed in the carbon used in production of soil nematodes among G1, G2, and G3 in the 10–20 cm soil layer.

Effect of grazing intensity on soil nematode metabolic footprints

In the 0–10 cm soil layer, G3 decreased the metabolic footprints of plant parasites, fungivores and total soil nematodes compared to G0 (Table 4). G2 decreased the metabolic footprints of plant parasites and fungivores compared to G0. There was a trend of larger soil nematode metabolic footprints in G1 compared to G0, but the differences were not significant for any of the trophic groups. The metabolic footprints of plant parasites, omnivores/predators and total soil nematodes were higher in G1 than in G3. In the 10–20 cm soil layer, G3 decreased the metabolic footprints of bacterivores, fungivores, omnivores/predators and total soil nematodes relative to G0 (Table 4), and

### Table 3  Carbon used in production of soil nematodes (μg 100 g−1 dry soil) in the 0–10 cm and 10–20 cm soil layers across a grazing intensity gradient

| Grazing intensity | PPc  | Bac  | Fuc  | Opc  | Toc  |
|-------------------|------|------|------|------|------|
| 0–10 cm           |      |      |      |      |      |
| G0                | 5.4 ± 0.8a | 11.5 ± 0.4a | 3.5 ± 0.9a | 2.6 ± 0.7b | 23.0 ± 2.8a |
| G1                | 5.0 ± 0.4a | 13.1 ± 2.2a | 3.0 ± 0.3ab | 4.5 ± 0.9a | 25.6 ± 3.7a |
| G2                | 2.3 ± 0.4b | 10.9 ± 2.0a | 1.9 ± 0.4b | 2.8 ± 0.4b | 18.0 ± 2.4ab |
| G3                | 2.5 ± 0.5b | 8.8 ± 1.8a | 2.1 ± 0.4bc | 1.7 ± 0.2b | 15.1 ± 2.7b |
| 10–20 cm          |      |      |      |      |      |
| G0                | 2.9 ± 0.3a | 7.8 ± 0.8a | 1.8 ± 0.3a | 2.0 ± 0.2a | 14.5 ± 1.3a |
| G1                | 2.1 ± 0.7a | 6.7 ± 1.1ab | 1.4 ± 0.2ab | 0.8 ± 0.2b | 11.0 ± 2.1ab |
| G2                | 1.7 ± 0.4a | 6.5 ± 2.1ab | 1.0 ± 0.4b | 0.5 ± 0.2b | 9.8 ± 2.8ab |
| G3                | 1.7 ± 0.5a | 4.0 ± 0.9b | 0.9 ± 0.2b | 0.8 ± 0.1b | 7.4 ± 1.4b |

Values are means ± standard errors (n = 3)

PPc, Bac, Fuc, Opc, and Toc represent the carbon used in production of plant parasites, bacterivores, fungivores, omnivores/predators, and total soil nematodes, respectively. Grazing intensities G0, G1, G2, and G3 indicate 0.00, 0.23, 0.46, and 0.92 AU ha−1, respectively. Means in the same column, the same depth and followed by the same lower case letter are not significantly different (p > 0.05)

### Table 4  Metabolic footprints of soil nematodes (μg 100 g−1 dry soil) in the 0–10 cm and 10–20 cm soil layers across a grazing intensity gradient. Values are means ± standard errors (n = 3)

| Grazing intensity | PPf  | Baf  | Fuf  | Opf  | Tof  |
|-------------------|------|------|------|------|------|
| 0–10 cm           |      |      |      |      |      |
| G0                | 70.5 ± 11.7a | 92.9 ± 5.2a | 37.9 ± 9.9a | 44.8 ± 12.4b | 246.2 ± 38.6ab |
| G1                | 62.9 ± 5.8a | 108.3 ± 17.7a | 35.3 ± 4.3ab | 72.4 ± 15.1a | 278.9 ± 40.8a |
| G2                | 29.5 ± 5.3b | 88.5 ± 15.7a | 20.9 ± 4.0b | 45.6 ± 5.7ab | 184.5 ± 20.2bc |
| G3                | 33.5 ± 6.2b | 71.6 ± 14.5a | 22.8 ± 4.6b | 26.4 ± 3.2b | 154.3 ± 26.1c |
| 10–20 cm          |      |      |      |      |      |
| G0                | 37.1 ± 3.7a | 59.6 ± 6.3a | 19.1 ± 2.6a | 30.6 ± 3.5a | 146.3 ± 13.4a |
| G1                | 25.9 ± 8.2a | 55.9 ± 8.8ab | 15.6 ± 2.5ab | 11.2 ± 2.6b | 108.7 ± 20.9ab |
| G2                | 22.1 ± 5.4a | 52.3 ± 16.9ab | 10.6 ± 3.7b | 8.1 ± 2.8b | 93.2 ± 25.7b |
| G3                | 21.4 ± 5.9a | 31.0 ± 6.9b | 10.0 ± 1.9b | 11.6 ± 1.6b | 74.1 ± 13.4b |

PPf, Baf, Fuf, Opf, and Tof represent metabolic footprints of plant parasites, bacterivores, fungivores, omnivores/predators, and total soil nematodes, respectively. Grazing intensities G0, G1, G2, and G3 indicate 0.00, 0.23, 0.46, and 0.92 AU ha−1, respectively. Means in the same column, the same depth and followed by the same lower case letter are not significantly different (p > 0.05)
G2 decreased the metabolic footprints of fungivores, omnivores/predators and total soil nematodes relative to G0. There were no differences in the metabolic footprints of soil nematodes among G1, G2, and G3.

The total area of footprints plotted on structure and enrichment coordinates indicates the functional metabolic footprints of soil nematodes. In the 0–10 cm soil layer, the metabolic footprints of soil nematodes were greater in G1 than in G0, and G3 clearly decreased the functional metabolic footprints of soil nematodes (Fig. 2). G0, G1, and G2 were located in the structured quadrant in the 0–10 cm soil layer, and G3 was partly in the degraded quadrant. The structured quadrant indicates a structured soil food web and undisturbed soil ecosystem. In the 10–20 cm soil layer, all grazing intensities were correspondingly smaller than those of the 0–10 cm soil layer, and all grazing treatments decreased the functional metabolic footprints of soil nematodes compared to G0. In the 10–20 cm soil layer, all grazing treatments moved to the degraded quadrant, but G0 remained in the structured quadrant.

Relationship between soil environmental factors and soil nematode community structure

Grazing affected the composition of soil nematode genera based on principal component analysis (PCA) (Fig. 3a and b). The first two components of PCA explained, respectively, 55.1% and 21.5% of the variance in nematode genus data in the 0–10 cm layer and 50.5% and 24.6% of the variance in nematode genus data in the 10–20 cm layer. At 0–10 cm depth, G2 and G3 were clearly separated from G0 and G1 on PCA axis 1 (Fig. 3a). G3 was characterized by *Aphelenchus*, *Acrobeles* and *Cricone-mella*. G2 was characterized by *Monhystera* and *Wilsonema*. G0 was characterized by *Discolaimus*, *Protorhabditis* and *Heterodera*. G1 was characterized by *Diploaimeloides*, *Tylenceholaimellus* and *Mesodorylaimus*. The first axis was mainly driven by AGB, BGB, soil moisture, Shannon diversity of grass and SBD, and the main driving factors of axis 2 were soil moisture, BGB and Margarlef of grass. At 10–20 cm, G3 was clearly separated from G0, G1, and G2, and G1 and G2 were also separated from G0 on axis 2 (Fig. 3b). G3 was characterized by *Acrobeles*, *Protorhabditis*, *Tylenceholaimus*, *Eudorylaimus* and *Tylenceholaimellus*. G2 was characterized by *Trischistoma* and *Criconemella*. G1 was characterized by *Cervidellus*. G0 was characterized by *Paratrichodorus*, *Trichodorus*, *Xiphinema*, *Longidorus*, *Wilsonema*, *Diphtherophora* and *Dorylaimellus*. PCA axis 1 was mainly driven by AGB, pH and soil moisture, and PCA axis 2 was...
mainly driven by soil moisture, BGB, SBD and Shannon diversity of grass.

The SEM model showed that grazing significantly and negatively affected grass AGB and soil moisture in the 0–10 cm soil layer ($p < 0.05$) (Fig. 4a). Grass AGB had significant effects on soil moisture and $H'$ of soil nematodes. Grazing and soil moisture positively affected $H'$ of soil nematodes. In the 10–20 cm soil layer, grazing significantly and negatively affected the grass AGB and BGB and $H'$ of soil nematodes (Fig. 4b). However, neither AGB nor BGB had significant effect on $H'$ of soil nematodes either directly or indirectly.
Discussion

Effect of grazing on abundance of soil nematodes

In our study, we found intensive grazing decreased the abundance of total soil nematodes, plant parasites, bacterivores and omnivores/predators. This is consistent with the previous finding that grazing decreased the abundance of total soil nematodes, bacterivores, plant parasites and omnivores/predators by 32, 42, 46 and 93%, respectively (Wang et al. 2020). This is likely due to intensive grazing reducing plant cover or growth and disturbing the soil ecological environment, thereby reducing the abundance of soil nematodes. This is especially true for plant parasites that feed on plant roots and omnivores/predators that are sensitive to environmental disturbance. Grazing decreased the relative abundance of plant parasites but increased the relative abundance of bacterivores in our study. Similar results were observed in subtropical grassland (Wang et al. 2006). This is likely because grazing has a greater negative impact on plant parasites; plant parasites are more dependent on plants for food (Van der Putten and Van der Stoel 1998). Faeces of grazing animals deposited on the soil provides resource for the soil microorganisms, which in turn also provide food for the bacterivores. This partially compensates for any negative impact of grazing on bacterivores but not on other nematode trophic groups, which could explain the increase the relative abundance of bacterivores in grazing grassland.

Grazing affected the abundance of soil nematodes, and the effect of grazing intensity on soil nematode abundance was weakened in the 10–20 cm soil layer compared to the 0–10 cm soil layer (Table 1). This is likely because the effect of grazing on the soil environment is greater at 0–10 cm near the surface soil layer. Another reason may be that soil nematodes in the 0–10 cm soil layer are normally more abundant than those in the 10–20 cm soil layer, so the changes in the abundance of soil nematodes in the 0–10 cm layer caused by external factors were more obvious. Previous studies have found that biological soil crusts had a stronger impact on soil nematodes in the topsoil layers than in deeper soil layers (Liu et al. 2013; Guan et al. 2018). Our results demonstrated that the effect of grazing on the soil nematode community structure was lower in the deeper soil layer.

Effect of grazing on community diversity of soil nematodes

Ecological indices of soil nematodes consolidate the characteristics, activities and functions of a large number of soil nematodes and nematode genera into a single metric and can provide a deeper understanding of the grazing effect on the soil nematode community and ecological function (Yeates 2003). In the 0–10 cm soil layer, both G2 and G3 decreased the H’ value of soil nematodes, and the H’ value showed a decreasing trend with an increase in grazing intensity from G1 to G3. This indicates that serious disturbance by intensive grazing decreases the diversity of soil nematodes. This is inconsistent with previous findings of no significant difference in the Shannon diversity of soil nematodes in grazing grassland (Zolda 2006; Schon et al. 2010; Hu et al. 2015). The different grassland environments, grazing intensities, and grazing animals could explain the different findings. We conducted our study in Hulun Buir meadow steppe with four grazing intensities of 0, 0.4, 0.8 and 1.6 mature cattle ha$^{-1}$, and Hu et al. (2015) conducted their study in Tibetan Plateau meadows with three grazing intensities, 1, 1.1, and 1.5 yaks ha$^{-1}$; all of their grazing intensities were higher than our grazing intensities except for most intensive grazing.

The MI value decreased with an increase in grazing intensity, suggesting that grazing disturbs soil ecosystems based on communities of free-living soil nematodes. Other studies have found that intensive grazing resulted in the lower MI value (Schon et al. 2010; Hu et al. 2015). Zolda (2006) also reported that donkey grazing decreased MI value. This is due to a decrease in the proportion of omnivores/predators with higher c-p value accompanied by an increase in the proportion of bacterivores with lower c-p value in grazing grassland. However, our results are inconsistent with the findings of Wang et al. (2006) that higher MI occurred in grazed plots. The different results are likely due to the voided faeces effect of herbivores on soil nematodes. Wang et al. (2006) collected soil samples at least 1 m away from any visible animal droppings, while in our random sampling, we avoided sampling within a faeces deposit but allowed sampling within a one-metre radius. The input of animal faeces can increase the abundance of bacterivores and fungivores with low c-p values (Mills et al. 2011),
which leads to a low MI value. Forge et al. (2005) reported that the addition of dairy manure slurry to sward also resulted in a decrease in the MI.

Effect of grazing intensity on carbon utilization of soil nematodes

In both the 0–10 cm and 10–20 cm soil layers, G3 and G2 showed trends of decreasing carbon used in production of soil nematodes compared to G0 (Table 3). This is likely due to intensive grazing reducing the BGB of grass and the corresponding organic matter input (Zhang et al. 2020). Plant roots provide an important carbon source for soil microbes in grassland ecosystems (Coleman et al. 1983). However, intensive grazing reduced root biomass and consequently decreased the carbon aggregation surrounding the root. Grass growth and AGB is reduced in heavily grazed plots, thus reducing the carbon returned to the soil from plant litter, although approximately half of the carbon in the AGB of grass is returned to the soil as faeces. The reduction in the carbon source used by microorganisms will naturally affect the carbon utilization located at high-level positions in the soil food web. This may explain the lower carbon used in production of soil nematodes in G2 and G3. There was a gradient effect of grazing on the carbon used in production of soil nematodes in the 0–10 cm soil layer, but the effect was weakened in the 10–20 cm soil layer, demonstrating that the grazing influence on the activity of soil nematodes is mainly confined to the uppermost soil layer. This is likely because organic matter input via faeces and soil disturbance by grazing animal foot traffic have stronger influences on the topsoil layer than on the deeper soil layer.

The metabolic footprints of soil nematodes represent the carbon entering the soil food web via nematode channels (Ferris 2010). In both the 0–10 cm and 10–20 cm soil layers, G3 and G2 showed trends of decreasing the metabolic footprints of soil nematodes (Table 4). This is in line with the above results that intensive grazing reduced the abundance and carbon used in production of nematodes (Tables 1 and 3). The metabolic footprints are the combination of carbon used for production and respiration of soil nematodes. Yan et al. (2017) found that CO₂ flux significantly decreased with increasing grazing intensity. Our results are in agreement and indicate that intensive grazing reduces the metabolic activity of soil nematodes. The changing trend of the soil nematode metabolic footprint is the same as that of the soil CO₂ flux under different grazing intensities. A previous study has shown that nematode activity contributes CO₂ flux (Ferris et al. 1995).

The functional metabolic footprints of soil nematodes are the total area of the footprints plotted on structure and enrichment coordinates. In the 0–10 cm soil layer, G3 clearly decreased the functional metabolic footprints of soil nematodes, while there was a small increase from G0 to G1 (Fig. 2). Wang et al. (2018) reported an increasing trend of structure and enrichment footprints in grazed meadows with shrub vegetation. This may be attributed to light grazing increasing root exudation, which then promotes the activity of soil biota. However, intensive grazing can seriously decrease root biomass and soil ecological processes. Previous studies have found that clipping wheatgrass can increase root exudation (Bokhari and Singh 1974), and defoliation of white clover and Italian ryegrass can increase root efflux of nitrate and ammonium nitrogen (McDuff and Jackson 1992). Our results suggest that light grazing can promote the contribution of soil nematodes to soil carbon cycling, but intensive grazing decreases the function of soil nematodes in the soil food web in the 0–10 cm soil layer. In the 10–20 cm soil layer, the functional metabolic footprints of soil nematodes of all grazing intensities were correspondingly lower than those of the 0–10 cm soil layer (Fig. 2), suggesting that the contribution of soil nematodes to carbon cycling is larger in topsoil than in the deeper soil layer and that grazing will not alter the function of soil nematodes in the deeper soil layer.

Potential driving factors of grazing on soil nematode community structure

Intensive grazing changed the composition of soil nematode genera based on NMDS and PCA analysis (Figs. 1 and 3). In the 0–10 cm soil layer, G3 was distinguished from other grazing intensities by the increased abundance of fungivore *Aphelenchus* and the plant parasite *Criconemella*. This is consistent with previous studies showing that grazing can increase the abundance of fungivores in shortgrass steppe and the Tibetan Plateau (Wall-Frekman and Huang 1998; Hu et al. 2015). In contrast, G2 was distinguished by the bacterivores *Monhystera* and *Wilsonema*. Previous studies also showed that grazing stimulated bacterivores (Sørensen et al. 2009; Wang et al. 2018). This is
likely due to manure amendment from animals under moderate grazing increasing the growth and activity of bacteria (Xun et al. 2018), as manure is bacterivorous food. In the 10–20 cm soil layer, G3 was characterized by different nematode genera from those in the 0–10 cm soil layer, and the main driving factors of PCA axis 1 were AGB, soil pH, and soil moisture, which were also different from those in the 0–10 cm soil layer (Fig. 3b). Both AGB and soil moisture were also among the main driving factors of the community structure of soil nematodes in the 0–10 cm layer, suggesting that these two environmental factors are stable drivers of soil nematode composition under grazing in both soil layers. The close relationship between soil pH and soil nematodes has been proven by previous studies (Fiscus and Neher 2002; Li et al. 2010; Pan et al. 2016). Our results show that grazing changes the community composition of soil nematodes, and the selective pressures of grazing as the driving factors on soil nematode community structure are different in different soil layers.

Our study found that grazing affected soil nematode diversity by different paths in the 0–10 cm and 10–20 cm soil layers (Fig. 4a and b). In the 0–10 cm soil layer, grazing had significant direct effect on the Shannon diversity of soil nematodes, and it also indirectly affected the Shannon diversity of soil nematodes by modifying grass AGB and soil moisture. Our results were in line with previous findings that soil moisture can influence soil nematode community structure (Landesman et al. 2011). SEM analysis showed that grazing had positive effect on soil nematode diversity in 0–10 cm soil layer, which is not inconsistent with the low soil nematode diversity of intensive grazing above, because grazing also regulates the Shannon diversity of soil nematodes via negative effects on soil moisture and grass AGB. However, soil moisture and grass AGB both had a positive effect on soil nematode diversity. Our result was supported by previous study that higher species richness of soil nematodes was found on a seriously over-grazed site (Hu et al. 2015). This is probably because grazing increased the diversity of available food resources for soil nematodes, such as animal waste can increase the abundance of soil microorganisms upon which bacterivores and fungivores feed. In the 10–20 cm soil layer, grazing negatively and directly affected soil nematode diversity (Fig. 4b). This may be due to differences in the root distribution and distribution of cattle faeces in different soil layers. Several studies have shown that root exudation is significantly affected by aboveground defoliation and herbivory (McDuff and Jackson 1992; Shand et al. 1994). Root exudation affects the community structure of soil microorganisms, which provides food resources for soil microfauna. Soil microorganisms are the food of bacterivores, fungivores and omnivores, so a shift in their abundance and diversity will also influence diversity of soil nematodes. Grass roots are mainly distributed in topsoil (Wang and Zhang 2010), and cattle faeces is deposited on the soil surface and is mixed with topsoil by rain, animal foot traffic, and earthworms; therefore, grazing could modify soil nematode diversity via grass AGB and soil physical and chemical properties in the 0–10 cm soil layer. However, there are fewer grass roots and less mixing of cattle faeces in the 10–20 cm soil layer, so grazing has a more prominent effect on soil nematodes than other factors. Our results suggest that grazing affects the soil nematode community, but the paths by which the effects occur are different in different soil layers. In grasslands, grazing may affect the structure and function of soil nematodes in belowground ecosystems via other biotic or abiotic factors (Wang et al. 2018), such as vegetation type and soil type, which needs further research.

Conclusions

Our results showed that grazing affects the community structure and activity of soil nematodes in both the 0–10 cm and 10–20 cm soil layers. However, the effect of grazing gradients was weaker in the 10–20 cm soil layer than in the 0–10 cm soil layer. Light grazing showed trends of increasing the abundance, carbon used in production and metabolic footprints of soil nematodes at 0–10 cm. Intensive grazing changed the composition of soil nematodes and degraded the food web structure of soil nematodes in both soil layers. Soil physical and chemical properties, AGB and BGB played important roles in determining soil nematode community composition. In the 0–10 cm soil layer, grazing directly and indirectly affected the soil nematode diversity via AGB and soil moisture; however, grazing only directly affected the soil nematode diversity in the 10–20 cm soil layer. Our findings indicate that grazing affects soil nematode community structure and function via different paths in different soil layers. Our study also provides evidence for increasing the understanding of the linkage between aboveground and
belowground ecosystems. The community structure of soil nematodes, widely used as bio-indicators, can well reflect the impact of grazing on the soil biodiversity of grassland ecosystems and can also reflect the sustainability of grazing grassland ecosystems.

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