Effects of Mowing Frequency on Soil Nematode Diversity and Community Structure in a Chinese Meadow Steppe

Jinling Zhao 1,2,†, Jiale Chen 3,†, Honghui Wu 3,*, Linghao Li 1 and Fengjuan Pan 4,*

1 State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China; zhaojl@126.com (J.Z.); llinghao@ibcas.ac.cn (L.L.)
2 College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China
3 Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing 100081, China; jialechen320@163.com
4 Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Harbin 150081, China
* Correspondence: wuhonghui@caas.cn (H.W.); Panfj@iga.ac.cn (F.P.)
† Jinling Zhao and Jiale Chen contributed equally to this work.

Abstract: Soil nematodes are one of the most important components in terrestrial ecosystems and the critical factor driving the belowground process. The grasslands of Northeast China have been subject to mowing for ages, which theoretically should have had substantial effects on the processes associated with soil nematodes. However, relevant studies have barely been conducted to date. This study examined variations in soil nematode abundance, biomass, diversity, and community structure, with respect to varying mowing frequencies. The results showed that a higher mowing frequency significantly reduced the abundance of soil nematodes, biomass, diversity, and community structure stability in the ecosystem, while intermediate mowing frequency enhanced these parameters to different extents. Our findings indicate that the changing patterns of the nematode indices with mowing frequency conform to the intermediate disturbance theory. This study provides a theoretical basis for formulating grassland-related management measures and maintaining the stability of grassland ecosystems.

Keywords: grassland; nematodes; biodiversity; mowing frequency

1. Introduction

Grassland ecosystems are the single largest terrestrial biosphere in the world and play a crucial role in primary production and ecosystem functioning [1]. They support the livelihood of over one-fifth of the world’s population and maintain the largest soil carbon and nitrogen pools on Earth. More and more studies show that most ecological functions are substantially dependent on belowground processes, notably carbon and nitrogen cycling, in which soil nematodes are the predominant driving force [2].

Soil nematodes may appear at various trophic levels of the soil food chain, being highly sensitive to changes in vegetation-soil-related aspects [3], which is largely due to their high diversity at species to trophic level. Four trophic or feeding habit-associated groups are most predominant in the free-living soil nematodes, namely bacterivores, fungivores, plant parasitic nematodes, and omnivores/predators [4]. These groups differ substantially in ecological functioning and have rather differential, niche widths in soils. Bacterivores and fungivores consume soil microbes in large amounts, thus imposing significant impacts on soil organic matter decomposition and nutrient release, while plant parasitic nematodes have direct impacts on vegetation growth, because they mainly feed on fresh organs that are most important in the primary production of plant communities, such as leaves and fine roots. They also use root exudation and thus affect the rhizospheric absorption of nutrients and water [5]. Omnivores and predatory nematodes have significant impacts on soil fauna appearing at lower food chain positions, and thus alleviate the feeding activity of soil animals on microbes [6].
A number of studies show that soil nematode abundance and biomass vary significantly with season and site-specific conditions, which is due mainly to variations in soil temperature, moisture, aeration, and soil carbon availability [7–9]. By contrast, the genus diversity is much more related to the plant species composition and the shoot to root ratio of the vegetation in question [2,10–13], with dominant plant species in particular [14]. It is likely that the soil nematode should be affected by mowing and the response might be altered by the frequency of mowing. This is because mowing has a notable effect on soil temperature, moisture, aeration, and soil carbon availability, and the frequency of mowing mediates the magnitude of these responses [15,16]. Studies have shown that moderate cutting can increase the diversity of vegetation [15]. On the other hand, heavy mowing will also increase the pH of the soil, reducing the carbon distribution in the above-ground part and the abundance of soil biomass. Therefore, different levels of cutting have different effects on the environmental factors of soil nematodes [16–18]. However, few studies have investigated the effect of mowing and its frequency on soil nematodes.

Studies on soil nematode ecology in grassland ecosystems are conducted mostly in North American prairies and much less in Eurasian steppes. Although most of these studies examined the effects of livestock grazing on the abundance aspect, only a few dealt with its impacts on the ecological functional aspects [3]. By contrast, our knowledge about the effects of mowing on soil nematode communities in grasslands is extremely limited. The Hulun Buir steppe of Inner Mongolia is a temperate meadow steppe in nature, which is highly representative of the Eurasian steppe. Mowing is the most dominant human practice in this region, especially in the last several decades. Because the soil is more fine-textured and xeric, while water-logging occurs frequently in wet years, the meadow steppe is assumed to be unique and significant in terms of soil animal-related aspects. However, studies on soil nematode communities with respect to mowing have been poorly documented [1].

In the present study, we examined the impact of mowing frequency on the soil nematode community structure and genus diversity in a grassland ecosystem of northeastern Inner Mongolia. Three objectives were addressed, including: (1) to quantitatively evaluate the effect of mowing frequency on the individual density and cumulative biomass of soil nematodes at trophic group and community levels; (2) to estimate the change trend of soil nematode diversity and community structure, under different mowing frequencies, and (3) to unravel the relations and controls with respect to mowing-resultant variations in community structure and diversity of soil nematodes.

2. Materials and Methods

2.1. Site Description

The field survey was conducted in a meadow steppe ecosystem located in northeastern Inner Mongolia (49°33’ N and 120°05’ E). The relief is gently undulating, being between 670 and 677 m in elevation. The continental climate is prevalent, generally being muted and semi-arid. The mean annual temperature varies between −5 and 2 °C, and the frost-free period lasts around 110 days. The annual precipitation averages about 376 mm, with 80% falling in summer. The vegetation is dominated by *Leymus chinensis*, a widespread, rhizomatous grass species. Important companion species include *Stipa baicalensis*, *Carex duriuscula*, *Galium verum*, *Bupleurum scorzonerifolium*, and *Filifolium sibiricum*. Chestnut soil is predominant, which is equivalent to Castanozems in the soil taxonomic system of the FAO, being neutral to slightly alkaline and sandy-loam in texture [18,19]. The experiment was built on a meadow, fenced in 2005 to avoid the influence of large herbivores. The mowing treatments were started in 2005, with six treatments being randomly arranged: high mowing frequency (M1), with the pasture being mowed once a year; intermediate mowing frequency (M2 and M3), mowed once every 2 and 3 years; low mowing frequency (M6 and M12), mowed once every 6 and 12 years; and control (CK), not mowed throughout. In each treatment, five replicates were set in an
even manner, each with an area of 0.4 ha. Pastures under all treatments were mowed in mid-August of the relevant years.

2.2. Extraction and Identification of Soil Nematodes

Soils were sampled from a 0–20 cm soil layer with a 5 cm diameter auger in August 2018. Ten soil samples were collected from each replication, and a composite soil sample was derived from 5 sampling spots across each replicate of a treatment. Due to the limitation of laboratory space, nematodes in M3 and M12 were extracted 5 days late. Soil nematodes were extracted by a modified Baermann funnel method, with 100 g of fresh soil being used for one sampling spot \[20,21\]. The nematodes were submerged in hot water at 60 °C for at least 10 min and sacrificed, and then were kept in a triethanolamine formaldehyde solution. The nematode suspension was drawn out with a pipette for identification and counting after being shaken well by hand. The initially recognized 100 nematode individuals were identified to a genus level, under a compound microscope at 400× or 1000× magnification. The total soil nematode abundance was estimated by counting the number of all individuals using an anatomical lens with an accuracy of 25× to 60×. The relative abundances of four trophic groups were separately determined, namely plant parasitic nematodes, bacterivores, fungivores, and omnivores/predators \[4\]. Each nematode genus was given a c-p value of 1–5 according to the scheme of Bongers \[22\]. The biomass of each nematode group was determined based on the relevant abundance of soil nematodes, in combination with the body size characteristics of different genera and was converted to a unit weight per 100 g of dry soil.

2.3. Calculations of Ecological Indices

The Shannon–Weaver index (H’) and richness index (SR) are used to characterize the abundance of soil nematode communities. The genus dominance index (λ) and evenness index (J’) are necessary parameters for judging the distribution of dominant species and other non-dominant species in the soil nematode community; the above parameters are used to describe the diversity of soil nematode communities. The maturity index (MI) \[22\], Wasilewska index (WI), and plant parasitic index (PPI) were used to describe the distribution of soil nematodes in different trophic groups, and reflect the function of soil nematodes \[22,23\]. The body length (L) and maximum body width (D) of the nematodes were used to determine the average body weight \(W, \mu g\) of the nematodes, and to determine the biomass of each nematode trophic group. The fresh weight quantification formula is \[24\]:

\[
W = (L^2 \times L)/(1.6 \times 10^6)
\]

2.4. Statistical Analysis

A significance test was performed using SPSS 20.0 (IBM Corp., Armonk, NY, USA). The effects of different mowing treatments on the soil nematode-related parameters were statistically assessed by the Tukey test, with one-way ANOVA \((p < 0.05)\).

3. Results

3.1. Soil Nematode Abundance

Our results show that with increasing mowing frequency, the abundance of soil nematodes basically increased first and then decreased (Figure 1). The results showed that the total abundances of soil nematodes of M2, M6, and M12 were significantly higher than those of M1, M3, and CK. The nematode abundance of each trophic group also showed a similar trend with variable mowing frequencies to that of the total abundance. Among them, the abundances of plant parasitic nematodes (Pp) and bacterivores (Ba) were significantly higher under M6 treatment than other treatments, while fungivores (Fu) and omnivores/predators (Op) had the highest abundances at M2; there was no significant difference between M6 and M12. No significant difference in the abundance of nematodes for each trophic group was detected between M1 and CK, except for fungivores. At the
same time, differences in the proportional abundance of each trophic group were also not significant between different mowing frequencies (Figure 2). The average proportion of bacterivores was the highest (30.0%), while the average proportion of omnivores/predators was the lowest (16.5%).

Figure 1. Variations in total and group abundances of soil nematodes (individuals per 100g of dry soil), across different mowing frequencies. (a) Total; (b) Plant parasitic nematodes; (c) Bacterivores; (d) Fungivores; (e) omnivores/predators. M1: mowing once per year; M2: mowing once every two years; M3: mowing once every three years; M6: mowing once every six years; M12: mowing once every twelve years; CK: without mowing. Values include means ± standard errors (n = 5). Bars marked with different lowercase letters indicate they are significantly different between treatments at p < 0.05.
3.2. Soil Nematode Biomass

Under different mowing treatments, the total biomass of soil nematodes ranged from 211.2 to 441.8 µg per 100 g dry of soil (Table 1). Among all trophic groups, the average proportion of the biomass of bacteria-eating nematodes was the highest (Figure 3), which was 35.7%, and the biomass range was 87.4–158.8 µg per 100 g of dry soil; the average proportion of the biomass of fungi-eating nematodes was the lowest, at 14.6%, the biomass range was 17.8–70.4 µg per 100 g of dry soil.

Table 1. Mean biomass values of different soil nematode groups (µg per 100g dry of soil) with respect to mowing frequency.

|          | M1       | M2       | M3       | M6       | M12      | CK       |
|----------|----------|----------|----------|----------|----------|----------|
| Ppw      | 46.9 ± 5.0a | 108.1 ± 9.7b | 54.9 ± 5.7a | 103.9 ± 9.2b | 76.9 ± 6.9ab | 52.3 ± 5.5a |
| Baw      | 90.5 ± 8.8a | 126.3 ± 11.7ab | 101.0 ± 13.0a | 158.8 ± 15.8b | 121.3 ± 9.0ab | 87.4 ± 10.9a |
| Fuw      | 17.8 ± 1.9a | 70.4 ± 7.8d | 36.3 ± 2.8ab | 61.4 ± 5.5bcd | 62.9 ± 7.0cd | 44.6 ± 8.0bc |
| Opw      | 56.0 ± 7.7a | 132.3 ± 9.0c | 71.0 ± 5.5ab | 117.6 ± 8.4c | 103.1 ± 12.9bc | 66.2 ± 8.8ab |
| Tow      | 211.2 ± 20.9a | 437.1 ± 24.6c | 263.2 ± 23.4ab | 441.8 ± 28.6c | 364.2 ± 26.2bc | 250.5 ± 25.0a |

Abbreviations are the same as in Figure 2. Values are means ± standard errors (n = 10). Values in a row with different lowercase letters indicate they are significantly different at \( p < 0.05 \).
M6 treatment. The nematode biomass of each trophic population was not significantly different between M2 and M6.

3.3. Soil Nematode Ecological Indices

3.3.1. Soil Nematode Diversity Indices

The soil nematode richness was expressed by the number of species (S) and richness index (SR). With increasing mowing frequency, the S and SR values of soil nematodes showed a single-peak trend (Table 2). The S value of soil nematodes ranged from 33 to 39, and the S values under low mowing frequencies (M6 and M12) were significantly higher than those under other treatments. The maximum S value appeared under the M6 and M12 treatments. The trend of SR across the treatments was similar to that of S, with the maximal value of SR occurring under M12. No significant differences in S and SR were detected between the intermediate, severe frequency, and control treatments.

Table 2. Variations in nematode diversity indices with decreasing mowing frequency.

|       | M1         | M2         | M3         | M6         | M12        | CK         |
|-------|------------|------------|------------|------------|------------|------------|
| S     | 33 ± 1a    | 35 ± 1ab   | 35 ± 1ab   | 39 ± 1b    | 39 ± 1b    | 33 ± 2a    |
| SR    | 4.74 ± 0.09ab | 4.46 ± 0.13a | 4.83 ± 0.1ab | 4.96 ± 0.09ab | 5.08 ± 0.13b | 4.53 ± 0.17a |
| H'    | 3.29 ± 0.02a | 3.40 ± 0.04ab | 3.34 ± 0.04ab | 3.56 ± 0.03c | 3.43 ± 0.04b | 3.29 ± 0.05a |
| J'    | 0.94 ± 0.00a | 0.95 ± 0.00ab | 0.94 ± 0.00a | 0.97 ± 0.01b | 0.94 ± 0.00a | 0.94 ± 0.01a |
| λ     | 0.047 ± 0.001c | 0.039 ± 0.001ab | 0.043 ± 0.002bc | 0.034 ± 0.001a | 0.039 ± 0.001ab | 0.045 ± 0.002bc |

S: species richness (genus number); SR: richness index; H': Shannon–Weaver index; J': evenness index; λ: genus dominance index. Values in a row with different lowercase letters indicate they are significantly different at p < 0.05.

Under different treatments, the H’ of M6 was significantly higher than those of other treatments, reaching 3.56, which was an increase of 7.6% compared with the control; there was no significant difference between M1 and CK.

The maximum value of J’ appeared in M6, which was 0.97. The J’ of M6 was significantly higher than those of other treatments, except M6, while there were no significant differences between M1, M3, M12 and CK.

The dominance index (λ) is used to reflect the distribution of dominant genera in soil nematodes. The larger the value, the more it indicates that the dominant genera of soil nematodes play a greater role in the community. The change of λ value under different treatments basically showed an opposite trend to H’, and its change range was from 0.034 to 0.047, which was the largest in M1 and the smallest in M6. The λ of M6 was significantly lower than those of all other treatments, and it was reduced by 24.4% compared to CK. In addition, no significant difference in the λ value was detected between M1 and CK.

3.3.2. Soil Nematode Community Structure Indices

The maturity index (MI) reflects the degree of impact on the soil environment. The greater the MI, the higher the maturity of the soil ecosystem, and the smaller the degree of impact. Among the various treatments, the average MI value of M2 was the largest at 2.87. The average MI value under the M1 treatment was the smallest at 2.70, which was significantly smaller than the MI values of M2 (Table 3).

Table 3. Variations in indices of nematode community structure with decreasing mowing frequency.

|       | M1          | M2          | M3          | M6          | M12         | CK          |
|-------|-------------|-------------|-------------|-------------|-------------|-------------|
| PPI   | 2.90 ± 0.03a | 2.82 ± 0.05a | 2.74 ± 0.03a | 2.83 ± 0.06a | 2.78 ± 0.10a | 2.74 ± 0.11a |
| MI    | 2.70 ± 0.04a | 2.87 ± 0.05b | 2.75 ± 0.04ab | 2.76 ± 0.04ab | 2.78 ± 0.04ab | 2.77 ± 0.08ab |
| WI    | 1.63 ± 0.07a | 1.59 ± 0.13a | 1.83 ± 0.05ab | 1.87 ± 0.12ab | 1.96 ± 0.10ab | 2.07 ± 0.24b |

MI: maturity index; PPI: plant parasite index; WI: Wasilewska index. Values in a row with different lowercase letters indicate they are significantly different at p < 0.05.
The plant parasite index (PPI) is based on the maturity index of plant parasitic
nematodes. A low value indicates that mowing measures have little effect on the survival
conditions of plant parasitic nematodes. The minimum PPI value appears in M3 and CK,
but there is no significant difference between mowing treatment and CK, but the standard
error of CK is larger.

The Wasilewska index (WI) can reflect the mineralization pathway of the soil food
chain and the health of the soil. The WI values under different treatments were all higher
than 1. With an increase in mowing frequency, WI showed a gradual decrease trend. The
average WI values of M12 and CK were 1.96 and 2.07, which amounted to increases of
20.2% and 27.0%, respectively, compared with M1.

4. Discussion

4.1. The Effect of Mowing on Soil Nematode Abundance and Biomass

The results of this study show that, in addition to the M3 treatment, intermediate
mowing (M2) and light mowing (M6 and M12) had significantly increased the abundance
and biomass of soil nematodes, both at community and trophic group levels (Figure 1;
Table 1). There was no significant difference between high mowing frequency (M1) and
control (CK), but the abundance and biomass of soil nematodes in M1 were slightly lower
than CK. The results of Hu et al. in the alpine meadow grassland showed that the frequency
of fungivores was the highest under intermediate disturbance [25]. Tan also found that
bacterivores and fungivores had the highest abundance values under the M2 treatment
in a mowing experiment conducted at the same location [17]. These results indicate that
intermediate mowing is beneficial to the growth of soil microbial nematode communities,
which is in line with the intermediate disturbance theory. This result may be related to the
effect of mowing on grassland vegetation. Studies have shown that intermediate mowing
may increase plant species diversity [15]. The increase in plant diversity is conducive to
the presence and growth of more species of soil plant parasitic nematodes, due to their
host specificity [2].

The abundance and biomass of soil nematode communities under the no-mowing
treatment were close to those of the heavy mowing treatment, the reasons for which may
be multifaceted. For the CK treatment, the reason may lie in that the accumulation of
excessive litter had lowered the growth season soil temperature, while increasing the soil
moisture [16]. High mowing frequency, on the one hand, may have reduced the amount
of carbon allocated underground, limiting the nutrient access to soil nematodes [17],
thereby affecting the abundance and biomass of soil nematodes. At the same time, heavy
mowing should also limit the abundance of soil microorganisms [18], thereby affecting
the food sources of soil fungi-eating nematodes and bacteria-eating nematodes. The
omnivores/predators that were higher in the food chain would also be limited by the
reduction in food. In addition, heavy mowing can increase soil pH [17], whereas studies
have shown that under acidic conditions, the number of soil nematodes will increase [26].
The nematodes of each trophic group did not show significant differences in the biomass
ratios under different mowing treatments. This indicates that the trophic group structure
of the soil nematode community had not changed significantly with mowing frequency,
and the fungus-eating nematodes had occupied a dominant position.

4.2. The Effect of Mowing on the Soil Nematodes Ecological Index

The diversity index is an important indicator that reflects the number of species
in the community and the complexity and stability of the food web. The higher the
Shannon–Wiener index (H'), the evenness index (J'), and the richness index (SR), the more
stable the community; the lower the dominance index (λ), the higher the diversity of the
community. In the present study, the H' and SR of the soil nematode communities under
the intermediate and low mowing frequency treatments were higher than those of the high
mowing frequency and the control, which accorded with the intermediate interference
theory. Previous studies have shown that intermediate disturbance may lead to varying
degrees of increase in the diversity of nematodes in grassland ecosystems [25,27]. The soil environment, plant species, and effective nutrient content play an important role in maintaining the community diversity of soil nematodes. These not only affect the number and quality of soil nematodes to a large extent, but also determine their survival or death [28,29]. For soil nematodes of different trophic groups, the influencing factors are different. Plant parasitic nematodes are mainly affected by their hosts [2]. Studies have shown that as the degree of mowing increases, the dominance of rhizomatous herbs increases significantly, while those of other types of plants significantly decrease [20]. The increase in rhizomatous herbs may provide more hosts for plant parasitic nematodes. For bacterivores, the soil microbial flora is the main influencing factor [30]. At the same time, fungivores are more sensitive to soil acidity and available nutrients [20]. However, some studies have shown that mowing may reduce the diversity of soil nematodes. Wang found in an experiment on *Leymus chinensis* meadow grassland that the soil nematode *H*’ and *J*’ in swards mowed every other year were significantly lower than those subject to continuous mowing and enclosure [31]. This may be related to the difference in soil pH, resulting from the impact of litter on the soil, with respect to mowing.

The maturity index (MI) values in this study were slightly higher under the intermediate and low mowing frequencies than those under the high mowing frequency and control. This suggests that low and intermediate mowing frequencies can increase the stability of the soil nematode community structure, thereby increasing the stability of the soil ecosystem. However, the slightly higher PPI value under the heavy mowing frequency (Table 3) was difficult to explain. The reason may be that in the case of heavy mowing, fast-growing plants need more nutrients to quickly restore growth and maintain normal reproduction speed [32]. Studies have shown that the soil nitrogen mineralization rate and carbon turnover rate become faster under the condition of heavy mowing, which may be a reason for the higher PPI value under high mowing frequency [32]. WI is used to reflect the mineralization pathway of the soil food web and the health of the soil. In this study, the WI values under different mowing treatments were all higher than 1, indicating that the proportion of plant parasitic nematodes was relatively low, and the soil health was good. When WI is less than 1, the probability of plant nematode disease outbreak is greater [33].

5. Conclusions

We revealed that mowing impacts the abundance, biomass, diversity, and community structure of soil nematodes in this steppe ecosystem, which were all highly dependent on the mowing frequency. Under different mowing frequencies, the change patterns of soil nematode-related indices basically accorded with the theory of moderate interference. Moderate mowing can promote soil nematode abundance, biomass, and diversity, while excessive mowing would have the opposite effect. However, the mechanism of cutting frequency on soil nematode communities still needs to be further explored, especially with regard to the interaction between the aboveground and underground parts. This study hints that moderate mowing can promote the favorable functions of the soil nematode community as a whole and maintain the stability of the soil ecosystem at the same time. We propose that controlling the intensity of grassland use plays an important role in maintaining the sustainability of grassland use.

**Author Contributions:** Conceptualization, F.P. and L.L.; methodology, H.W.; software, J.C.; validation, F.P., L.L. and H.W.; formal analysis, F.P.; investigation, J.Z.; writing—original draft preparation, J.Z.; writing—review and editing, J.Z. and J.C.; visualization, J.C.; supervision, H.W.; project administration, F.P. and H.W.; funding acquisition, F.P. and L.L. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by National Key Research and Development Program of China (2017YFE0104500), the Major State Research Development Program of China (2016YFC0500601), and National Natural Science Foundation of China (41877342 and 32071636).

**Institutional Review Board Statement:** Not applicable.
Informed Consent Statement: Not applicable.

Acknowledgments: We owe our sincere thanks to the staff of the Hulun Buir Grassland Ecosystem Observation and Research Station. Yu, Q. kindly helped in the statistical analysis. Jiang Y. kindly helped us collect the soil samples.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results. Jinling Zhao and Jiale Chen contributed equally to this work.

References

1. Li, L.; Chen, J.; Zhang, W.; Han, X. *Chinese Grassland Ecosystems*; Springer: Berlin, Germany, 2020; pp. 176–220.

2. De Deyn, G.B.; Raaijmakers, C.E.; Ruijven, J.V.; Berendse, F.; van der Putten, W.H. Plant species identity and diversity effects on different trophic levels of nematode species in the soil food web. *Oikos* **2004**, *106*, 576–586. [CrossRef]

3. Wang, B.; Wu, L.; Chen, D.; Wu, Y.; Hu, S.; Li, L.; Bai, Y. Grazing simplifies soil micro-food webs and decouples their relationships with ecosystem functioning in grasslands. *Global Chang. Biol.* **2020**, *26*, 960–970. [CrossRef]

4. Yeates, G.; Bongers, T.; De Goede, R.; Freckman, D.; Georgieva, S. Feeding habits in soil nematode families and genera: An outline for soil ecologists. *J. Nematol.* **1993**, *25*, 315–331. [PubMed]

5. Denton, C.S.; Bardgett, R.D.; Cook, R.; Hobbs, P.J. Low amounts of root herbivory positively influence the rhizosphere microbial community in a temperate grassland soil. *Soil Biol. Biochem.* **1998**, *31*, 155–165. [CrossRef]

6. Laakso, J.; Setälä, H. Population- and ecosystem-level effects of predation on microbial-feeding nematodes. *Oecologia* **1999**, *120*, 27–286. [CrossRef]

7. Neher, D.A.; Weicht, T.R.; Savin, M.; Görres, J.H.; Amador, J.A. Grazing in a porous environment. 2. Nematode community structure. *Plant Soil* **1999**, *212*, 85–99. [CrossRef]

8. Ruan, W.; Sang, Y.; Chen, Q.; Zhu, X.; Lin, S.; Gao, Y. The Response of Soil Nematode Community to Nitrogen, Water, and Grazing History in the Inner Mongolian Steppe, China. *Ecosystems* **2012**, *15*, 1121–1133. [CrossRef]

9. Sohlenius, B.; Bostrom, S. Effects of climate change on soil factors and metazoan microfauna (nematodes, tardigrades and rotifers) for soil ecologists. *J. Nematol.* **1999**, *31*, 25–36. [CrossRef]

10. Kardol, P.; Wardle, D.A. How understanding aboveground–belowground linkages can assist restoration ecology. *Trends Ecol. Evol.* **2010**, *25*, 670–679. [CrossRef] [PubMed]

11. Zhao, J.; He, X.; Nie, Y.; Zhang, W.; Fu, Z.; Wang, K. Unusual soil nematode communities on karst mountain peaks in southwest China. *Soil Biol. Biochem.* **2015**, *88*, 414–419. [CrossRef]

12. Yeates, G.; Bongers, T. Nematode diversity in agroecosystems. *Agr. Ecosyst. Environ.* **1999**, *74*, 113–135. [CrossRef]

13. Diakhate, S.; Villenave, C.; Diallo, N.H.; Ba, A.O.; Djigal, D.; Masse, D.; Sembène, P.M.; Chapuis-Lardy, L. The influence of a shrub-based intercropping system on the soil nematofauna when growing millet in Senegal. *Eur. J. Soil Biol.* **2013**, *57*, 35–41. [CrossRef]

14. Van der Putten, W.H.; van der Stoel, C.D. Plant parasitic nematodes and spatiotemporal variation in natural vegetation. *Appl. Soil Ecol.* **1998**, *10*, 253–262. [CrossRef]

15. Baoyin, T.; Li, F.Y.; Minggagud, H.; Bao, Q.; Zhong, Y. Mowing succession of species composition is determined by plant growth forms, not photosynthetic pathways in Leymus chinensis grassland of Inner Mongolia. *J. Zhejiang Univ.* **2015**, 82, 101–110, (Abstract in English).

16. Shao, C.; Chen, J.; Li, L.; Zhang, L. Ecosystem responses to mowing manipulations in an arid Inner Mongolia steppe: An energy perspective. *J. Arid Environ.* **2012**, *79*, 1–10. [CrossRef]

17. Li, X.; Chen, L.; Fan, R.; Wu, X.; Xie, Y. Effects of four typical plant community litter input on soil physical and chemical properties under the fenced condition in desert steppe. *J. Zhejiang Univ. Appl.* **2015**, *41*, 101–110. (Abstract in English).

18. Chen, Y.; Hu, H.; Han, H.; Du, Y.; Wan, S.; Xu, Z.; Chen, B. Abundance and community structure of ammonia-oxidizing Archaea and Bacteria in response to fertilization and mowing in a temperate steppe in Inner Mongolia. *FEMS Microbiol. Ecol.* **2014**, *89*, 67–79. [CrossRef]

19. Yang, S.; Jin, J.; Wei, Z.; Sun, S.; Yan, R.; Liu, W. Effect of mowing on community characteristics in grassland for hay in Hulunbuir. *Chin. J. Grassland* **2015**, 37, 90–96. (Abstract in English).

20. Tan, H. Study on Impact of Grazing and Mowing on Soil Microbial Properties and Aboveground Vegetation. Master’s Thesis, Chinese Academy of Agricultural Sciences Dissertation, Beijing, China, 2015.

21. Barker, K.R. Nematode extraction and bioassays. In *An Advanced Treatise on Meloidogyne*; Barker, K.R., Carter, C.C., Sasser, J.N., Eds.; North Carolina State University Graphics: Raleigh, NC, USA, 1985.

22. Bongers, T. The maturity index: An ecological measure of environmental disturbance based in nematode species composition. *Oecologia* **1990**, 83, 14–19. [CrossRef]

23. Wasilewksa, L. Differences in development of soil nematode communities in single-and multi-species grass experimental treatments. *Appl. Soil Ecol.* **1995**, *2*, 53–64. [CrossRef]

24. Ferris, H. Form and function: Metabolic footprints of nematodes in the soil food web. *Eur. J. Soil Biol.* **2010**, *46*, 97–104. [CrossRef]
25. Hu, J.; Wu, J.; Ma, M.; Nielsen, U.N.; Wang, J.; Du, G. Nematode communities response to long-term grazing disturbance on Tibetan plateau. *Eur. J. Soil Biol.* 2015, 69, 24–32. [CrossRef]

26. Pan, F.; Yang, L.; Wang, C.; Yan, R.; Li, C.; Hu, Y.; Jiang, Y.; Cao, J.; Tan, H.; Xin, X. Effects of mowing frequency on abundance, genus diversity and community traits of soil nematodes in a meadow steppe in northeast China. *Plant Soil* 2020. [CrossRef]

27. Wang, X.; Nielsen, U.N.; Yang, X.; Zhang, L.; Zhou, X.; Du, G.; Li, G.; Chen, S.; Xiao, S. Grazing induces direct and indirect shrub effects on soil nematode communities. *Soil Biol. Biochem.* 2018, 121, 193–201. [CrossRef]

28. Pan, F.; Han, X.; Li, N.; Yan, J.; Xu, Y. Effect of Organic Amendment Amount on Soil Nematode Community Structure and Metabolic Footprints in Soybean Phase of Soybean-Maize Rotation in Mollisols. *Pedosphere* 2020, 30, 544–554. [CrossRef]

29. Li, L.H. *Chinese Vegetation and Environmental Change*; China Agricultural University Press: Beijing, China, 2021; pp. 346–351, in press.

30. Steinauer, K.; Chatzinotas, A.; Eisenhauer, N. Root exudate cocktails: The link between plant diversity and soil microorganisms? *Ecol. Evol.* 2016, 6, 7387–7396. [CrossRef]

31. Wang, J.; Li, M.; Zhang, X.; Liu, X.; Li, L.; Shi, X.; Hu, H.; Pan, G. Changes in soil nematode abundance and composition under elevated [CO$_2$] and canopy warming in a rice paddy field. *Plant Soil* 2019, 445, 425–437. [CrossRef]

32. Schrama, M.J.J.; Cordlandwehr, V.; Visser, E.J.W.; Elzenga, T.M.; de Vries, Y.; Bakker, J.P. Grassland cutting regimes affect soil properties, and consequently vegetation composition and belowground plant traits. *Plant Soil* 2013, 366, 401–413. [CrossRef]

33. Li, M. Effects of Long-Term Fertilization on Soil Nematode Community Structure in Wheat-Maize Rotation System. Master’s Thesis, Zhengzhou University, Zhengzhou, China, 2017.