Plant Soil
https://doi.org/10.1007/s11104-024-07067-x

RESEARCH ARTICLE

Altered energy dynamics of soil nematode food web modify multifunctionality under precipitation regime change in a temperate grassland

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Received: 14 July 2024 / Accepted: 27 October 2024

Abstract

Background Precipitation regimes in arid and semi-arid regions are exhibiting a trend of increase in rainfall intensity but reduction in frequency, affecting soil communities and ecosystem functions. Soil nematodes are essential components of soil communities, partaking in multiple energy channels and underpinning various crucial ecosystem functions. Understanding the impact of precipitation regime changes on energy fluxes within soil nematode food webs has a decisive impact on ecosystem function under global climate change.

Methods This study conducted a long-term field experiment established in 2012 to simulate precipitation regime changes (the total precipitation added was 80 mm unchanged, but the size and frequency of applied precipitation events were varied) in a semi-arid grassland of Inner Mongolia. We quantified the metabolism and energetic structure of soil nematodes. We further investigated the responses of metabolic rate of trophic groups and energy fluxes within soil nematode to changes in precipitation regime, and how such changes in nematode energy dynamics affect ecosystem multifunctionality (EMF).

Results We found that heavy precipitation intensity increased the metabolic rates and energy fluxes of all trophic groups, and the EMF index was maximized. The EMF values were positively correlated with the metabolic rates and energy fluxes of bacterivores and omnivores/predators.

Conclusions These results suggest that a shift toward higher-intensity and lower-frequency precipitation events could lead to an increase in energy fluxes within soil nematode food webs, thereby enhancing their contributions to EMF. These findings provide insights into the role of energy dynamics in affecting EMF under various scenarios of precipitation pattern changes.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-024-07067-x.

Responsible Editor: EGaowen Yang.

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Published online: 05 November 2024

Keywords Precipitation regime · Energy flux · Ecosystem multifunctionality · Soil nematode food web

Introduction

Climate models predict variabilities in precipitation regimes (IPCC 2013), potentially leading to variations in precipitation volume, seasonal distribution, precipitation frequency, and extreme rainfall events (O'Gorman 2012; Peng et al. 2013). Temperate regions experience a general shift toward lower-frequency and higher-intensity precipitation events, whereas the overall precipitation amount remains largely unchanged (Easterling et al. 2000; Radu and Duval 2018). Such changes in precipitation regimes can affect soil water dynamics and terrestrial ecosystem functionality (Knapp et al. 2008). Most studies have focused on the impacts of changes in precipitation amount and seasonal distribution (Peng et al. 2013; Wang et al. 2022; Zhang and Xi 2021), however, little is known about the impacts of the shift to larger but fewer rainfall events on grassland ecosystems, especially belowground communities.

Nematodes are dominant soil organisms dwelling in water films (Neher 2010), which distribute across multiple trophic levels and play key roles in ecosystem functions (Zhang et al. 2024). Variations in precipitation are likely significant determinants of alterations in the composition and function of soil nematodes (Landesman et al. 2011). For instance, greater precipitation increases the abundance of predaceous nematodes that consume and limit the abundance of nematodes lower in the trophic structure in mesic grassland (Franco et al. 2019). Furthermore, such water pulses may enhance diversity by suppressing dominant species in mesic grasslands (Song et al. 2016). Ecologists are increasingly recognizing the importance of traits to understand the responses of soil nematodes to environmental changes, rather than abundance or/and diversity (de Bello et al. 2021; Zhang et al. 2024). For example, large bodied soil nematodes benefit from higher long-term water availability (i.e. mesic conditions select for larger-bodied taxa) (Andriuzzi et al. 2020). Differences in nematode diversity, community structure and traits have been proved that are related to changes in precipitation. However, there is limited empirical evidence on how the energy dynamics of the soil nematode food web respond to changing precipitation regimes.

Emerging evidence suggests that energy dynamic across trophic levels serves as a vital descriptor of key ecosystem processes (Barnes et al. 2018; Moore 2012). For instance, the energy distributions across multiple trophic groups directly affect the stability of soil food webs and carbon flux between food resources/preys and consumers/predators (Potapov 2022; Trap et al. 2016; Xing 2024). Generally, increased water availability may result in more energy fluxes channeling to lower trophic groups and facilitate meeting top predators' energy demands (Potapov et al. 2019, 2021). Adequate energy supply for trophic groups can promote faunal metabolism and thereby increase their contributions to soil total CO_2flux (Liao et al. 2023). Nematode metabolic rate is a physiological trait related to growth rate and carbon cycling (Zhang et al. 2024) and consists of production carbon and respiration carbon (Ferris 2010). By integrating metabolic theories with assimilation efficiency and energy losses, the energy flux from each resource node to the corresponding consumer within soil nematode food web could serve as a metric for assessing ecosystem-level impacts (Barnes et al. 2014, 2018; Zhu et al. 2023). Ecosystem multifunctionality (EMF) is the capacity of an ecosystem to simultaneously provide multiple functions and services, such as carbon and nutrient cycling(Garland et al. 2020). Therefore, clarifying the connection between energy dynamics of soil nematode food web and EMFwill enhance our understanding of the consequences of alterations in precipitation regimes on biodiversity and the energy flow within soil food web.

In this study, we conducted an 8-year precipitation experiment in a temperate grassland to explore the responses of soil nematode energy dynamics to the precipitation regime changes and their impact on ecosystem multifunctionality. We hypothesized that higher-intensity precipitation regimes would promote the energy dynamics of the soil nematode food web by enhancing soil water availability, and such positive changes in nematode energy dynamics further increase ecosystem multifunctionality.

Materials and methods

Site and experimental design

This study was conducted at the Duolun Restoration Ecology Research Station of the Institute of Botany,

Chinese Academy of Sciences, Inner Mongolia, China (42°02′ N, 116°17′ E). The study area was located in a semi-arid temperate steppe (Zhou et al. 2013). The mean annual precipitation (MAP) was 383 mm, with 90% distributed from May to October. The mean annual temperature (MAT) was 2.1 °C. The soil was classified as Haplic Calcisols according to the FAO classification. Soil bulk density was 1.31 g cm^{-3}(Xia et al. 2009). The nitrogen (N) and phosphorus (P) contents were 0.17% and 0.028%, respectively. The plant community at the site was dominated by*Stipa krylovii*, *Agropyron cristatum*, and *Artemisia frigida.*

The precipitation manipulative experiment began in May 2012. A randomized block design with four replicate blocks was adopted; each block consisted of six randomly distributed treatment plots (3 × 4 m). Different precipitation intensities (the total precipitation unchanged, but the size and frequency of precipitation varied) were selected to simulate the precipitation regime changes: 0 mm (control), 2 mm (40 times), 5 mm (16 times), 10 mm (8 times), 20 mm (4 times) and 40 mm (2 times), totaling 24 experimental plots. We considered the manipulation of the degree of precipitation change was quite arbitrary, ranging from 5 to 100%. In this study, 20% of average annual precipitation of the research station was taken as intended precipitation, which is a magnitude mostly used (Beier et al. 2012; Wu et al. 2011). And an increase in 20% makes the total annual precipitation near the 80th percentile of the past 40-year record. Therefore, eighty millimeters of water were evenly added to each plot from June to August, during which period the grassland productivity is the highest every year. Soil sampling was done at the end of the growing season (September) in 2020. It has undergone eight years since soil sampling, and we can believe the responses caused mainly by the effects of treatments.

Soil and plant sampling

Soil samples were collected in September 2020, at the end of the growing season. Seven soil cores (2.5 cm in diameter) were randomly collected from the surface (0–10 cm) and mixed as one composite sample per plot. Soil samples were stored at 4 °C before analyzing soil nutrients and nematodes.

Plant samples were collected in August 2020. The number of plant species was recorded as plant species richness in each plot. The vegetation clipped in each quadrat (0.2 × 1.0 m) was oven-dried at 65 °C for 48 h and weighted as aboveground biomass (AGB). After removing the standing vegetation, the roots were sampled (0–10 cm) by randomly mixing three soil cores (5.0 cm in diameter) from each plot. The roots that were separated from the soil by washing, oven-dried at 65 °C and weighted as belowground biomass (BGB).

Nematode energetic structure

Nematodes were extracted from 50 g fresh soil by using a modified cotton-wool filter method (Oostenbrink 1960). After counting, at least 100 individuals were randomly selected from each sample and identified at the genus level. Nematodes are classified into bacterivores, fungivores, herbivores, and omnivores/predators according to their feeding habits (Yeates et al. 1993). The fresh biomass of the nematodes was estimated using data fromhttp://nemaplex.ucdavis.edu. The individuals of nematodes (per m^2) were calculated as follows (Liao et al. 2023):

$$N = D \times 1 \times G \times 10^6 \times A$$

where D is the soil sampling depth (m), 1 represents 1 m^2, G is the soil bulk density (g cm^{-3}), 10^6 is the conversion coefficient from m^3 to cm^3, and A is the individuals of nematodes per gram of soil sample.

Nematode metabolic rate is a physiological trait related to growth rate and carbon cycling (Zhang et al. 2024) and consists of production carbon and respiration carbon (Ferris 2010). By combining the production carbon ($0.1W_i/12\mathrm{cp}._i$) with respiration carbon ($0.0159W_i^{0.75}$) of an individual, the metabolic rate of nematodes (mg C m^{-2} d^{-1}) was calculated using the following equation (Ferris 2010; van den Hoogen et al. 2019):

$$M = \sum (N_i \times (0.1W_i/12cp_i + 0.0159W_i^{0.75})$$

where N_i is the number of individuals of genus i (per m^2), W_i is the fresh biomass of genus i (mg), and $\mathrm{cp}._i$ is the colonizer-persister value of genus i. Next, the metabolic rate of each trophic group was calculated by summing the metabolic rates at the genus level within the corresponding trophic group.

The energy flux of each trophic group (mg C m^{-2} d^{-1}) was calculated as follows:

$$F = (M_j + L)/e_a$$

where M is the total metabolic rate of all individuals in trophic group j (mg C m^{-2} d^{-1}), L is the energy loss to the corresponding consumer, and $e_a$is the assimilation efficiency (0.60, 0.38, 0.25 and 0.50 for bacterivores, fungivores, herbivores, and omnivores/predators, respectively) (De Ruiter et al. 1993; Schwarz et al. 2017). First, the energy flux of omnivores/predators was calculated as$F_{OP} = M_{OP}/e_a$, because there is no predator of omnivores/predators (i.e., the energy loss L was zero) in our study. Next, the energy loss of each lower trophic group to omnivores/predators could be calculated as $F_{OP}\times P_j$ (where P_j is the proportional abundance to the total lower trophic group abundance of trophic group j).

Ecosystem Multifunctionality

Ecosystem multifunctionality metrics potentially summarize the ability of ecosystems to deliver multiple functions and services simultaneously, and aim to understand ecosystem functioning from multidimensional patterns (Manning et al. 2018). In this study, the selection of functions is based on their theoretical links with grassland belowground ecosystem functions. We used 11 measurements related to three key belowground ecosystem functions: (a) water regulation (soil moisture), (b) soil nutrient supply (total nitrogen, total phosphorus, available nitrogen, ammoniacal nitrogen, nitrate nitrogen, microbial biomass carbon and microbial biomass nitrogen), and (c) vegetation properties (plant richness, aboveground biomass, and belowground biomass). Detailed measurements of these indicators and their importances are provided in Supplementary information (TableS1).

The averaging approach is an intuitive and effective method to evaluate changes in several ecosystem functions and enables the calculation of EMF (Hooper and Vitousek 1998; Maestre et al. 2012). The Z scores of the 11 functions under each treatment were calculated first by the formula $Z_{ij}= (x_{ij}- \mu_j)/\sigma_j$, where the Z_{ij} is the Z-score of function i under treatment j, x_{ij} is the value of function i under treatment j, μ_i is the average of function i under six treatments and σ_i is the standard deviation of function i within six treatments. The EMF index under different precipitation treatments was the average of the Z scores of the 11 functions.

Data analysis

Data were analyzed using R 4.3.2 version. Linear mixed-effects models were used to evaluate the effects of precipitation regime changes on soil moisture, ecosystem multifunctionality (EMF) index, metabolic rate, and energy flux of each nematode trophic group, in which the precipitation intensity treatment was fixed factor, and block was a random factor. Before statistical analysis, all data were tested for normality and homoscedasticity of variance. One-way analysis of variance (ANOVA) followed by the least significant difference (LSD) post hoc test ($P<0.05$) was used to test the effect of precipitation regime changes on the soil moisture, ecosystem multifunctionality (EMF) index, metabolic rate, and energy flux of each nematode trophic group. Linear regressions were used to reveal the relationships between metabolic rate and EMF index and the relationships between energy flux and EMF indices of all trophic groups.

Results

Soil moisture and ecosystem multifunctionality

Heavy precipitation intensity (20 mm) significantly increased the soil moisture (Fig. 1A, Table S2, $P<0.01$), and changes in the precipitation intensity significantly affected the EMF index (Fig. 1B, Table S2, $P<0.05$). The EMF values were lower under 0-, 2-, and 10-mm precipitation intensity treatments than those under the other treatments. The maximum EMF value of 0.46 was achieved under the heavy precipitation treatment (20 mm).

Energetic structure of the soil nematode food web

Changes in precipitation intensity had significant effects on the metabolic rates of all nematode trophic groups (Fig. 2A, Table S2, $P<0.01$). The metabolic rates of bacterivores under the heavy and extreme precipitation treatments were higher than those under the other treatments ($P<0.01$). The 10-, 20- and 40-mm precipitation treatments significantly increased the metabolic rate of fungivores, and herbivores compared with the other precipitation intensity treatments ($P<0.01$). The metabolic rate of omnivores/predators was the highest under the heavy precipitation treatment ($P<0.01$).

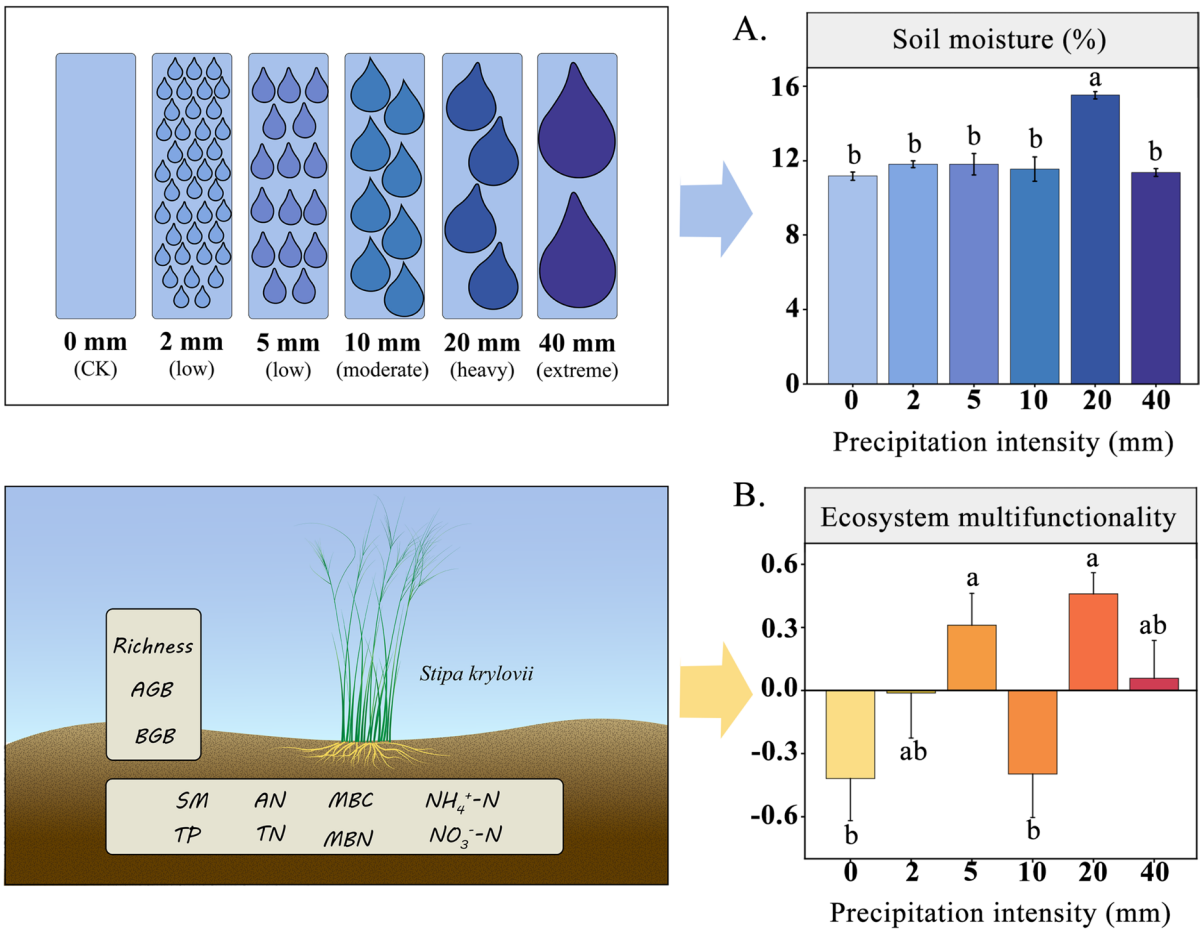

Fig. 1 The response of soil moisture and ecosystem multifunctionality (EMF) index to the precipitation intensity change. Vegetation was presented by a dominant species (*Stipa krylovii*). SM, Soil moisture; TP, total phosphorus; TN, Total nitrogen; AN, available nitrogen; MBC, Microbial biomass carbon; MBN, Microbial biomass nitrogen; NH_4^+-N, Ammoniacal nitrogen; NO_3^--N, Nitrate nitrogen; AGB, aboveground biomass; BGB, belowground biomass. Error bar means standard error (S.E.). Different letters indicate significant differences among different precipitation intensities. The number of replicates was 4 ($n=4$)

Variations in precipitation regimes significantly affected the energy flux from basal resources to the nematode trophic groups (Fig. 2B, Table S2, $P<0.01$). The energy flux of bacterivores was significantly higher under 20 mm precipitation treatment than those under the other treatments ($P<0.01$). The energy fluxes of fungivores under 10-, 20- and 40-mm precipitation treatments were higher than those under the low precipitation treatments ($P<0.01$). Changes in precipitation intensity significantly enhanced the energy fluxes of herbivores and omnivores/predators under 10 mm and 20 mm precipitation treatments ($P<0.01$).

Changes in precipitation intensity altered nematode biomass distribution and energy flux within the soil nematode food web (Fig. 2C). Under the heavy precipitation treatment (20 mm), more energy fluxes flowed from basal resources to nematodes in lower trophic level than those under the other treatments. Additionally, there were more energy fluxes flowing from each lower trophic group to omnivores/predators under the 20 mm precipitation treatment than under the other treatments. Correspondingly, the biomass of omnivores/predators peaked under heavy precipitation treatment, followed by those under moderate, extreme, and low precipitation treatments.

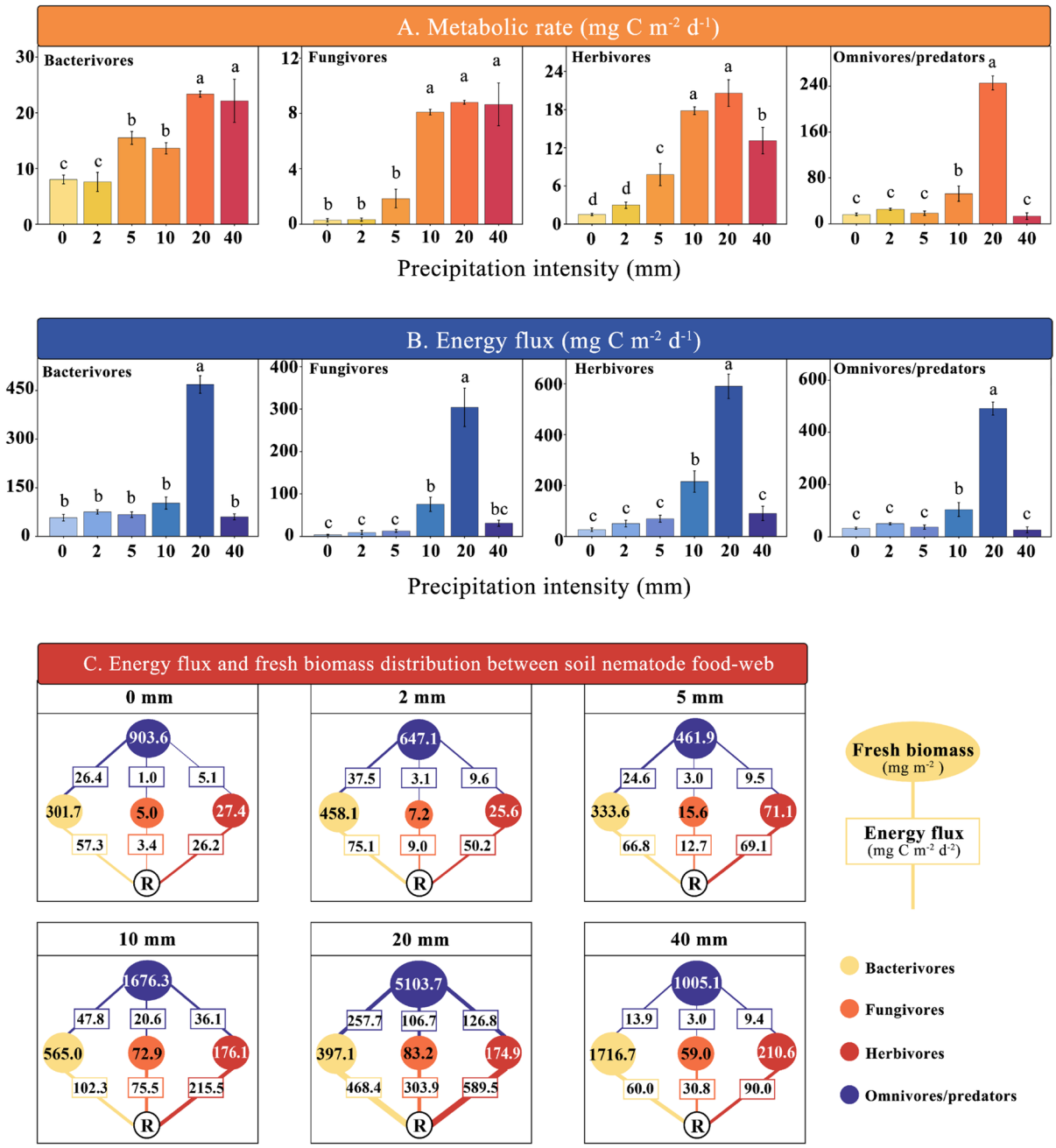

Fig. 2 The effects of precipitation intensity on metabolic rate and energy flux of each trophic group (A and B). Changes in energy flux and fresh biomass distribution between soil food-web under different precipitation intensity (C). Values in nodes indicate fresh biomass (mg m^{-2}). Values in boxes indicate energy fluxes (mg C m^{-2} d^{-1}). For each precipitation intensity, a five-node food web was constructed with bacterivores, fungivores and herbivores, receiving energy from basal resources (R), and omnivores/predators receiving energy from lower trophic groups of nematodes. Error bar means standard error (S.E.). Different letters indicate significant differences among different precipitation intensities. The number of replicates was 4 ($n = 4$)

Relationships between the nematode energetical structure and EMF

The EMF increased with the increasing metabolic rate of bacterivores and omnivores/predators (Fig. 3A, D, $P < 0.05$), and the EMF indices were positively correlated with the energy fluxes of bacterivores and omnivores/predators (Fig. 3E, H, $P < 0.05$).

Discussion

Impact of precipitation regime changes on energy structure of soil nematode food web

Soil water availability is one of the most crucial parameters regulating soil biota activity (Schnürer et al. 1986). In this study, we demonstrated that a heavy-intensity and low-frequency precipitation regime elevated the energy

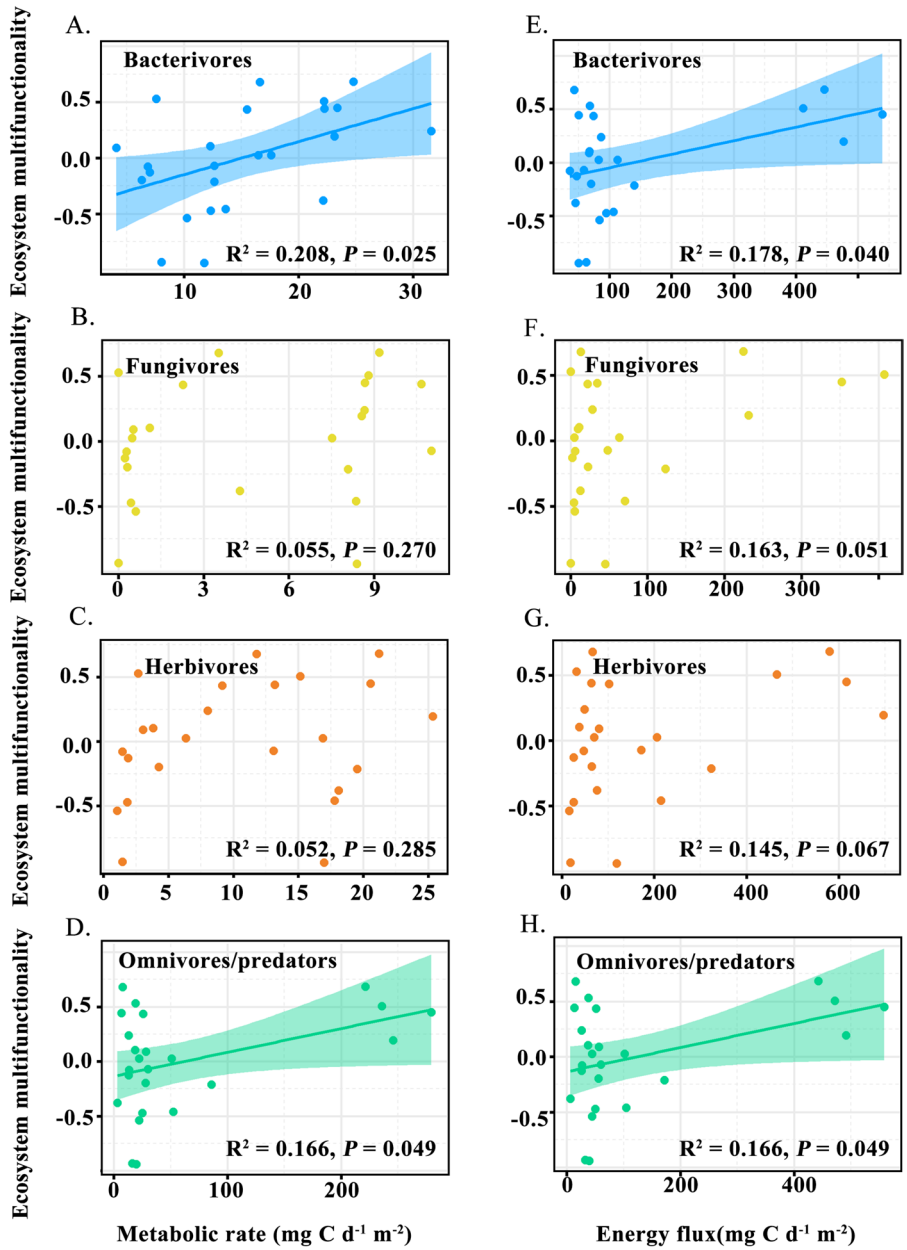

Fig. 3 The relationships between metabolic rate and ecosystem multifunctionality index (**A**-**D**). The relationships between energy flux and ecosystem multifunctionality index (**E**-**H**)

fluxes of nematodes by augmenting soil water availability, supporting our hypothesis. Studies have shown that an increase in soil moisture due to low rainfall is prone to evaporative loss, and heavy rainfall can effectively replenish soil water availability more (Peng et al. 2013; Wythers et al. 1999). The reason for this is that heavy rainfall can penetrate deeper into the soil layers, reducing the proportion of evaporative loss and maintaining soil moisture at a relatively high level (Heisler-White et al. 2009). Many studies have demonstrated that higher soil water availability potentially stimulates plant growth in water-limited grasslands (Lin et al. 2024; Ren et al. 2015). Our results also support that increased precipitation intensity promotes aboveground biomass and provides more resource inputs for herbivores, improving their energy fluxes. Increases in energy fluxes of microbivorous nematodes under heavy-intensity and low-frequency precipitation regime can be explained by the two reasons. Firstly, increased root exudation caused by increased soil water availability may favor rhizosphere microorganisms, facilitating the flow of resources to microbivorous nematodes (Bardgett and van der Putten 2014; Todd et al. 1999). Secondly, there was a sudden release of easily available energy and carbon from cells when the soil was rewetted (Schnürer et al. 1986). This phenomenon potentially enhanced the carbon uptake of microbivorous nematodes, further fostering the transfer of energy to nematode food webs. A precipitation regime shifting toward higher intensity and lower frequency benefits soil nematode energy fluxes, and the energy flux under 40 mm precipitation may deviate from this trend. Extreme precipitation may intensify the amplitude of soil moisture fluctuations and prolong the water stress period between two consecutive rainfall events (Knapp et al. 2002, 2008), potentially exerting adverse effects on nematodes that are highly sensitive to soil water availability.

Notably, omnivores/predatory nematodes exhibited a significantly higher metabolic rate under 20 mm precipitation than under other precipitation conditions. Soil nematodes live and movement through the water film within soil pores (Neher 2010). When soils are saturated, the flow of gravitational water toward tile drainage may ease the movement of soil nematodes (Neher 1999), which can improve the metabolic rate of the nematode community by promoting their general activity. This effect is more pronounced for omnivores/predatory nematodes because they are highly sensitive to soil water availability (Vandegehuchte et al. 2015). The metabolic rates of microbivorous nematodes and herbivores generally showed an increasing trend with increasing precipitation intensity. However, this might not be caused by the contingent effect of mean soil moisture but by factors such as water fluctuations. Research has shown that increases in rainfall intensity with concomitant decreases in frequency amplify soil water fluctuations in shallow soil layers (Knapp et al. 2008), changing the degree and duration of water stress. Different trophic groups may have variable upper and lower water stress thresholds for ecological processes, exhibiting different metabolic rates under soil fluctuation. In conclusion, our findings demonstrate that heavy-intensity and low-frequency rainfall events have a positive impact on the energy flux of soil nematodes by altering soil water availability. Furthermore, these results imply that energy flux may serve as a more direct indicator of environmental changes than metabolic rate to some extent.

Impact of soil nematode energy dynamic change on EMF

Emerging evidence indicates that the energy dynamic of the soil food web can serve as a crucial tool to comprehend the impact of environmental change drivers on EMF (Barnes et al. 2018; Wan et al. 2022), owing to functions driven by trophic interactions underpinning a spectrum of vital ecosystem functions (Wan et al. 2024). Partially consistent with our hypothesis, there were significant positive responses of EMF to metabolic rates of bacterivores and omnivores/predators (Fig.3). This finding agrees with a study that reported, the metabolism of bacterivores improved with increasing precipitation, possibly resulting in high rates of carbon and nutrients mineralization (Franco et al. 2022). It can be explained that bacterivores multiply most rapidly among the four trophic groups, which accelerate their metabolic processes and accumulations (Bongers 1990).

We also found significant positive responses of EMF to energy fluxes of bacterivores and omnivores/predators. The carbon flow through decomposers is pivotal for carbon sequestration and nutrient turnover rate (Morriën et al. 2017). Omnivores/predators had higher metabolic rate in the present study, which can explain why they played important roles in driving energy flux and EMF. Generally, individuals with high biomass require more energy to sustain their life activities (Potapov et al. 2021). In line with this, our results showed that bacterivores with higher biomass

have higher energy flux from basal level (Fig.2). Consequently, the energy demands of omnivores/predators drive the energy flow of bacterial channel by top-down control, because the feeding preference of omnivores/predators for trophic groups depended on community density (Cui et al. 2018). Although the energy flux of fungivores contributed less to EMF in our study, it is undeniable that fungivores help lengthen the time nutrients are retained within the soil food web, thereby protecting from loss (Whalen et al. 2013). Overall, our study indicated that the effect of precipitation intensity on the energy dynamics of the soil nematode food web is strongly determined by water availability, which affects the metabolic rates of trophic groups and energy flux within the soil food web and ultimately altering multifunctionality.

Conclusions

In this study, we demonstrated that heavy precipitation significantly enhanced the energy fluxes of all soil nematode trophic groups and promoted ecosystem multifunctionality. Additionally, the EMF increased with increasing metabolic rates and energy fluxes of bacterivores and omnivores/predators. Our results imply that a shift toward lower-frequency and higher-intensity precipitation events could increase the energy flux within the soil nematode food web, thereby increasing their contributions to EMF. These insights contribute to a better understanding of the role of energy dynamics within the soil nematode community in ecosystem multifunctionality under changing global scenarios.

Acknowledgements We greatly appreciate the Duolun Restoration Ecology Research Station of the Institute of Botany, Chinese Academy of Sciences for the field help.

Authors' contributions XM: Formal analysis, Data curation, Writing - review & editing. YZ: Data curation, Writing - review. SH: Methodology. ZH: Review & editing. GZ: Review & editing, Project administration, Funding acquisition. SC: Conceptualization, Methodology, Writing - review & editing, Investigation.

Funding This work was supported by the National Natural Science Foundation of China (NSFC-31970410), Liaoning Revitalization Talents Program (XLYC2002083).

Data availability The data supporting the findings of this study will be shared on reasonable request to the corresponding author.

Declarations

Conflict of interest The authors declare that they have no competing interests.

References

Andriuzzi WS, Franco AL, Ankrom KE, Cui S, de Tomasel CM, Guan P, Gherardi LA, Sala OE, Wall DH (2020) Body size structure of soil fauna along geographic and temporal gradients of precipitation in grasslands. Soil Biol Biochem 140:107638. https://doi.org/10.1016/j.soilbio.2019.107638

Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. Nature 515:505–511. https://doi.org/10.1038/nature13855

Barnes AD, Jochum M, Mumme S, Haneda NF, Farajallah A, Widarto TH, Brose U (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. Nat Commun 5:5351. https://doi.org/10.1038/ncomms6351

Barnes AD, Jochum M, Lefcheck JS, Eisenhauer N, Scherber C, O'Connor MI, de Ruiter P, Brose U (2018) Energy Flux: the link between Multitrophic Biodiversity and Ecosystem Functioning. Trends Ecol Evol 33:186–197. https://doi.org/10.1016/j.tree.2017.12.007

Beier C, Beierkuhnlein C, Wohlgemuth T, Penuelas J, Emmett B, Körner C, de Boeck H, Christensen JH, Leuzinger S, Janssens IA, Karin H (2012) Precipitation manipulation experiments–challenges and recommendations for the future. Ecol Lett 15:899–911. https://doi.org/10.1111/j.1461-0248.2012.01793.x

Bongers T (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83:14–19. https://doi.org/10.1007/BF00324627

Cui S, Liang S, Zhang X, Li Y, Liang W, Sun L, Wang J, Martijn Bezemer T, Li Q (2018) Long-term fertilization management affects the C utilization from crop residues by the soil micro-food web. Plant Soil 429:335–348. https://doi.org/10.1007/s11104-018-3688-4

de Bello F, Lavorel S, Hallett LM, Valencia E, Garnier E, Roscher C, Conti L, Galland T, Goberna M, Májeková M, Montesinos-Navarro A (2021) Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. Trends Ecol Evol 36:822–836. https://doi.org/10.1016/j.tree.2021.05.001

De Ruiter PC, Van Veen JA, Moore JC, Brussaard L, Hunt HW (1993) Calculation of nitrogen mineralization in soil food webs. Plant Soil 157:263–273. https://doi.org/10.1007/bf00011055

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns L (2000) Climate extremes: observations, modeling, and impacts. Science 289:2068–2074. https://doi.org/10.1126/science.289.5487.2068

Ferris H (2010) Form and function: metabolic footprints of nematodes in the soil food web. Eur J Soil Biol 46:97–104. https://doi.org/10.1016/j.ejsobi.2010.01.003

Franco ALC, Gherardi LA, De Tomasel CM, Andriuzzi WS, Ankrom KE, Shaw EA, Bach EM, Sala OE, Wall DH (2019) Drought suppresses soil predators and promotes root herbivores in mesic, but not in xeric grasslands.

Proc Natl Acad Sci USA 116:12883–12888. https://doi.org/10.1073/pnas.1900572116

Franco ALC, Guan P, Cui S, de Tomasel CM, Gherardi LA, Sala OE, Wall DH (2022) Precipitation effects on nematode diversity and carbon footprint across grasslands. Glob Change Biol 28:2124–2132. https://doi.org/10.1111/gcb.16055

Garland G, Banerjee S, Edlinger A, Miranda Oliveira E, Herzog C, Wittwer R, Philippot L, Maestre FT, van der Heijden MGA, Hector A (2020) A closer look at the functions behind ecosystem multifunctionality: a Rev. J Ecol 109:600–613. https://doi.org/10.1111/1365-2745.13511

Heisler-White JL, Blair JM, Kelly EF, Harmoney K, Knapp AK (2009) Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Glob Chang Biol 15:2894–2904. https://doi.org/10.1111/j.1365-2486.2009.01961.x

Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. Ecol Monogr 68:121–149. https://doi.org/10.1890/0012-9615(1998)068[0121:EOPCAD]2.0.CO;2

IPCC (2013) Climate Change 2013 – the physical science basis Working Group I contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 1–30. https://doi.org/10.1017/CBO9781107415324.004

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK (2002) Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205. https://doi.org/10.1126/science.1076347

Knapp AK, Beier C, Briske DD, Classen AT, Luo Y, Reichstein M, Smith MD, Smith SD, Bell JE, Fay PA, Heisler JL (2008) Consequences of more extreme precipitation regimes for terrestrial ecosystems. Bioscience 58:811–821. https://doi.org/10.1641/B580908

Landesman WJ, Treonis AM, Dighton J (2011) Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. Pedobiologia 54:87–91. https://doi.org/10.1016/j.pedobi.2010.10.002

Liao X, Fu S, Zhao J (2023) Altered energy dynamics of multitrophic groups modify the patterns of soil CO2 emissions in planted forest. Soil Biol Biochem 178:108953. https://doi.org/10.1016/j.soilbio.2023.108953

Lin X, Zhao H, Zhang S, Singh VP, Li R, Luo M, Wang S, Zhao X, Lv S, Chen X (2024) Global response of different types of grasslands to precipitation and grazing, especially belowground biomass. Agr Ecosyst Environ 363:108852. https://doi.org/10.1016/j.agee.2023.108852

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, García-Gómez M, Bowker MA, Soliveres S, Escolar C, García-Palacios P, Berdugo M, Valencia E, Gozalo B, Gallardo A, Aguilera L, Arredondo T, Blones J, Boeken B, Bran D, Conceição AA, Cabrera O, Chaieb M, Derak M, Eldridge DJ, Espinosa CI, Florentino A, Gaitán J, Gatica MG, Ghiloufi W, Gómez-González S, Gutiérrez JR, Hernández RM, Huang X, Huber-Sannwald E, Jankju M, Miriti M, Monerris J, Mau RL, Morici E, Naseri K, Ospina A, Polo V, Prina A, Pucheta E, Ramírez-Collantes DA, Romão R, Tighe M, Torres-Díaz C, Val J, Veiga JP, Wang D, Zaady E (2012) Plant species richness and ecosystem multifunctionality in global drylands. Science 335:214–218. https://doi.org/10.1126/science.1215442

Manning P, van der Plas F, Soliveres S, Allan E, Maestre FT, Mace GM, Whittingham MJ, Fischer M (2018) Redefining ecosystem multifunctionality. Nat Ecol Evol 2:427–436. https://doi.org/10.1038/s41559-017-0461-7

Moore JC, de Ruiter PC (2012) Energetic food webs: an analysis of Real and Model ecosystems. Oxford University Press, Oxford, UK. Retrieved May 8, 2024 from https://academic.oup.com/book/2389

Morriën E, Hannula SE, Snoek LB, Helmsing NR, Zweers H, de Hollander M, Soto RL, Bouffaud ML, Buée M, Dimmers W, Duyts H, Geisen S, Girlanda M, Griffiths RI, Jørgensen HB, Jensen J, Plassart P, Redecker D, Schmelz RM, Schmidt O, Schmidt O, Thomson BC, Tisserant E, Uroz S, Winding A, Bailey MJ, Bonkowski M, Faber JH, Martin F, Lemanceau P, de Boer W, van Veen JA, van der Putten WH (2017) Soil networks become more connected and take up more carbon as nature restoration progresses. Nat Commun 8:14349. https://doi.org/10.1038/ncomms14349

Neher DA (1999) Soil community composition and ecosystem processes: comparing agricultural ecosystems with natural ecosystems. Agroforest Syst 45:159–185. https://doi.org/10.1023/A:1006299100678

Neher DA (2010) Ecology of plant and free-living nematodes in natural and agricultural soil. Annu Rev Phytopathol 48:371–394. https://doi.org/10.1146/annurev-phyto-073009-114439

O'Gorman PA (2012) Sensitivity of tropical precipitation extremes to climate change. Nat Geosci 5:697–700. https://doi.org/10.1038/ngeo1568

Oostenbrink M (1960) Estimating nematode populations by some selected methods. In: Sasser JN, Jenkins WR (eds) Nematology. University of North Carolina Press, Chapel Hill, pp 85–102. Retrieved May 8, 2024 from https://scholar.google.com/scholar_lookup?title=Estimating%20nematode%20populations%20by%20some%20selected%20methods&author=M.%20Oostenbrink&publication_year=1960

Peng S, Piao S, Shen Z, Ciais P, Sun Z, Chen S, Bacour C, Peylin P, Chen A (2013) Precipitation amount, seasonality and frequency regulate carbon cycling of a semi-arid grassland ecosystem in Inner Mongolia, China: a modeling analysis. Agric Meteorol 178–179:46–55. https://doi.org/10.1016/j.agrformet.2013.02.002

Potapov AM (2022) Multifunctionality of belowground food webs: resource, size and spatial energy channels. Biol Rev 97:1691–1711. https://doi.org/10.1111/brv.12857

Potapov AM, Tiunov AV, Scheu S (2019) Uncovering trophic positions and food resources of soil animals using bulk natural stable isotope composition. Biol Rev 94:37–59. https://doi.org/10.1111/brv.12434

Potapov AM, Rozanova OL, Semenina EE, Leonov VD, Belyakova OI, Bogatyreva VY, Degtyarev MI, Esaulov AS, Korotkevich AY, Kudrin AA, Malysheva EA, Mazei YA, Tsurikov SM, Zuev AG, Tiunov AV (2021) Size compartmentalization of energy channeling in terrestrial belowground food webs. Ecology 102:03421. https://doi.org/10.1002/ecy.3421

Radu DD, Duval TP (2018) Precipitation frequency alters peatland ecosystem structure and CO_2 exchange: contrasting effects on moss, sedge, and shrub communities. Glob Chang Biol 24:2051–2065. https://doi.org/10.1111/gcb.14057

Ren H, Xu Z, Huang J, Lü X, Zeng D, Yuan Z, Han X, Fang Y (2015) Increased precipitation induces a positive plant-soil feedback in a semi-arid grassland. Plant Soil 389:211–223. https://doi.org/10.1007/s11104-014-2349-5

Schnürer J, Clarholm M, Boström S, Rosswall T (1986) Effects of moisture on soil microorganisms and nematodes: a field experiment. Microb Ecol 12:217–230. https://doi.org/10.1007/bf02011206

Schwarz B, Barnes AD, Thakur MP, Brose U, Ciobanu M, Reich PB, Rich RL, Rosenbaum B, Stefanski A, Eisenhauer N (2017) Warming alters the energetic structure and function but not resilience of soil food webs. Nat Clim Chang 7:895–900. https://doi.org/10.1038/s41558-017-0002-z

Song M, Li X, Jing S, Lei L, Wang J, Wan S (2016) Responses of soil nematodes to water and nitrogen additions in an old-field grassland. Appl Soil Ecol 102:53–60. https://doi.org/10.1016/j.apsoil.2016.02.011

Todd TC, Blair JM, Milliken GA (1999) Effects of altered soil-water availability on a tallgrass prairie nematode community. Appl Soil Ecol 13:45–55. https://doi.org/10.1016/s0929-1393(99)00022-0

Trap J, Bonkowski M, Plassard C, Villenave C, Blanchart E (2016) Ecological importance of soil bacterivores for ecosystem functions. Plant Soil 398:1–24. https://doi.org/10.1007/s11104-015-2671-6

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

Vandegehuchte ML, Sylvain ZA, Reichmann LG, de Tomasel CM, Nielsen UN, Wall DH, Sala OE (2015) Responses of a desert nematode community to changes in water availability. Ecosphere 6:1–15. https://doi.org/10.1890/es14-00319.1

Wan B, Liu T, Gong X, Zhang Y, Li C, Chen X, Hu F, Griffiths BS, Liu M (2022) Energy flux across multitrophic levels drives ecosystem multifunctionality: evidence from nematode food webs. Soil Biol Biochem 169:108656. https://doi.org/10.1016/j.soilbio.2022.108656

Wan B, Barnes AD, Potapov A, Yang J, Zhu M, Chen X, Hu F, Liu M (2024) Altered litter stoichiometry drives energy dynamics of food webs through changing multiple facets of soil biodiversity. Soil Biol Biochem 191:109331. https://doi.org/10.1016/j.soilbio.2024.109331

Wang C, Vera-Vélez R, Lamb EG, Wu J, Ren F (2022) Global pattern and associated drivers of grassland productivity sensitivity to precipitation change. Sci Total Environ 806:151224. https://doi.org/10.1016/j.scitotenv.2021.151224

Whalen JK, Kernecker ML, Thomas BW, Sachdeva V, Ngosong C (2013) Soil food web controls on nitrogen mineralization are influenced by agricultural practices in humid temperate climates. CABI Revi 8:1–18. https://doi.org/10.1079/pavsnnr20138023

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob Chang Biol 17:927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Wythers KR, Lauenroth WK, Paruelo JM (1999) Bare-soil evaporation under semi-arid field conditions. Soil Sci Soc Am J 63:1341–1349. https://doi.org/10.2136/SSSAJ1999.6351341X

Xia J, Niu S, Wan S (2009) Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe. Glob Chang Biol 15:1544–1556. https://doi.org/10.1111/j.1365-2486.2008.01807.x

Xing W, Hu N, Li Z, Feng L, Zhang W, du Preez G, Zhang H, Li D, Lu S, Chang S, Zhang Q, Lou Y (2024) Soil enzyme profile analysis for indicating decomposer micro - food web. iMeta 3:161. Retrieved August 22, 2024 from https://onlinelibrary.wiley.com/doi/10.1002/imt2.161

Yeates GW, Bongers T, De Goede RG, Freckman DW, Georgieva S (1993) Feeding habits in soil nematode families and genera-an outline for soil ecologists. J Nematol 25:315–331. https://doi.org/10.1006/jipa.1993.1100

Zhang C, Xi N (2021) Precipitation changes regulate plant and soil microbial biomass *via* plasticity in plant biomass allocation in grasslands: a meta-analysis. Front Plant Sci 12:614968. https://doi.org/10.3389/fpls.2021.614968

Zhang C, Wright IJ, Nielsen UN, Geisen S, Liu M (2024) Linking nematodes and ecosystem function: a trait-based framework. Trends Ecol Evol 39:644–653. https://doi.org/10.1016/j.tree.2024.02.002

Zhou X, Chen C, Wang Y, Xu Z, Han H, Li L, Wan S (2013) Warming and increased precipitation have differential effects on soil extracellular enzyme activities in a temperate grassland. Sci Total Environ 444:552–558. https://doi.org/10.1016/j.scitotenv.2012.12.023

Zhu B, Wan B, Liu T, Zhang C, Cheng L, Cheng Y, Tian S, Chen X, Hu F, Whalen JK, Liu M (2023) Biochar enhances multifunctionality by increasing the uniformity of energy flow through a soil nematode food web. Soil Biol Biochem 183:109056. https://doi.org/10.1016/j.soilbio.2023.109056