Geoderma 401 (2021) 115318

Contents lists available at ScienceDirect

Geoderma

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

Response of the soil food web to warming and litter removal in the Tibetan Plateau, China

Yang Wu [a,1], HuaKun Zhou [b,c,1], WenJing Chen [a], Yue Zhang [a], Jie Wang [a], HongFei Liu [d], ZiWen Zhao [a], YuanZe Li [a], QiMing You [e], Bing Yang [f], GuoBin Liu [a,g], Sha Xue [a,g,*]

[a] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Northwest A&F University, Yangling 712100, PR China
[b] Qinghai Provincial Key Laboratory of Restoration Ecology in Cold Regions, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810000, PR China
[c] State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining 810000, PR China
[d] Department of Agroecology, University of Bayreuth, Bayreuth, Germany
[e] Qunjia State Forest Farm, Huangzhong County, Xining 810000, PR China
[f] Sichuan Academy of Giant Panda, Chengdu 610041, PR China
[g] Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry Water Resources, Yangling 712100, PR China

ARTICLE INFO

Handling Editor: Diego Abalos

Keywords:
Soil nematode
Nematode metabolic footprint
Soil food web
Qinghai-Tibet Plateau
Warming and litter removal

ABSTRACT

Both climate warming and litter removal alter soil nematode communities and the structure, stability, and function of soil food webs. The soil nematode metabolic carbon footprint, based on nematode biomass and respiration, can be used to indicate ecosystem function and the response of nematodes to nutrient enrichment in the ecosystem. However, it is unclear whether or how climate warming and litter removal affect the metabolic carbon footprint of soil nematodes and soil food webs. In this study, we investigated four warming and litter removal treatments in the Qinghai-Tibet Plateau, China, to determine the effects of climate warming and litter removal on soil microbial food webs. The treatments included: (1) control (CK), (2) warming, (3) litter removal, (4) warming + litter removal. We found that warming and litter removal had significant negative effects on the diversity and richness of soil nematodes. In addition, our results showed warming indirectly and directly affected vegetation diversity, thereby altering soil nematode diversity. Vegetation played an important role in the maintenance of soil nematode community diversity. The enrichment and structural footprints reflected nematodes that could respond most rapidly to resource enrichment and those with higher trophic levels in soil food webs, respectively. Overall, warming and litter removal significantly negatively affect the enrichment metabolic footprint, indicating they could significantly reduce the external resource inputs into the food web. Both warming and litter removal reduced the structural metabolic footprint of the soil food web, although the changes were not significant, indicating that the metabolic activity of nematodes of high nutrient levels decreased and the ability to regulate the food web from top-bottom effects was weakened under warming and litter removal. The nematode functional metabolic footprints indicated that litter removal could aggravate the effect of warming on the soil food web and result in more severe degradation. The combination of warming and litter removal significantly inhibited the connectance of the bacterial channel, but had no significant effect on the fungal channel. These results suggest that the soil food web enhanced resistance to the environment by increasing the proportion of the fungal channel. It is critical to understand the responses of soil food webs to climate warming and litter removal to better predict how ecosystem functions will change in the future.

1. Introduction

Soil carbon (C) storage is roughly twice that of atmospheric CO2-C storage and five times that of plant C storage (Davidson et al., 2000), and it plays a key role in maintaining the function of terrestrial ecosystems (Schmidt et al., 2011). However, soil C storage is sensitive to

* Corresponding author at: Xinong Rd. 26, Institute of Soil and Water conservation, Northwest A&F University, Yangling, Shaanxi 712100, PR China.
E-mail address: xuesha100@163.com (S. Xue).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.geoderma.2021.115318
Received 31 January 2021; Received in revised form 13 June 2021; Accepted 18 June 2021
Available online 25 June 2021

changes in the external environment by biotic and abiotic stresses (Jackson et al., 2017). Soil nematode communities play an important role in soil C storage through indirect effects on microbial communities (Fox et al., 2006; Neher, 2010). Soil nematodes significantly affect soil C pools by stimulating microbial basic respiration (Alphei et al., 1996), changing turnover rates of SOC pools by predation (Jiang et al., 2013), and inducing plant-derived C release into soil (Wardle et al., 2004). Therefore, it is important to study soil nematodes to elucidate the accumulation and cycling of organic carbon in soil ecosystems.

Soil nematodes occupy a central position in the soil food web and include microbivorous nematodes (bacterivores and fungivores), predatory nematodes (omnivores-predators), and herbivores. These species have important ecological functions, such as nutrient cycling, decomposition, and pest and pathogen population regulation (Ekschmitt et al., 2001; Neher et al., 2012), and they have an irreplaceable role in soil ecosystems (Carrascosa et al., 2014; Sauvadet et al., 2016; Fu et al., 2017; Sechi et al., 2018; Richter et al., 2019). Nematodes contribute to the following three main pathways for carbon flows through soil food webs: (1) bacterial channel; (2) fungal channel; and (3) root channel (Guan et al., 2018). In order to better understand carbon flows through soil food webs, Ferris (2010) proposed the nematode metabolic footprint (NMF) concept to provide information on the response of carbon flows in soil food webs and their contribution to ecosystem functions. The NMF is obtained by calculating the carbon content during the nematode lifecycle (including growth and egg production) and carbon utilization in metabolic activities and dividing the sum into an enrichment footprint and a structural footprint (Ferris, 2010). The enrichment footprint shows the responsiveness to external resources, whereas the structural footprint shows the effect on metabolic activity at higher trophic levels in the food web and responses to soil food web stability (Ferris, 2010; Ferris et al., 2012; Zhang et al., 2015). Consequently, soil nematode metabolic footprints are increasingly often used to reflect the carbon flow in the soil food web (Ferris, 2010; Guan et al., 2018; Wu et al., 2021).

Global warming has increased since the industrial revolution because of the combustion of fossil fuels, and the potential environmental effects have garnered research attention (Edenhofer and Seyboth, 2013). Soil organic carbon pools are known to be sensitive to warming (Li et al., 2018, 2020). Warming leads to the loss of soil carbon pools and causes changes in carbon flows by stimulating microbial activity, enhancing soil enzyme activity, and degrading the labile carbon pool (Li et al., 2018). The decomposition of soil organic matter mainly depends on complex biological and physicochemical interactions, but biochemical reactions are strongly regulated by temperature; this regulation is affected by several other factors, leading to uncertainties in the response of different ecosystems to climate warming (Nottingham et al., 2019). Previous studies have found that climate warming significantly affects the diversity of vegetation (Jin et al., 2020; Li et al., 2020), decomposition of litter (Chuckran et al., 2020), and underground microbial communities (Van Nuland et al., 2020; Zhang et al., 2020; Chen et al., 2021), thus affecting the soil carbon pool (Johnson et al., 2020; Tian et al., 2021). However, as nematodes play a role in linking the food web and heterogeneity of different environments, the impact of warming on soil nematode communities is still uncertain (Thakur et al., 2014, 2017b; De Long et al., 2016).

The C content (60 Tg C y^{-1}) released by litter is 11 times higher than that by fossil fuels at the global scale, and is one of the important sources of soil C pool (Walker, 1991). The changes in the quality and quantity of plant litter input cause changes in the decomposition of litter, which has a substantial effect on the dynamics of soil C pools (Wu et al., 2018). A previous study reported that aboveground litter is crucial for energy flow in the soil (Attiwill and Adams, 1993). Litter removal reduces the substrates available for microbes, thereby affecting the biochemical processes in the soil, leading to changes in the distribution of soil C (Leff et al., 2012; Philippot et al., 2013). Litter also has a clear effect on the soil microbial community (Fisk and Fahey, 2001; Marichal et al., 2011; Li et al., 2021). However, the interactive effects between warming and litter removal on nematode communities and C flow in the soil food web based on the nematode metabolic footprint are still unclear.

In this study, we examined how warming and litter removal in the Qinghai-Tibet Plateau in China could affect the soil nematode food web and carbon flow. We hypothesized the following: 1) warming and litter removal significantly decrease the abundance and diversity of soil nematode communities; and 2) warming promote carbon flow in the food web based on the nematode metabolic footprint; litter removal inhibit carbon flow in the food web based on the nematode metabolic footprint.

2. Material and methods

2.1. Site description

The study area is located in the Haibei Research Station (37°36′ N, 101°19′ E, 220 m above sea level), which is situated in Haibei, Qinghai, China, on the northeastern Qinghai-Tibet Plateau. The mean annual temperature is −1.7 °C (ranging from −15.2 °C to 9.9 °C), average annual rainfall is 561 mm, and the growing season is from May to September (Chen et al., 2020). The main soil type is Mollic-Cryic Cambisol (Zhao and Zhou, 1999). Plant communities mainly consist of Kobresia humilis, Festuca ovina, Elymus nutans, Poa pratensis, Carex scabrirostris, Scripus distigmaticus, Gentiana straminea, G. farreri, Leontopodium nanum, Blysmus sinocompressus, Potentilla nivea, and Dasiphora fruticose (He et al., 2006).

2.2. Experimental design and soil sampling

The research site is located in an alpine meadow community, dominated by *K. humilis*. In 2011, we fenced areas on slopes <1° and used fiberglass open top chambers (OTCs) to simulate the effects of climate warming on ecosystems. The bottom diameter of each OTC was 2.05 m, the top diameter was 1.60 m, and height was 1.5 m. OTCs were constructed with Sun-Lite HP 1.0 mm thick fiberglass (Solar Components Corporation, Manchester, NH, USA) (Zhang et al., 2017). During the growing season, the OTCs increased the average daytime temperature by 1.58 °C-5.24 °C and average nighttime temperature by 1.22 °C-4.28 °C at a height of 0.1 m from the ground. Therefore, we compared removing the effects of dead leaves with and without warming. We removed dead leaves from the ground in April or early May every year by hand picking. There were four treatments, namely, control (CK), warming, litter removal, and warming + litter removal, and each of the four treatments was set up with five replicate plots. All plots were randomly distributed to avoid experiment error.

Soil samples were collected in August 2018, and 10 samples were randomly collected in each plot using a 5-cm diameter soil drill. After mixing the samples from each plot and removing excess roots and stones, soil samples were passed through a 2-mm screen and divided into two parts. One part was placed in liquid nitrogen to transport to the laboratory and stored at −80 °C until further analysis of the microbes. The other part was maintained at 4 °C and transported to the laboratory. In the laboratory, we divided the soil maintained at 4 °C into two parts; one part was stored in a refrigerator at 4 °C for the analysis of soil nematodes and the other part was air dried naturally and then sieved into 1-mm and 0.25-mm samples for the analysis of soil properties.

2.3. Physical and chemical analyses of soil

Soil organic carbon and soil total N content was measured using the H_2SO_4-$K_2Cr_2O_7$ oxidation and Kjeldahl methods, respectively (Bremner and Mulvaney, 1982). Soil total P concentration was measured using colorimetric analysis after digestion with H_2SO_4 and $HClO_4$(Olsen et al., 1982). Soil available P was extracted using 0.5 M $NaHCO_3$ at pH 8.5 and measured colorimetrically using a UV spectrophotometer and the

molybdate-ascorbic acid method. Soil moisture content was determined at 110 °C for 10 h. Soil ammonium (NH + 4-N) and nitrate N (NO-N) were filtered using 2.0 mol/L KCl and measured using a flow injection autoanalyzer (Table 1).

2.4. Soil fatty-acid analysis (PLFAs and NLFAs)

We used a solution of citrate buffer, chloroform, and methanol to extract fatty acids from 3.0 g of lyophilized soil (Zelles, 1999). The NLFAs and PLFAs were separated from the neutral and glycolipid fatty acids by solid phase extraction chromatography and analyzed using a gas chromatograph (GC7890A, Agilent Technologies, USA) equipped with MIDI Sherlock software (Microbial ID, Inc., Newark, USA). Quantification was performed using an external standard of 19:0 methyl ester. We used iso- and anteiso-branched fatty acids and monounsaturated fatty acids as indicators of gram-positive and gram-negative bacteria, respectively. The indicators of gram-positive bacteria were i14:0, i15:0, a15:0, i16:0, a16:0, i17:1, and a17:0. The indicators of gram-negative bacteria were 16:1 ω9c, 16:1 ω7c, i17:1 ω9c, 17:1 ω8c, 18:1 ω7c, 18:1 ω5c, cy17:0 ω7c, and cy19:0 ω7c. The lipid 18:2w6c was used as an indicator of fungal PLFAs, whereas 16:1 ω5c was used as an indicator of arbuscular mycorrhizal fungi (AMF) PLFAs. The lipids 16:0 10-methyl, 17:0 10-methyl, and 18:0 10-methyl indicated actinomycetes. In addition, we used the sum of gram-positive bacteria (G^+), gram-negative bacteria (G^-), and 14:0, 15:0, 16:0, 17:0, 18:0, and 20:0 as total bacteria (Mckinley et al., 2005; Bach et al., 2010; Guan et al., 2018). Here, 363.6 nmol PLFA = 1 mg bacterial biomass carbon; 11.8 nmol PLFA = 1 mg fungal biomass carbon; and 1.047 nmol neutral lipid fatty acid = 1 μg AMF biomass carbon (Olsson et al., 1995; Vries et al., 2013).

2.5. DNA extraction, amplification, sequencing, and processing of sequencing data

To extract the DNA sequence, 0.25 g of frozen soil was analyzed using a Power Soil DNA Isolation kit (MO BIO Laboratories). We used a NanoDrop 2000 spectrophotometer (Thermo Scientific, Waltham, MA, USA) and 1% agarose gel electrophoresis to check DNA concentration, purity, and quality; the purified DNA was stored at −80 °C until further assay and processing. The bacterial 16S rRNA gene (V3-V4 region) was amplified using PCR with the following universal primer pair: forward primer *338F* (5′-ACTCCTACGGGAGGCAGCA-3′) and reverse primer *806R* (5′-GGACTACHVGGGTWTCTAAT-3′) (Yu et al., 2019). The ITS region of the ribosome was used as the universal primers for fungi: forward primers *ITS1F* (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and reverse primer *ITS2-2043R* (5′-GCTGCGTTCTTCATCGATGC-3′) (Yan et al., 2017). The total volume of the PCR mixture was 50 μL, containing 0.2 μL of High-Fidelity DNA Polymerase, 10 μL of High GC Enhancer, 1 μL of dNTP, 10 μM of each primer, and 60 ng of genome DNA. We then adjusted the volume of the system to 50 μL with ddH_2O. The PCR thermal cycling conditions (bacteria and fungi) were as follows: 98 °C for 5 min for initial denaturation; 25 cycles at 98 °C for 1 min, 50 °C for 1 min, and 72 °C for 1 min; final extension at 72 °C for 7 min. On the basis of the first PCR, we conducted a second PCR. The total volume of the PCR mixture was 40 μL, containing 20 μL of 2 × Phusion HF MM, 8 μL of ddH_2O, 10 μM of each primer, and 10 μL of PCR products from the first step. The PCR thermal cycling conditions were as follows: 98 °C for 30 s for initial denaturation; 10 cycles at 98 °C for 10 s, 65 °C for 30 s, 72 °C for 30 s; and final extension at 72 °C for 5 min. We used the QIAquick gel extraction kit (Qiagen, Germany) to purify the products and Quant-iT™ dsDNA HS Reagent to quantify PCR products of the two rounds; the products were then pooled.

The high-throughput sequencing analysis of bacteria and fungi was performed with the purified pooled sample using the Illumina Hiseq 2500 platform (2 × 250 paired ends) at Biomarker Technologies Corporation, Beijing, China. We used the QIIME quality control process to obtain high-quality clean tags from raw tags and combined the same barcode into the same sample (Bokulich et al., 2013). Bacterial and fungal tags were compared with reference databases (Gold database, http://drive5.com/uchime/uchime_download.html; and Unite database, https://unite.ut.ee/, respectively) using the UCHIME algorithm to detect chimera sequences. The chimera sequences were removed to obtain the effective tags (Chen et al., 2020; Wang et al., 2019). The sequences were clustered using UPARSE software and assigned to OTUs at similarities of 97%. Bacterial taxonomy was identified using the Silva reference database (http://www.arb-silva.de) via the RDP classifier. The fungi were identified using the Unite database (https://unite.ut.ee/) with the BLAST tool and QIIME software (http://qiime.org/index.html). A total of 389 genera of bacteria and 238 genera of fungi were identified.

2.6. Soil nematode community analysis

We used the modified Baermann funnel method (Ingham and Santo, 1994) to extract soil nematodes from a sample of fresh soil (100 g). After the nematodes were killed at 60 °C and fixed with triethanolamine formalin, they were transferred to flame slides and observed and counted using an inverted compound microscope. Then, 100 specimens were randomly chosen from fixed soil nematodes and the genera were identified using the method developed by UNL Nematode Laboratory (https://nematode.unl.edu/nemakey.htm)(Bongers, 1988). The Shannon diversity index (H') and Margalef index (SR) were calculated based on the following formulas: $\acute{H} = -\Sigma P_i \ln P_i$ and SR= (S-1)/logN to response diversity and richness of the community. Owing to the different characteristics of soil nematode, r- and K-selection characteristics, soil nematodes were divided into a 1–5 colonizer-persister (c-p) scale. On the basis of this scale, nematodes were divided into four trophic groups, namely, plant parasites (Ppx), bacterivores (Bax), fungivores (Fux), and

Table 1
Soil physicochemical and vegetation properties.

	Treatments (means ± standard error)				W	RL	W × RL
	CK(n = 5)	W (n = 5)	RL (n = 5)	WRL (n = 5)			
SOC	150.29 ± 19.85	164.97 ± 22.76	148.37 ± 26.03	193.88 ± 72.60	0.08	0.42	0.35
TN	7.98 ± 0.49a	4.31 ± 3.14ab	3.75 ± 3.44b	8.52 ± 1.61a	0.63	0.99	0.002**
TP	0.62 ± 0.13b	0.76 ± 0.06ab	0.67 ± 0.22ab	0.86 ± 0.15a	0.03*	0.27	0.69
AP	20.82 ± 4.04	23.82 ± 4.33	20.11 ± 4.14	18.15 ± 7.28	0.82	0.18	0.29
NO_ 3-N	23.47 ± 3.15	22.46 ± 4.03	39.39 ± 29.35	27.22 ± 5.48	0.35	0.15	0.43
NH + 4-N	128.88 ± 13.09ab	153.48 ± 53.76a	97.80 ± 33.50b	87.96 ± 25.81b	0.64	0.009**	0.29
pH	7.76 ± 0.19	7.96 ± 0.08	7.92 ± 0.16	7.79 ± 0.38	0.74	0.98	0.13
Vegetation diversity	3.10 ± 0.07a	2.76 ± 0.09b	3.01 ± 0.14a	2.65 ± 0.29b	0.0006**	0.2	0.91
Vegetation abundance	25.60 ± 3.29ab	23.40 ± 3.51b	29.00 ± 4.30a	23.80 ± 1.10b	0.03*	0.22	0.33

* $P < 0.05$ ** $P < 0.01$

Note: CK, control; W, Warming; LR, Litter removal; WLR, Warming + Litter removal; Soil organic carbon, SOC(g·kg-1); Soil total nitrogen, TN(g·kg-1); Soil total phosphorus, TP(g·kg-1); Available phosphorus, AP(mg·kg^{-1}); NO_ 3-N, Nitrate nitrogen(mg·kg^{-1}); NH + 4-N, Ammonium nitrogen(mg·kg^{-1}). Different letters in table indicate significant difference *($P < 0.05$)* by the ANOVA and Tukey's multiple test, and used mixed linear model to response warm and grazing effect.

omnivores/predators (OPx), where x = 1–5 on the c-p scale. A value of 1–2 represented low trophic level nematodes, while 3–4 indicated high trophic level nematodes (Yeates et al., 1993).

The formula for enrichment index (EI) and structural index (SI) were as follows: EI = 100 × e/(b + e) and SI = 100 × s/(b + s), where b, e, and s represent the abundance of individuals in guilds in the basal component (Ba_2 and Fu_2), enrichment component (Ba_1 and Fu_2), and structural component (Ba_3-Ba_5, Fu_3-Fu_5, and OP_3-OP_5) weighted by their kb, ke, and ks values, respectively (Ferris et al., 2001). The formula for the carbon content in nematode biomass was 52% × 20% Wt/100 (μg g-1), where Wt represented the fresh weight of soil nematodes (the dry weight of soil nematodes was 20% of the fresh weight, and the carbon content in nematodes was 52% of the dry weight) (Ferris, 2010). The nematode metabolic footprints (NMF) was the amount of carbon and energy entering the soil food web represented by the formula, NMF = Σ [Nt (0.1 wt/mt + 0.273 (W0.75)], where Nt represents the number of individuals in the genus t, wt and mt represent the body weight and c-p values of the genus t, respectively (Ferris et al., 2012). The NMF was divided into enrichment footprints (Ba_1 and Fu_2) and structural footprints (Ba_3-Ba_5, Fu_3-Fu_5, and OP_3-OP_5). The enrichment footprints indicated the degree of response of soil nematodes to inputs from external resources and the structural footprints indicated nematode metabolic activity at higher trophic levels in the food web (Ferris et al., 2012; Zhang et al., 2015). For the nematode functional metabolic footprint (FMF), the structural index and enrichment index were presented on the x-axis and y-axis, respectively; they were depicted by joining sequential points, i.e., (SI-0.5sfoot/k, EI), (SI + 0.5sfoot/k, EI), (SI, EI-0.5efoot/k), and (SI, EI + 0.5efoot/k). The adjusted k value was 1.

Connectance indicates the degree of co-occurrence between the predator and the prey in each food web channel (Sanchez-Moreno et al., 2011; Ferris et al., 2012). We assumed that the contact between the predator and the prey in the food web was not hindered. We used high-throughput sequencing analysis to obtain numbers of bacteria and fungi genera. The numbers of bacteria and fungi prey and of bacterivore and fungivore predators were used to calculate the bacterial channel and fungal channel, respectively. The omnivore–predator channel used bacterivores and fungivores as prey and omnivores–predators as predators in calculations. The parameters a and b represented the number of occurrences of predator and prey in each replication, S = ab; A and B indicated the number of occurrences of all replication predators and prey in a treatment, F = AB. Connectance = S/F (Ferris et al., 2012; Wu et al., 2021).

2.7. Statistical analysis

We used SPSS 20.0 (SPSS, Inc., Chicago, IL, USA) to perform the one-way ANOVA with Tukey's multiple comparisons test ($P < 0.05$) to analyze soil physicochemical and vegetation properties, nematode diversity index, soil nematode metabolic footprints, nematodes abundance, soil microbial and nematode biomass carbon and connectance of nematodes channels and used the mixed linear model to evaluate the response effect of warming and litter removal using the R package "lme4." In this model, warming (YES/NO) and litter removal (YES/NO) and their interaction was treated as fixed factors; block was treated as a random factor. The response variables of the mixed linear model were soil physicochemical and vegetation properties, nematode diversity index, nematode metabolic footprints, nematode relative abundance, soil microbial and nematode biomass carbon and connectance *($P < 0.05$)*. We used partial least squares path modeling (PLSPM) to evaluate the response relationship among soil nutrient, vegetation, and nematodes using the R package "PLSPM." The multi-response permutation procedure (MRPP) based on a group distance to the mean within the group mean of a randomly assigned group was used to examine differences in soil nematode community composition (Weand et al., 2010). Principal coordinates analysis (PCoA) was performed using R packages "FactoMineR" and "factoextra," and the MRPP significance test was performed using the R "vegan" package to indicate differences in the composition of the nematode genus. To identify the relative importance of bacterial diversity, fungal diversity, and soil properties in explaining variations in soil nematodes diversity, variation partitioning analysis (VPA) was conducted using the redundancy analysis (RDA) with the varpart function in the "vegan" package in R.

3. Results

3.1. Nematode community composition and diversity

A total of 38 nematode genera were detected in the soil under the four different treatment combinations (Table S1). Warming negatively affected the relative abundance of bacterivores (Table S2, $P < 0.05$). The abundance of other nematodes did not change significantly (Table S2). Warming negatively affected the SR index and Shannon-Wiener index (Table 2, $P < 0.05$). The results of the PCoA showed that warming and litter removal did not significantly change the nematode community composition; PCoA1 accounted for 17.18% of the variance, whereas PCoA2 accounted for 11.87% (Fig. 1, MRPP, $P = 0.231$).

3.2. Soil microbial and nematode biomass carbon and metabolic footprints

Both warming and litter removal significantly reduced the biomass carbon values in bacterivores (Table S3, $P < 0.05$). The biomass carbon values in bacteria, fungus, fungivores, herbivores, and omnivores-predators were not significantly affected by the treatments (Table S3, $P < 0.05$). Warming and litter removal negatively affected the nematode enrichment metabolic footprint (Table 3, $P < 0.05$). Warming, litter removal and the interaction effect of warming and litter significantly affected the bacterivore metabolic footprint (Table 3, $P < 0.05$). Litter removal had much stronger effect on bacterivore metabolic footprint under ambient temperatures conditions than under warming conditions (Table 3, $P < 0.05$). The structural footprint, fungivore footprint, and omnivore footprint did not significantly change in response to warming and litter removal (Table 3, $P < 0.05$). The nematode functional metabolic footprint (FMF) of the control was significantly greater than that of the other treatments (Fig. 4, $P < 0.05$). The interaction effect of warming and litter removal significantly affected the connectance of the bacterial channel. Under litter removal conditions, warming has a positive effect, while under control conditions warming has a negative effect (Fig. 5, $P < 0.05$). Warming negatively affected the connectance of the omnivore–predator channel (Fig. 5, $P <$ 0.05). The connectance of the fungal channel was not significantly different among the treatments (Fig. 5).

Table 2
Nematode diversity index under different treatments.

	Treatments (means ± standard error)				W	LR	W × LR
	CK(n = 5)	W (n = 5)	LR (n = 5)	WLR (n = 5)			
SR Index	3.91 ± 0.20	3.42 ± 0.75	4.01 ± 0.65	3.36 ± 0.44	0.03*	0.34	0.51
Shannon-Wiener Index	2.33 ± 0.16	1.91 ± 0.25	2.34 ± 0.16	2.31 ± 0.17	0.04*	0.06	0.07

* $P < 0.05$ ** $P < 0.01$
Note: CK, control; W, Warming; LR, Litter removal; WLR, Warming + Litter removal; Different letters in table indicate significant difference *($P < 0.05$)* by the ANOVA and Tukey's multiple test, and used mixed linear model to response warm and grazing effect.

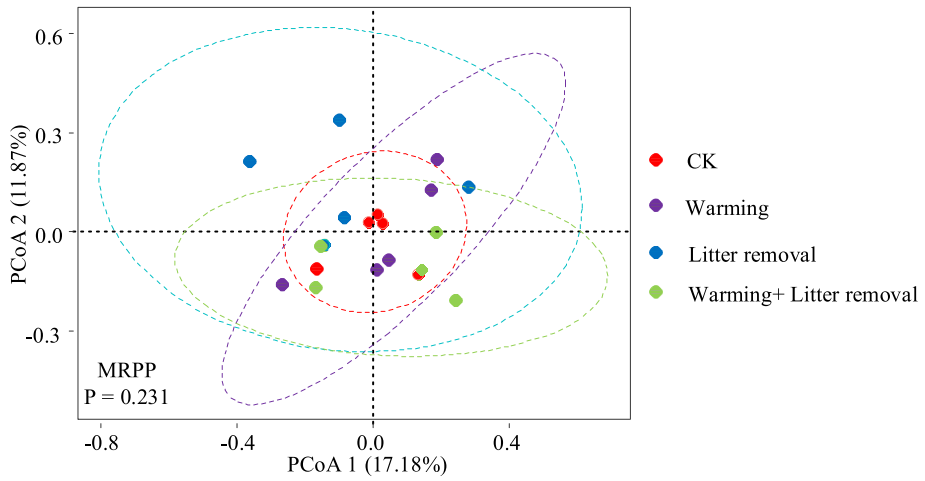

Fig. 1. PCoA of nematode genus composition under different treatments.

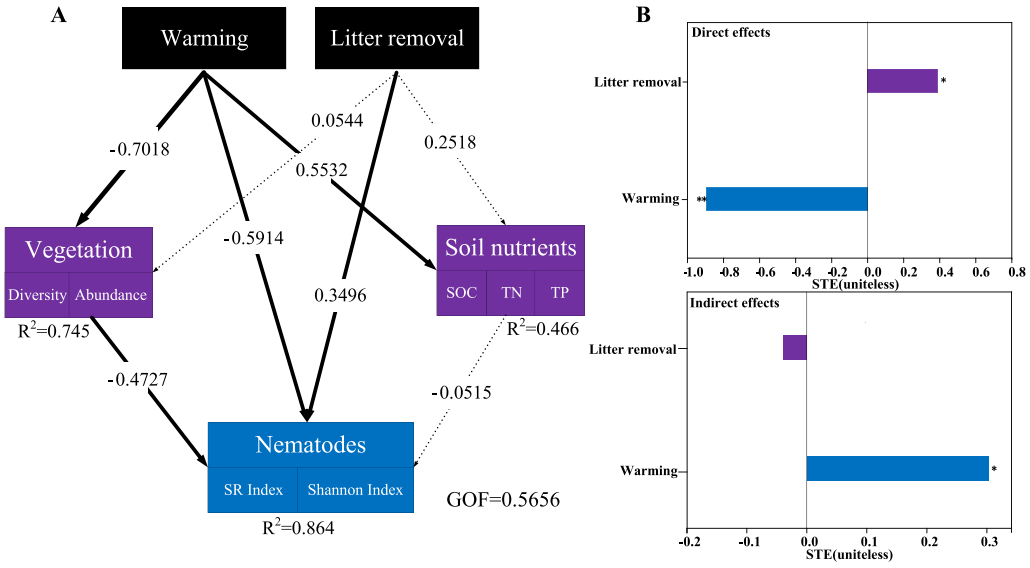

Fig. 2. A the Partial Least Squares Path Modeling (PLSPM) of soil nutrient, vegetation, and nematode. Solid thick arrows indicate a significant difference ($P < 0.05$). B Standardized direct and indirect effect of warming and Litter removal on nematodes (* $P < 0.05$, ** $P < 0.01$).

3.3. Factors controlling soil nematode community and soil micro-food webs

The results of the PLSPM showed that warming significantly negatively affected vegetation diversity ($R^2 = 0.745$) and nematode diversity ($R^2 = 0.864$). Warming significantly positively affected soil nutrients ($R^2 = 0.466$). Litter removal significantly positively affected soil nematode diversity. Vegetation significantly negatively affected nematode diversity (Fig. 2A). Among the factors tested in this study, warming had the largest direct and indirect effect on nematode diversity (Fig. 2B). The VPA showed that bacterial diversity, fungal diversity, and soil properties explained 12%, 13%, and 67% of nematode diversity variations, respectively, in non-warming sites (Fig. 3A). In warming sites, bacterial diversity, fungal diversity, and soil properties explained 20%, 27%, and 47% of nematode diversity variations, respectively (Fig. 3B). In non-litter removal sites, bacterial diversity and soil properties explained 66% and 17% of nematode diversity variation, respectively (Fig. 3C). In litter removal sites, bacterial diversity and soil properties explained 21% and 35% of nematode diversity variation, respectively (Fig. 3D).

4. Discussion

4.1. The effect of warming and litter removal on the soil nematode community.

The response of soil nematode communities as indicator taxa of climate warming has garnered extensive attention (Mueller et al., 2016; Schwarz et al., 2017; Ma et al., 2018). However, the effect of warming on soil nematode communities remains uncertain. Some studies have reported that warming may not cause changes in soil nematode communities, including in community structure and nematode abundance (Thakur et al., 2014; De Long et al., 2016). However, our results showed that warming may significantly lower soil nematode diversity and reduce the relative abundance of bacterivores. Several studies have reported that the changes in nematode communities and abundance may be underlain by changes in vegetation and soil nutrients caused by warming (Ruess et al., 1999; Mueller et al., 2016; Thakur et al., 2017a). However, in our study, although warming had significant negative and positive effects on soil total phosphorus, vegetation diversity and abundance, and PLSPM showed that warming has a significant positive effect on soil nutrients, soil nutrients had no significant effects on soil

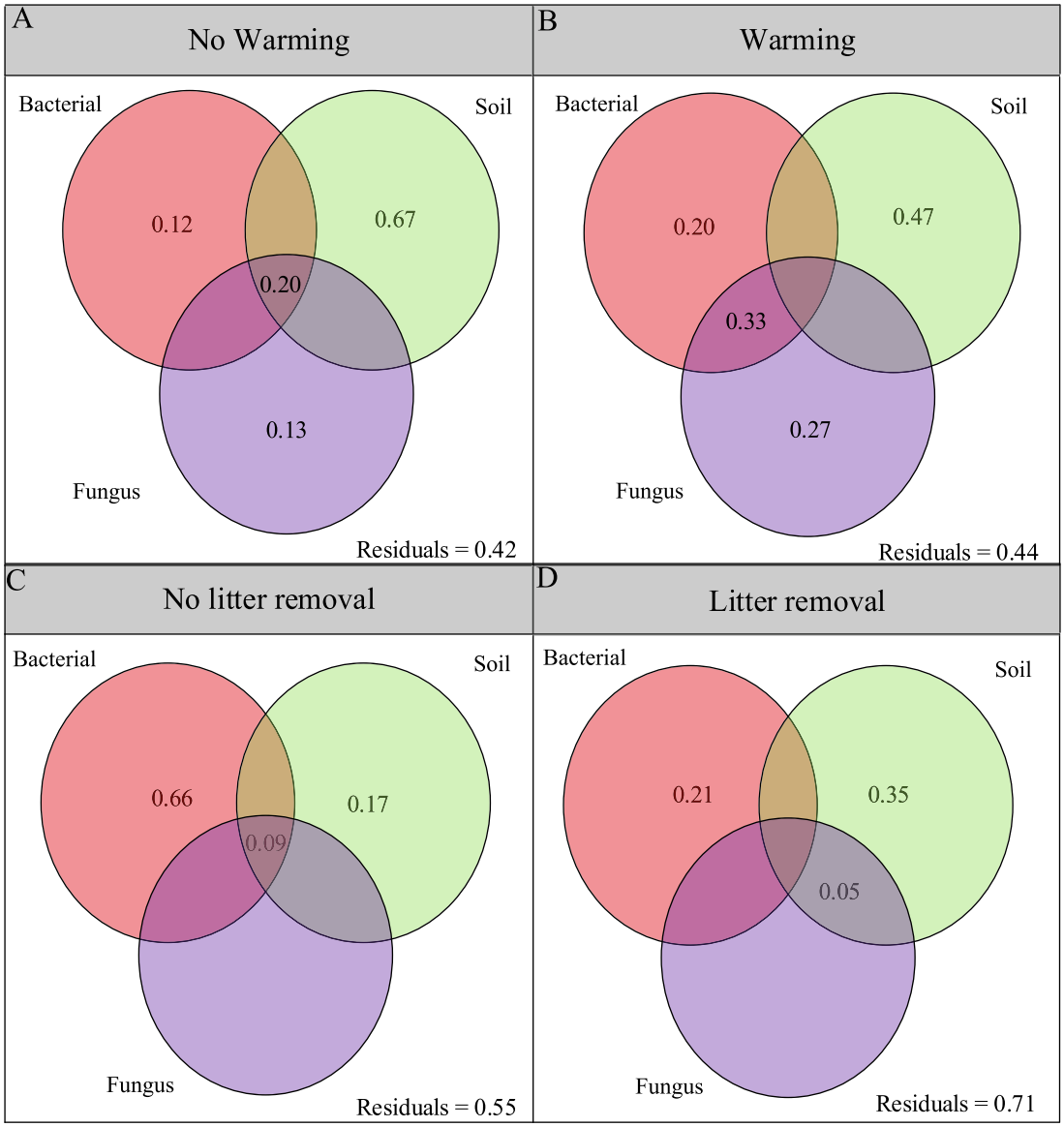

Fig. 3. Variation partitioning analysis (VPA) showing the effects of bacterial diversity, fungal diversity and soil on nematode diversity under unremoved litter and removed litter. Soil properties include SOC, total soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; NO_ 3-N: nitrate nitrogen; NH + 4-N: ammonium nitrogen and pH.

Table 3
Soil nematode metabolic footprints under different treatments (μg C kg^{-1}soil).

	Treatments (means ± standard error)				W	LR	W × LR
	CK(n = 5)	W (n = 5)	LR (n = 5)	WLR (n = 5)			
Enrichment footprint	9.40 ± 4.57a	2.08 ± 2.85ab	3.59 ± 3.41ab	1.09 ± 0.55b	0.005**	0.03*	0.12
Structure footprint	20.14 ± 10.46	16.32 ± 12.35	13.83 ± 11.74	27.54 ± 15.26	0.4	0.67	0.15
Herbivore footprint	26.92 ± 19.84	13.17 ± 12.93	8.63 ± 3.79	14.77 ± 8.35	0.52	0.17	0.11
Bacterivore footprint	14.08 ± 6.23a	4.59 ± 2.52b	5.58 ± 3.58b	3.19 ± 1.59b	0.004**	0.01*	0.05*
Fungivore footprint	1.45 ± 0.80	1.16 ± 1.32	1.62 ± 1.11	1.29 ± 0.95	0.52	0.76	0.97
Omnivore and Predators footprint	19.71 ± 10.91	15.57 ± 12.67	12.55 ± 11.27	27.23 ± 15.24	0.37	0.70	0.12

*p < 0.05 ** p < 0.01
Note: CK, control; W, Warming; LR, Litter removal; WLR, Warming + Litter removal; Different letters in table indicate significant difference (P < 0.05) by the ANOVA and Tukey's multiple test, and used mixed linear model to response warm and grazing effect.

nematode communities. Thus, our results suggest that warming has direct and indirect effects on soil nematode communities through negative changes in vegetation diversity.

The feedback between nematodes and vegetation has become a research hotspot (Wilschut and Geisen, 2020). Some studies have confirmed that plants play an important top-down role in changing soil nematode communities (Shao et al., 2012; Nico et al., 2013; Zhang et al., 2015). However, we found that warming and litter removal had significant negative effects on the carbon biomass of bacterivores, but limited effect on the carbon level of soil nematodes of high nutrient levels. This

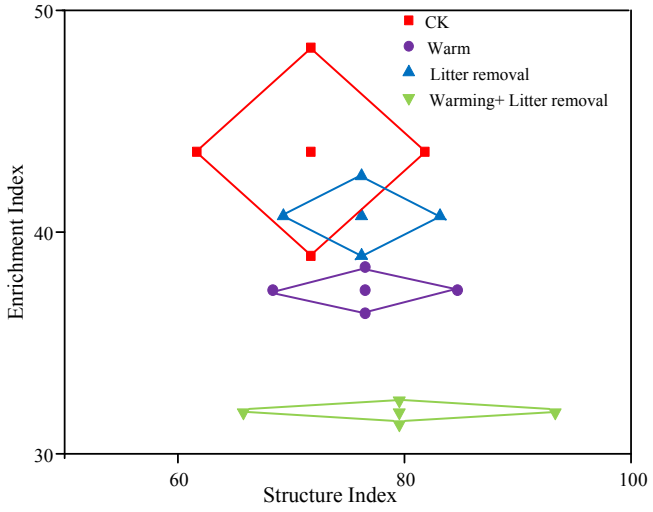

Fig. 4. Functional metabolic footprints of nematode communities under different treatment. The functional metabolic footprint is depicted by the sequentially joining points: (SI-0.5sfoot/k, EI); (SI + 0.5sfoot/k, EI); (SI, EI-0.5efoot/k); and (SI, EI + 0.5efoot/k). The adjusted k value is 1.

indicated that the top-down control ability of high-nutrient nematodes on vegetation is weak, consistent with the findings of Yan et al. (2020). The study suggested vegetation mainly affected nematodes with low nutrient levels in soil and changed nematode communities with high nutrient levels through nutritional cascade effects (Zhang et al., 2015). However, it is surprising that combined warming and litter removal effects significantly inhibited vegetation diversity and abundance but had no effect on nematode community diversity. This may be because although the supply of soil nutrients is reduced by litter removal, warming increased soil microbial metabolic activity (Bradford et al., 2008; Leff et al., 2012; Philippot et al., 2013; Sun et al., 2019). We observed that combined warming and litter removal effects increased the carbon biomass of bacteria and fungi. Due to the bottom-up effect of the soil food web, the stability of soil nematode diversity was maintained. The VPA test confirmed this result. After warming, the effect of soil microbial diversity on nematodes diversity increased; the effect of soil nutrients on nematode diversity decreased. Thus, our results indicated that the soil nematode diversity can be maintained stable by removing litter under climate warming in the future.

4.2. The effect of warming and litter removal on the nematode microbial food web and metabolic footprint

The nematode enrichment metabolic footprint is an indicator of the external resources entering the soil ecosystem that affect the soil food web (Ferris et al., 2012). In our study, warming and litter removal negatively affected the enrichment metabolic footprint, indicating that both warming and litter removal would significantly reduce the external resource inputs into the food web. First, warming and litter removal significantly reduce vegetation biomass and diversity, which lead to a decrease in the soil nutrient input (Leff et al., 2012; Philippot et al., 2013). In addition, the acceleration of soil biochemical reactions caused by warming accelerates the degradation of soil organic compounds (Davidson and Janssens, 2006; Hopkins et al., 2012; Blagodatskaya et al., 2016), resulting in a decline in soil nutrient content. The structural metabolic footprint generally reflects the net resource output of the food web and the metabolic activity of the higher trophic level nematodes, which typically have a regulatory role in the food web and stability of the soil food web (Ferris et al., 2012; Zhang et al., 2015). Warming and

	Warm	Litter removal	Warm× Litter removal
Bacterial channel	0.19	0.35	0.0003**
Fungal channel	0.23	0.72	0.09
Omnivore-Predator channel	0.04*	0.26	0.42

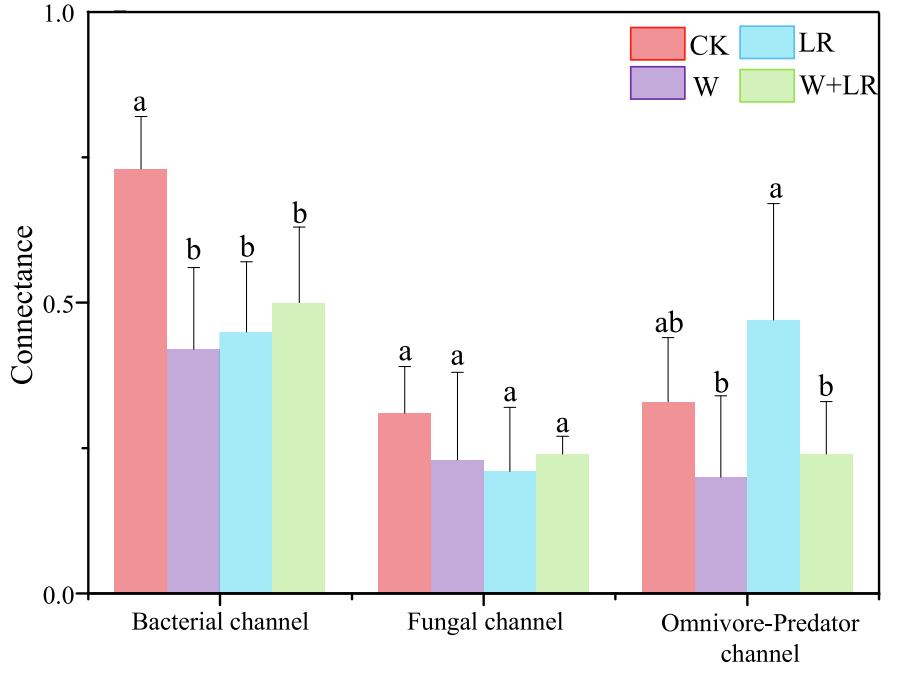

Fig. 5. Connectance of nematodes channels under different treatment. W: Warming; LR: Litter removal; W + LR: Warming + Litter removal. Different letters indicate a significant difference ($P < 0.05$) by the ANOVA and Tukey's multiple testand used mixed linear model to response warm and grazing effect. The values are means ± standard error.

litter removal reduced the structural metabolic footprint of the soil food web. Although the changes were not significant, the results showed that the metabolic activity of omnivores and predators in the food web decreased under warming and litter removal. Therefore, with the combined warming and litter removal, the regulatory effect of the soil food web weakened, and the food sources became more unstable.

The nematode functional metabolic footprint (FMF) is the total area of the two functional footprints (enrichment and structure) indicating the input of carbon resources in the food web (Ferris, 2010; Zhang et al., 2012, 2015). Our results showed that warming and litter removal had negative effects on the FMF. A larger FMF indicated that more carbon was input into the soil food webs. In this study, warming and litter removal reduced the amount of carbon entering the soil food web. Several researchers have used the FMF to reflect the basic information about the degree of degradation of the soil food web (Berkelmans et al., 2003; Ferris et al., 2012; Wu et al., 2021. Warming and litter removal had higher structural indexes and lower enrichment indexes, indicating that the nutrient enrichment of the soil food web worsened and that the food web tended towards fungal degradation channels, resulting in greater instability. Under the combined warming and litter removal, the enrichment of nutrients in the soil food web would become more difficult, and the food web would degrade. Therefore, we concluded that litter removal would aggravate the effect of warming on the soil food web, resulting in more severe degradation of the soil food web.

4.3. Effect of warming and litter removal on carbon flows in the soil food web

Climate warming and litter removal change the interactions between prey and predators, thus affecting the structure and function of the soil food web (Woodward et al., 2010; Fussmann et al., 2014; Thakur et al., 2014). Therefore, the connectivity between predator and prey can act as an indicator to reflect the stability of the soil food web. We used connectance to reflect the relationship between prey and predators in the soil food web. These were considered to be a measure of different nutrient channels, thereby reflecting the connectivity in different channels (Sanchez-Moreno et al., 2011; Guan et al., 2018). Generally, we expected that the metabolic activity was significantly positively correlated with warming, and the substrate would affect the metabolic activity of soil microorganisms to some extent (Stone et al., 2012; Qi et al., 2016; Ma et al., 2017). Therefore, warming would promote connectivity between predator and prey, and litter removal would inhibit the connectivity. However, we found that the combined warming and litter removal significantly positively inhibited connectance of the bacterial channel, but maintained connectivity of the fungal channel; warming significantly positively promoted the connectance of the omnivore-predator channel. Other studies have found that fungal channel was more likely to have stronger resistance to external conditions than the bacterial channel (de Vries et al., 2012; Andres et al., 2016). Therefore, our results were possibly because warming and litter removal increased the proportion of the fungal channel in the food web, thereby improving stress resistance of the food web.

5. Conclusions

In our study, climate warming significantly reduced soil nematode diversity. However, litter removal mitigated the effect of warming on the diversity of nematode communities. The maintenance of nematode diversity was significantly related to surface vegetation. However, we found that vegetation had a greater effect on nematodes with lower nutrient levels than on those with higher nutrient levels. In addition, our results indicated that both warming and litter removal significantly reduced the external resource inputs into the food web and decreased the metabolic activity of omnivores and predators in the food web, leading to food web degradation. With combined warming and litter removal, the nutrient enrichment of the soil food web became worse, and the food web tended towards fungal degradation channels. Furthermore, we concluded that warming and litter removal directly and indirectly affect vegetation diversity, thus affecting soil nematode community diversity, and that litter removal would aggravate the effect of warming on the soil food web, resulting in more severe degradation. Therefore, in the context of global warming, reducing mowing and grazing is conducive to the maintenance of soil ecosystems and functions. This study provides a deeper understanding of the ecosystems and functions through the soil food web with combined warming and litter removal under global climate warming.

Declaration of Competing Interest

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

Acknowledgements

Funding: This work was supported by the Qinghai innovation platform construction project by Chinese Academy of Sciences (2021- ZJ-Y01), Joint Research Project of Three-River- Resource National Park funded by Chinese Academy of Sciences and Qinghai Provincial People's Government (LHZX-2020-08), the Fundamental Research Funds for the Central Universities (2452021165), the Science Fund for Distinguished Young Scholars of Shaanxi Province, China (2021JC-50) and Qinghai Provincial Key Laboratory of Restoration Ecology in Cold Regions, Northwest Institute of Plateau Biology (2020-KF-04)

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.115318.

References

Alphei, J., Bonkowski, M., Scheu, S., 1996. Protozoa, Nematoda and Lumbricidae in the rhizosphere of Hordelymus europaeus (Poaceae): Faunal interactions, response of microorganisms and effects on plant growth. Oecologia 106 (1), 111–126.

Andres, P., Moore, J.C., Simpson, R.T., Selby, G., Cotrufo, F., Denef, K., Haddix, M.L., Shaw, E.A., de Tomasel, C.M., Molowny-Horas, R., Wall, D.H., 2016. Soil food web stability in response to grazing in a semi-arid prairie: The importance of soil textural heterogeneity. Soil Biol. Biochem. 97, 131–143.

Attiwill, P.M., Adams, M.A., 1993. Nutrient cycling in forests. New Phytol. 124 (4), 561–582.

Bach, E.M., Baer, S.G., Meyer, C.K., Six, J., 2010. Soil texture affects soil microbial and structural recovery during grassland restoration. Soil Biol. Biochem. 42 (12), 2182–2191.

Berkelmans, R., Ferris, H., Tenuta, M., van Bruggen, A.H.C., 2003. Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. Appl. Soil Ecol. 23 (3), 223–235.

Blagodatskaya, E., Blagodatsky, S., Khomyakov, N., Myachina, O., Kuzyakov, Y., 2016. Temperature sensitivity and enzymatic mechanisms of soil organic matter decomposition along an altitudinal gradient on Mount Kilimanjaro. Sci. Rep. 6 (1), 1–11.

Bokulich, N.A., Subramanian, S., Faith, J.J., Gevers, D., Gordon, J.I., Knight, R., Mills, D. A., Caporaso, J.G., 2013. Quality-filtering vastly improves diversity estimates from Illumina amplicon sequencing. Nat. Methods 10 (1), 57–59.

Bongers, A.M.T., 1988. De nematoden van Nederland. Pirota Schoorl Bibliotheek Uitgave Knnv Nr.

Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E., Reynolds, J.F., Treseder, K.K., Wallenstein, M.D., 2008. Thermal adaptation of soil microbial respiration to elevated temperature. Ecol. Lett. 11 (12), 1316–1327.

Bremner, J., Mulvaney, C., 1982. Nitrogen total. Methods of soil analysis. Part 2. Chemical and microbiological properties Soil Sci. Soc. Am. Inc Publisher, Madison, Wisconsin, USA.

Carrascosa, M., Sanchez-Moreno, S., Alonso-Prados, J.L., 2014. Relationships between nematode diversity, plant biomass, nutrient cycling and soil suppressiveness in fumigated soils. Eur. J. Soil Biol. 62, 49–59.

Chen, W., Zhou, H., Wu, Y., Wang, J., Zhao, Z., Li, Y., Qiao, L., Chen, K., Liu, G., Xue, S., 2020. Direct and indirect influences of long-term fertilization on microbial carbon and nitrogen cycles in an alpine grassland. Soil Biol. Biochem. 149, 107922.

Chen, W., Zhou, H., Wu, Y., Li, Y., Qiao, L., Wang, J., Zhai, J., Song, Y., Zhao, Z., Zhang, Z., Liu, G., Zhao, X., You, Q.M., Xue, S., 2021. Plant-mediated effects of long-

term warming on soil microorganisms on the Qinghai-Tibet Plateau. Catena 204, 105391.
Chuckran, P.F., Reibold, R., Throop, H.L., Reed, S.C., 2020. Multiple mechanisms determine the effect of warming on plant litter decomposition in a dryland. Soil Biol. Biochem. 145, 107799.
Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440 (7081), 165–173.
Davidson, E.A., Trumbore, S.E., Amundson, R., 2000. Soil warming and organic carbon content. Nature 408 (6814), 789–790.
De Long, J.R., Dorrepaal, E., Kardol, P., Nilsson, M.-C., Teuber, L.M., Wardle, D.A., 2016. Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient. Ecosystems 19 (2), 339–355.
de Vries, F.T., Liiri, M.E., Bjornlund, L., Bowker, M.A., Christensen, S., Setala, H.M., Bardgett, R.D., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nat. Clim. Change 2 (4), 276–280.
Edenhofer, O., Seyboth, K., 2013. Intergovernmental Panel on Climate Change (IPCC).
Ekschmitt, K., Bakonyi, G., Bongers, M., Bongers, T., Boström, S., Dogan, H., Harrison, A., Nagy, P., O'Donnell, A.G., Papatheodorou, E.M., Sohlenius, B., Stamou, G.P., Wolters, V., 2001. Nematode community structure as indicator of soil functioning in European grassland soils. Eur. J. Soil Biol. 37 (4), 263–268.
Ferris, H., 2010. Form and function: Metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46 (2), 97–104.
Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18 (1), 13–29.
Ferris, H., Sanchez-Moreno, S., Brennan, E.B., 2012. Structure, functions and interguild relationships of the soil nematode assemblage in organic vegetable production. Appl. Soil Ecol. 61, 16–25.
Fisk, M.C., Fahey, T.J., 2001. Microbial biomass and nitrogen cycling responses to fertilization and litter removal in young northern hardwood forests. Biogeochemistry 53 (2), 201–223.
Fox, O., Vetter, S., Ekschmitt, K., Wolters, V., 2006. Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. Soil Biol. Biochem. 38 (6), 1353–1363.
Fu, X., Guo, D., Wang, H., Dai, X., Li, M., Chen, F., 2017. Differentiating between root- and leaf-litter controls on the structure and stability of soil micro-food webs. Soil Biol. Biochem. 113, 192–200.
Fussmann, K.E., Schwarzmueller, F., Brose, U., Jousset, A., Rall, B.C., 2014. Ecological stability in response to warming. Nat. Clim. Change 4 (3), 206–210.
Guan, P., Zhang, X., Yu, J., Cheng, Y., Li, Q., Andriuzzi, W.S., Liang, W., 2018. Soil microbial food web channels associated with biological soil crusts in desertification restoration: The carbon flow from microbes to nematodes. Soil Biol. Biochem. 116, 82–90.
He, J.S., Wang, Z., Wang, X., Schmid, B., Zuo, W., Zhou, M., Zheng, C., Wang, M., Fang, J., 2006. A test of the generality of leaf trait relationships on the Tibetan Plateau. New Phytol. 170 (4), 835–848.
Hopkins, F.M., Torn, M.S., Trumbore, S.E., 2012. Warming accelerates decomposition of decades-old carbon in forest soils. PNAS 109 (26), E1753–E1761.
Ingham, R.E., Santo, G.S., 1994. Extraction methods Quantifying nematode control. Res. Rep. 149, 55–59.
Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., Piñeiro, G., 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. Annu. Rev. Ecol. Evol. Syst. 48, 419–445.
Jiang, Y., Sun, B., Jin, C., Wang, F., 2013. Soil aggregate stratification of nematodes and microbial communities affects the metabolic quotient in an acid soil. Soil Biol. Biochem. 60, 1–9.
Jin, K., Wang, F., Zong, Q., Qin, P., Liu, C., 2020. Impact of variations in vegetation on surface air temperature change over the Chinese Loess Plateau. Sci. Total Environ. 716, 136967.
Johnson, J.L., Raw, J.L., Adams, J.B., 2020. First report on carbon storage in a warm-temperate mangrove forest in South Africa. Estuar. Coast. Shelf Sci. 235, 106566.
Leff, J.W., Wieder, W.R., Taylor, P.G., Townsend, A.R., Nemergut, D.R., Grandy, A.S., Cleveland, C.C., 2012. Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. Glob. Change Biol. 18 (9), 2969–2979.
Li, S., Song, M., Jing, S., 2021. Effects of different carbon inputs on soil nematode abundance and community composition. Appl. Soil Ecol. 163, 103915.
Li, X., Xie, J., Zhang, Q., Lyu, M., Xiong, X., Liu, X., Lin, T., Yang, Y., 2020. Substrate availability and soil microbes drive temperature sensitivity of soil organic carbon mineralization to warming along an elevation gradient in subtropical Asia. Geoderma 364, 114198.
Li, Y., Qing, Y., Lyu, M., Chen, S., Yang, Z., Lin, C., Yang, Y., 2018. Effects of artificial warming on different soil organic carbon and nitrogen pools in a subtropical plantation. Soil Biol. Biochem. 124, 161–167.
Ma, Q., Yu, H., Liu, X., Xu, Z., Zhou, G., Shi, Y., 2018. Climatic warming shifts the soil nematode community in a desert steppe. Clim. Change 150 (3), 243–258.
Ma, X., Razavi, B.S., Holz, M., Blagodatskaya, E., Kuzyakov, Y., 2017. Warming increases hotspot areas of enzyme activity and shortens the duration of hot moments in the root-detritusphere. Soil Biol. Biochem. 107, 226–233.
Marichal, R., Mathieu, J., Couteaux, M.-M., Mora, P., Roy, J., Lavelle, P., 2011. Earthworm and microbe response to litter and soils of tropical forest plantations with contrasting C: N: P stoichiometric ratios. Soil Biol. Biochem. 43, 1528–1535.
Mckinley, V.L., Peacock, A.D., White, D.C., 2005. Microbial community PLFA and PHB responses to ecosystem restoration in tallgrass prairie soils. Soil Biol. Biochem. 37, 1946–1958.
Mueller, K.E., Blumenthal, D.M., Carrillo, Y., Cesarz, S., Ciobanu, M., Hines, J., Pabst, S., Pendall, E., de Tomasel, C.M., Wall, D.H., Eisenhauer, N., 2016. Elevated CO2 and warming shift the functional composition of soil nematode communities in a semiarid grassland. Soil Biol. Biochem. 103, 46–51.
Neher, D.A., 2010. Ecology of Plant and Free-Living Nematodes in Natural and Agricultural Soil. Annu. Rev. Phytopathol. 48.
Neher, D.A., Weicht, T.R., Barbercheck, M.E., 2012. Linking invertebrate communities to decomposition rate and nitrogen availability in pine forest soils. Appl. Soil Ecol. 54, 14–23.
Nottingham, A.T., Baath, E., Reischke, S., Salinas, N., Meir, P., 2019. Adaptation of soil microbial growth to temperature: Using a tropical elevation gradient to predict future changes. Glob. Change Biol. 25 (3), 827–838.
Olsen, S., Sommers, L., Page, A., 1982. Methods of soil analysis. Part 2. Chemical and microbiological properties of Phosphorus. ASA Monogr. 9, 403–430.
Olsson, P.A., Baath, E., Jakobsen, I., Soderstrom, B., 1995. The use of phospholipid and neutral lipid fatty acids to estimate biomass of arbuscular mycorrhizal fungi in soil. Mycol Res 99 (5), 623–629.
Philippot, L., Raaijmakers, J.M., Lemanceau, P., Van Der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev. Microbiol. 11 (11), 789–799.
Qi, R., Li, J., Lin, Z., Li, Z., Li, Y., Yang, X., Zhang, J., Zhao, B., 2016. Temperature effects on soil organic carbon, soil labile organic carbon fractions, and soil enzyme activities under long-term fertilization regimes. Appl. Soil Ecol. 102, 36–45.
Richter, A., Kern, T., Wolf, S., Struck, U., Ruess, L., 2019. Trophic and non-trophic interactions in binary links affect carbon flow in the soil micro-food web. Soil Biol. Biochem. 135, 239–247.
Ruess, L., Michelsen, A., Schmidt, I.K., Jonasson, S., 1999. Simulated Climate Change Affecting Microorganisms, Nematode Density and Biodiversity in Subarctic Soils. Plant Soil 212 (1), 63–73.
Sanchez-Moreno, S., Ferris, H., Young-Mathews, A., Culman, S.W., Jackson, L.E., 2011. Abundance, diversity and connectance of soil food web channels along environmental gradients in an agricultural landscape. Soil Biol. Biochem. 43 (12), 2374–2383.
Sauvadet, M., Chauvat, M., Cluzeau, D., Maron, P.A., Villenave, C., Bertrand, I., 2016. The dynamics of soil micro-food web structure and functions vary according to litter quality. Soil Biol. Biochem. 95, 262–274.
Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478 (7367), 49–56.
Schwarz, B., Barnes, A.D., Thakur, M.P., Brose, U., Ciobanu, M., Reich, P.B., Rich, R.L., Rosenbaum, B., Stefanski, A., Eisenhauer, N., 2017. Warming alters energetic structure and function but not resilience of soil food webs. Nat. Clim. Change 7 (12), 895–900.
Sechi, V., De Goede, R.G.M., Rutgers, M., Brussaard, L., Mulder, C., 2018. Functional diversity in nematode communities across terrestrial ecosystems. Basic Appl. Ecol. 30, 76–86.
Shao, Y.H., Zhang, W.X., Liu, Z.F., Sun, Y.X., Chen, D.M., Wu, J.P., Zhou, L.X., Xia, H.P., Neher, D.A., Fu, S.L., 2012. Responses of soil microbial and nematode communities to aluminum toxicity in vegetated oil-shale-waste lands. Ecotoxicology 21 (8), 2132–2142.
Stone, M.M., Weiss, M.S., Goodale, C.L., Adams, M.B., Fernandez, I.J., German, D.P., Allison, S.D., 2012. Temperature sensitivity of soil enzyme kinetics under N-fertilization in two temperate forests. Glob. Change Biol. 18 (3), 1173–1184.
Sun, S., Wu, Y., Zhang, J., Wang, G., DeLuca, T.H., Zhu, W., Li, A., Duan, M., He, L., 2019. Soil warming and nitrogen deposition alter soil respiration, microbial community structure and organic carbon composition in a coniferous forest on eastern Tibetan Plateau. Geoderma 353, 283–292.
Thakur, M.P., Kuenne, T., Griffin, J.N., Eisenhauer, N., 2017a. Warming magnifies predation and reduces prey coexistence in a model litter arthropod system. Proc. R. Soc. B Biol. Sci. 284 (1851), 20162570.
Thakur, M.P., Reich, P.B., Fisichelli, N.A., Stefanski, A., Cesarz, S., Dobies, T., Rich, R.L., Hobbie, S.E., Eisenhauer, N., 2014. Nematode community shifts in response to experimental warming and canopy conditions are associated with plant community changes in the temperate-boreal forest ecotone. Oecologia 175 (2), 713–723.
Thakur, M.P., Tilman, D., Purschke, O., Ciobanu, M., Cowles, J., Isbell, F., Wragg, P.D., Eisenhauer, N., 2017b. Climate warming promotes species diversity, but with greater taxonomic redundancy, in complex environments. Sci. Adv. 3 (7), e1700866.
Tian, L., Bai, Y., Wang, W., Qu, G., Deng, Z., Li, R., Zhao, J., 2021. Warm- and cold-season grazing affect plant diversity and soil carbon and nitrogen sequestration differently in Tibetan alpine swamp meadows. Plant Soil 458, 151–164.
Van Nuland, M.E., Smith, D.P., Bhatnagar, J.M., Stefanski, A., Hobbie, S.E., Reich, P.B., Peay, K.G., 2020. Warming and disturbance alter soil microbiome diversity and function in a northern forest ecotone. FEMS Microbiol. Ecol. 96.
Vries, F.T.D., Thébault, E., Liiri, M., Birkhofer, K., Tsiafouli, M.A., Bjørnlund, L., Jørgensen, H.B., Brady, M.V., Christensen, S., Ruiter, P.C.D., 2013. Soil food web properties explain ecosystem services across European land use systems. PNAS 110 (35), 14296–14301.
Walker, J.C., 1991. Biogeochemistry: An Analysis of Global Change. Science 253 (5020), 686–688.
Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van Der Putten, W.H., Wall, D. H., 2004. Ecological linkages between aboveground and belowground biota. Science 304 (5677), 1629–1633.
Wang, J., Liu, G., Zhang, C., Wang, G., Fang, L., Cui, Y., 2019. Higher temporal turnover of soil fungi than bacteria during long-term secondary succession in a semiarid abandoned farmland. Soil Tillage Res. 194, 104305.

Weand, M.P., Arthur, M.A., Lovett, G.M., Mcculley, R.L., Weathers, K.C., 2010. Effects of tree species and N additions on forest floor microbial communities and extracellular enzyme activities. Soil Biol. Biochem. 42 (12), 2161–2173.
Wilschut, R.A., Geisen, S., 2020. Nematodes as drivers of plant performance in natural systems. Trends Plant Sci. 26 (3), 237–247.
Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., Cross, W.F., Friberg, N., Ings, T.C., Jacob, U., Jennings, S., Ledger, M.E., Milner, A. M., Montoya, J.M., O'Gorman, E.J., Olesen, J.M., Petchey, O.L., Pichler, D.E., Reuman, D.C., Thompson, M.S.A., Van Veen, F.J.F., Yvon-Durocher, G., 2010. Ecological Networks in a Changing Climate. Adv. Ecol. Res. 42, 71–138.
Wu, J., Zhang, D., Chen, Q., Feng, J., Li, Q., Yang, F., Zhang, Q., Cheng, X., 2018. Shifts in soil organic carbon dynamics under detritus input manipulations in a coniferous forest ecosystem in subtropical China. Soil Biol. Biochem. 126, 1–10.
Wu, Y., Chen, W., Entemake, W., Wang, J., Liu, H., Zhao, Z., Li, Y., Qiao, L., Yang, B., Liu, G., 2021. Long-term vegetation restoration promotes the stability of the soil micro-food web in the Loess Plateau in North-west China. Catena 202, 105293.
Yan, G., Xing, Y., Xu, L., Wang, J., Dong, X., Shan, W., Guo, L., Wang, Q., 2017. Effects of different nitrogen additions on soil microbial communities in different seasons in a boreal forest. Ecosphere 8 (7), e01879.
Yan, J., Zhang, Y., Crawford, K.M., Chen, X., Wu, J., 2020. Plant genotypic diversity effects on soil nematodes vary with trophic level. New Phytol. 229, 575–584.
Yeates, G.W., Bongers, T., Goede, R.G., De, Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera-an outline for soil ecologists. J. Nematol. 25 (3), 315–331.
Yu, Y., Wu, M., Petropoulos, E., Zhang, J., Nie, J., Liao, Y., Li, Z., Lin, X., Feng, Y., 2019. Responses of paddy soil bacterial community assembly to different long-term fertilizations in southeast China. Sci. Total Environ. 656, 625–633.
Zelles, L., 1999. Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biol. Fertil. Soils 29 (2), 111–129.
Zhang, C., Willis, C.G., Klein, J.A., Ma, Z., Li, J., Zhou, H., Zhao, X., 2017. Recovery of plant species diversity during long-term experimental warming of a species-rich alpine meadow community on the Qinghai-Tibet plateau. Biol. Conserv. 213, 218–224.
Zhang, X., Guan, P., Wang, Y., Li, Q., Zhang, S., Zhang, Z., Bezemer, T.M., Liang, W., 2015. Community composition, diversity and metabolic footprints of soil nematodes in differently-aged temperate forests. Soil Biol. Biochem. 80, 118–126.
Zhang, X., Li, Q., Zhu, A., Liang, W., Zhang, J., Steinberger, Y., 2012. Effects of tillage and residue management on soil nematode communities in North China. Ecol. Ind. 13 (1), 75–81.
Zhang, Y., Zhang, N., Yin, J., Zhao, Y., Yang, F., Jiang, Z., Tao, J., Yan, X., Qiu, Y., Guo, H., Hu, S., 2020. Simulated warming enhances the responses of microbial N transformations to reactive N input in a Tibetan alpine meadow. Environ. Int. 141, 105795.
Zhao, X.Q., Zhou, X.M., 1999. Ecological basis of Alpine meadow ecosystem management in Tibet: Haibei Alpine Meadow Ecosystem Research Station. Ambio 28, 642–647.