Long-term vegetation restoration promotes the stability of the soil micro-food web in the Loess Plateau in North-west China

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A B S T R A C T

Soil nematode communities play a significant role in soil ecosystems. Indeed, soil nematode metabolic carbon footprint, based on nematode biomass, is used to evaluate ecosystem functioning and assess nematode response to ecosystem nutrient enrichment. However, it is unclear whether vegetation restoration affects the metabolic carbon footprint of soil nematodes and soil food webs. We selected five periods for this study including: (1) farmland (0 years), (2) grassland (30 years), (3) shrubland (60 years), (4) pioneer forest (100 years), and (5) climax forest (160 years). Community composition, diversity, and metabolic footprint of soil nematodes, and carbon flow changes through the food web were investigated. The Shannon diversity (H′) index of the soil nematode community increased in the process of restoration, and the Pielou index (J′) appeared to be lower at 30 years after vegetation restoration than at 60, 100, and 160 years. The connectance of the soil nematode food web values increased continuously, from 30 years to 160 years, reaching the highest value at 100 and 160 years, which indicated that the food web had the strongest carbon flow at 100 years after vegetation restoration on the Loess Plateau, indirectly reflecting the stability of the soil food web. Bacteria were more important than fungi in the carbon flow in the food web during vegetation restoration. The study demonstrated that vegetation restoration promoted the input of the availability of external resources, enhanced the metabolic activity of omnivorous carnivores and the soil carbon flow, and stabilized the soil food web. However, the increase in vegetation restoration time not only changed the species composition but also changed the carbon input, due to the lack of interference by agriculture. Therefore, the intrinsic mechanism needs to be studied further.

1. Introduction

Vegetation restoration on ex-agricultural lands is an effective way to increase species cover, diversity, plant net primary productivity (NPP) (Lozano et al., 2014), and improves soil ecosystem function. Studies have found that vegetation restoration on ex-agricultural lands significantly increases soil carbon pools (Gu et al., 2019), soil nitrogen pools (Liu et al., 2019; Yang et al., 2019), and soil microbial community diversity (Zhang et al., 2016), thereby improving microbial nutrient

limitation (Xiao et al., 2020), and changing soil N and P cycles (Zhong et al., 2018). The ecosystem function of soil is further affected due to changes in the above- and below-ground ecosystems in the process of vegetation restoration on ex-agricultural lands. Therefore, vegetation restoration on ex-agricultural lands has become a primary method for improving the environment as well as the function of the ecosystem.

Soil nematodes are an important part of the soil food web. Within the ecosystem, Soil nematodes participates in the decomposition of organic matter, nutrient cycling, maintenance of the ecological diversity, and

balance of the food web (Yeates et al., 1993; Ekschmitt et al., 2001; Yeates, 2003; Sánchez-Moreno and Ferris, 2007; Yeates, 2007; Sechi et al., 2018). Soil nematodes include bacterivores, fungivores, plant-parasitic, and omnivore-predator nematodes. They are divided into the following three carbon flow pathways: the bacterial channel, the fungal channel, and the root channel. Increasing evidence shows that the interconnections between these channels play a critical role in regulating soil food webs (Ferris, 2010; Ferris et al., 2012; Zhang et al., 2017b; Guan et al., 2018). In recent years, in order to better reflect the soil food web channel and the utilization of carbon in nematode production and respiration, Ferris (2010) proposed the soil nematode metabolic footprint (NMF) to reflect carbon flow in the soil nematode food web. The metabolic footprint is obtained by calculating the carbon content of the nematode lifetime (including growth and egg production) and carbon utilization in metabolic activities (Ferris, 2010). The metabolic footprint is divided into the enrichment metabolic footprint and the structural metabolic footprint. The enrichment footprint is the metabolic footprint of those nematodes that rapidly respond to the enrichment of environmental resources, while the structural metabolic footprint is a high trophic level metabolic footprint with regulatory functions in the food web (Sánchez-Moreno et al., 2009; Ferris, 2010; Zhang et al., 2015). The emergence of the concept has improved our understanding of carbon flow of soil food webs (Ferris, 2010; Ferris et al., 2012; Zhang et al., 2017b; Guan et al., 2018). Thus, the value of soil nematodes as bioindicators to reflect the effects of anthropogenic and edaphic disturbances on the soil food web has received increasing attention from scholars (Zhang et al., 2015; Hu et al., 2016; Guan et al., 2018).

A large number of studies used soil nematodes as an indicator to reflect soil energy and carbon flow (Sánchez-Moreno and Ferris, 2007; Pausch et al., 2016a; Pausch et al., 2016b; Sauvadet et al., 2016; Sechi et al., 2018). Therefore, changes in the composition and structure of soil nematodes have an important role in ecosystem function. Studies found that surface vegetation, vegetation diversity, and soil microbes have a significant impact on the diversity, composition and function of soil nematode communities after vegetation restoration (Cesarz et al., 2013; Zhang et al., 2015; Hu et al., 2016). Yeates (2007) also indicated that differences between the aboveground and underground inputs from different plant species and different soil or biogeographic factors could lead to changes in nematode communities. Further, the top-bottom effects of plant communities play a significant role in soil-shaping nematode communities (Zhang et al., 2015), which causes changes in soil carbon flow and ecosystem functions. However, vegetation restoration not only changes species composition and stimulates vegetation growth, but it also alters C input because of the lack of interference from agricultural activities. Therefore, the internal mechanisms of how vegetation restoration affects soil nematodes and thus changes the carbon flow of the food web require further study. Recently, there have been some studies on the soil carbon flow during vegetation restoration by elucidating the metabolic footprint of the soil nematodes, but consistent conclusions have not been reached on the trends of the soil carbon flow and driving mechanism during the vegetation restoration process (Zhang et al., 2015; Hu et al., 2016). In particular, the effects of different vegetation types on the soil carbon flow after vegetation restoration on ex-agricultural lands are still unclear.

The Loess Plateau in northwestern China has a long history of tillage (Li et al., 2008; Fu et al., 2010). Due to the special ecological environment and soil parent material, the Loess Plateau has severe soil erosion, making it one of the most vulnerable regions in the world (Li et al., 2008). Therefore, vegetation restoration has become one of the most effective ways to improve the ecological environment of the Loess Plateau. However, there are few reports on the changes in soil nematode communities and food webs after vegetation restoration on ex-agricultural lands on the Loess Plateau. Therefore, our aim was to investigate how vegetation restoration on ex-agricultural lands affects the structure and functions of the micro-food-webs. We hypothesized

that: 1) the abundance and diversity of soil nematodes will increase after vegetation restoration, 2) the metabolic footprint of soil nematodes will increase after vegetation restoration on the Loess Plateau, and 3) The soil micro-food-web system will be more stable after vegetation restoration.

2. Material and methods

2.1. Site description

We selected sampling sites located on the Lianjiabian Forest Farm of the Loess Plateau in northwestern China. This area belongs to the Heshui General in the Gansu Province within N (35°03′E–36°37′) and E (108°10′–109°18′), average altitude 1211–1453 m. The study area forms part of the Ziwu mountain area, which is 23,000 km^2 in size. The area is dominated by a temperate continental climate (Wu et al., 2020). Since 1842, the farmlands have been abandoned because of famine, war, and natural disasters. Studies showed that *Populus davidiana* achieved 70% cover in the Ziwuling forest area in about 100 years. In around 150 to 160 years, it was gradually replaced by *Quercus liaotungensis* (Chen, 1954; Zou et al., 2002). The secondary forests in the region have naturally changed from farmland to forest over approximately 160 years (Wang et al., 2010b). Other vegetation in the area consists of herb species including: *Bothriochloa ischaemum* (Linn.) Keng, *Carex lanceolata* Boott, *Potentilla chinensis* Ser., and *Stipa bungeana* Trin., with shrub species including *Sophora davidii* (Franch.) Skeels, *Hippophae rhamnoides* Linn., *Rosa xanthina* Lindl., and *Spiraea pubescens* Turcz., and *Populus davidiana* Dode, and *Betula platyphylla* Suk is the pioneer forest species. The climatic climax vegetation is deciduous broadleaf forest dominated by *Q. liaotungensis* Koidz. (Wang et al., 2010a) (Fig. 1).

2.2. Experimental design and soil sampling

We selected the following five stages of vegetation restoration as sampling sites by engaging residents and assessing the literature (Table 1): (1) farmland (0 years means still farming, main species: corn); (2) grassland (30 years, main species: *B. ischaemum*); (3) shrubland (60 years, main species: *R. xanthina*); (4) the pioneer forest (100 years, main species: *P. davidiana*); and (5) the climax forest (160 years, main species: *Q. liaotungensis*). Except for 300 kg ha^{-1} nitrogen and 750 kg ha^{-1} phosphate fertilizer applied during the annual sowing period in the farmland stage, all treatments have no other human interference.

Soil sampling was conducted in early September 2017. We selected five independent sampling points representing five different stages of vegetation restoration based on local conditions. We set up four replicates for each stage. The distances of the replicate plots were within the range of more than 100 m and less than 1 km for each stage. Because of the difference in surface vegetation, we refer to previous studies in this area and set up sample plots of different areas in different vegetation (Zhong et al., 2018). We set up 20 m × 20 m plots within a forest community. In the shrubland community, we installed 10 m × 10 m plots, and in grassland and farmland, we installed 5 m × 5 m plots. We used a soil drill of 5-cm diameter and collected 15 soil samples from four plots per vegetation community in a serpentine manner at an approximately 0 to 20-cm depth. The samples were hand-mixed and passed through a 2-mm screen. The soil samples were maintained at 4 °C and used to measure water organic carbon (WOC) and soil nematodes. Naturally air-dried soil was used for the analysis of soil properties, and the samples were passed through 1-mm and 0.25-mm screens.

2.3. Soil physical and chemical analysis

We used the H_2SO_4–$K_2Cr_2O_7$ oxidation and the Kjeldahl methods to measure soil organic carbon (SOC) and soil total N (TN) concentrations, respectively (Bremner and Mulvaney, 1982). Soil total phosphorus (TP) concentration was measured using colorimetric analysis after digestion
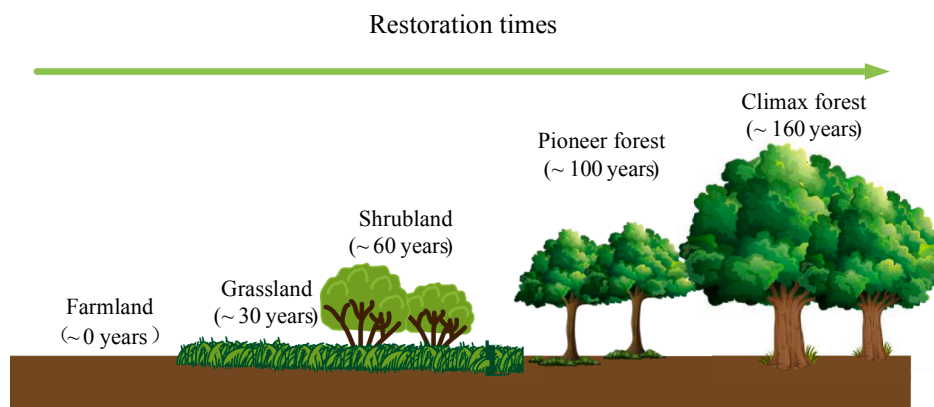
Fig. 1. Location of the study site on the Loess Plateau and conceptual diagram of the major stages during vegetation restoration stages.

Table 1

Geographical and vegetation characteristics with vegetation restoration in the Ziwuling forest region of the Loess Plateau.

Site	Succession stage (in year)	Biome	Altitude (m)	Slope (°)	Main plant species
S1	0 year	Farm	~1280	0°	*Corn*
S2	30 year	Grass	~1416	15°	*Bothriochloa ischaemum, Lespedeza dahurica*
S3	60 year	Shrub	~1346	21°	*Sophora davidii, Carex lanceolata, Hippophae rhamnoides*
S4	100 year	the pioneer forests	~1445	14°	*Populus davidiana, Spiraea schneideriana, Carex lanceolata*
S5	160 year	the climax forests	~1427	22°	*Quercus liaotungensis, Rosa hugonis, Carex lanceolata*

with H_2SO_4 and $HClO_4$ (Olsen et al., 1982). Soil available P (AP) was extracted using 0.5 M $NaHCO_3$ at pH 8.5 and measured colorimetrically by the molybdate-ascorbic acid method using a UV spectrophotometer. We used a pH-meter (Metrohm 702, Swiss) to measure soil pH at a ratio of 2.5:1 (water to soil). Soil moisture content was determined at 110 °C for 10 h. We used 2.0 mol/L KCl to extract and filter soil ammonium (NH_4^+-N) and nitrate N (NO_3^--N), which were measured on a flow injection autoanalyzer. A TOC analyzer (liquiTOC II, Elementar, Germany) was used to determined WOC concentrations.

2.4. Soil phospholipid fatty acid analysis (PLFA)

We extracted fatty acids from 3.0 g of lyophilized soil (Zelles, 1999) and analyzed them using a gas chromatograph (7890A GC, Agilent Technologies) equipped with MIDI Sherlock software (Microbial ID, Inc., Newark, USA). We used an external standard of 19:0 methyl ester to quantify the neutral lipid fatty acids (NLFAs) and phospholipid fatty acids (PLFAs). A particular NLFA and PLFA can refer to a specific microbial community; for example, iso- and anteiso-branched fatty acids and monounsaturated fatty acids are used as indicators of gram-positive bacteria 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 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 indicated fungal PLFAs, and the 16:1 ω5c indicated arbuscular mycorrhizal fungi (AMF) NLFAs. The lipid 16:0 10-methyl, 17:0 10-methyl, and 18:0 10-methyl indicated actinomycetes. In addition, the sum of the gram-positive bacteria (G $^+$), gram-negative bacteria (G $^-$) and 14:0, 15:0, 16:0, 17:0, 18:0, and 20:0 was used as total bacteria (Mckinley et al., 2005; Bach et al., 2010; Briar et al., 2011; Dempsey et al., 2013; Zhang et al., 2017a; Guan et al., 2018). The PLFAs were converted into microbial biomass carbon according to the following formulas: 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; Frostegård and Bååth, 1996; Vries et al., 2013; Guan et al., 2018).

2.5. Soil nematode community analysis

We used the modified Baermann funnel method (Ingham and Santo, 1994) to extract soil nematodes from fresh soil (100 g). Nematodes were killed at 60 °C and fixed with triethanolamine formalin, transferred to a

Table 2

Soil physicochemical properties with vegetation restoration.

Site	SOC g·kg⁻¹	TN g·kg⁻¹	TP g·kg⁻¹	WOC mg·kg⁻¹	AP mg·kg⁻¹	NO₃⁻-N mg·kg⁻¹	NH₄⁺-N mg·kg⁻¹	pH
0 years	10.64± (0.31)b	1.13± (0.04)b	0.077± (0.01)a	55.97± (3.48)b	9.46± (2.66)a	4.00± (1.95)a	6.16± (2.00)a	7.68± (0.17)a
30 years	12.81± (0.58)bc	1.30± (0.13)b	0.057± (0.00)b	60.25± (4.75)b	1.80± (0.19)b	0.73± (0.10)b	7.68± (1.43)a	7.48± (0.17)ab
60 years	16.41± (0.86)cd	1.58± (0.13)c	0.059± (0.00)b	70.16± (5.81)c	2.18± (0.28)b	0.83± (0.15)b	9.19± (0.06)b	7.33± (0.15)bc
100 years	18.69± (0.45)d	1.66± (0.04)cd	0.064± (0.00)b	78.4± (7.74)ac	2.52± (0.13)bc	1.27± (0.08)b	8.13± (0.32)b	7.13± (0.19)c
160 years	23.74± (5.98)a	1.93± (0.34)a	0.06± (0.00)b	86.05± (7.32)a	4.43± (1.41)c	1.20± (0.02)b	8.18± (1.26)b	7.15± (0.06)c

Note: Soil organic carbon: SOC, Soil total nitrogen: TN, Soil total phosphorus: TP, Water-soluble organic carbon: WOC, Available phosphorus: AP. The results are means ± (standard error) (n = 4). Different letters in table indicate significant difference (P < 0.05) by the ANOVA and LSD multiple test.

flame glass slide, and counted using an inverted composite microscope. According to the method adopted by Bongers (1988), 100 specimens were randomly selected from the fixed soil nematodes, and the genus was identified using the method developed by the UNL Nematology Lab (https://nematode.unl.edu/nemakey.htm). They were then categorized into plant parasites (PP), bacterivores (Ba), fungivores (Fu), and omnivores-predators (OP), according to (Yeates et al., 1993).

The Shannon diversity (H′) index and Pielou index (J′) were calculated according to the following formula: H′ = -ΣPilnPi and J′ = H′/lnS (Shannon and Weaver, 1950; Pielou, 1966). The c-p scale is assigned according to the r and K characteristics of soil nematodes. The nematodes were divided into four trophic groups: plant parasites (Ppx), bacterivores (Bax), fungivores (Fux), and omnivores-predators (OPx) (where x = 1–5), where x represents the c-p scale. Low nutrient level nematodes had a c-p value of 1–2, while high nutrient level nematodes had a c-p value of 3–5 (Ferris et al., 2001). The enrichment index (EI) and structural index (SI) were calculated according to EI = 100 * e/(b + e) and SI = 100 * s/(b + s), respectively, where b, e, and s represented the abundance of individuals in guilds in different nematode component (including basal component, enrichment component and structural component) weighted by their kb, ke and ks values, respectively, indicating the response of soil nematode to resources (Ferris et al., 2001). We assumed that the dry weight of soil nematodes was 20% of the fresh weight, and the carbon content in nematodes was 52% of the dry weight. The formula for calculating the carbon content in nematode biomass is 52% × 20% Wt / 100 (μg g^{-1}), where Wt indicates the fresh weight of soil nematodes (Ferris, 2010; Guan et al., 2018). The nematode metabolic footprint (NMF) uses the formula NMF = Σ (Nt [0.1 wt/mt + 0.273 (W0.75)]), where Nt represents the number of individuals in the genus t, while wt and mt represent soil nematode weight and c-p values, respectively (Ferris, 2010; Ferris et al., 2012; Guan et al., 2018). The nematode metabolic footprint (NMF) divides into enrichment footprints and structural footprints. The enrichment footprint (Fe) shows the responsiveness to resource pulses, and the structural footprint (Fs) shows the impact on higher trophic levels on the metabolic activity in the food web (Ferris, 2010; Ferris et al., 2012; Zhang et al., 2015).

The connectance is the potential for carbon flow in the food web (Sánchez-Moreno et al., 2011; Ferris et al., 2012). We assumed that all species in the soil sample can freely hunt for prey; S = ab, where the number of occurrences of any predator (a) and any prey (b) in each sampling points of the stages; F = AB, where the number of occurrences of predator (A) and prey (B) groups in all sampling points of a stage. Connection (C) = S/F (Ferris et al., 2012; Guan et al., 2018).

2.6. Statistical analysis

We used IBM SPSS Statistics 20.0 (IBM Corp, Armonk, NY, USA) to perform statistical analyses for one-way Analysis of Variance (ANOVA) with Least Significant Difference multiple comparisons test ($P < 0.05$). We used Redundancy Analysis (RDA) to analyze the effect of soil properties on nematode genera using CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA). The multi-response permutation procedure (MRPP) was used to statistically examine differences in soil nematode community composition (Weand et al., 2010). Principal coordinates analysis (PCoA) was used to compare nematode genus composition in relation to different stages using R packages (3.6.0) "FactoMineR" and "factoextra," and the multi-response permutation procedures (MRPP significance) test using the R "vegan" package. To identify the independent contribution (%) of environmental drivers (soil physical and chemical properties) on plant parasites, bacterivores, fungivores, and omnivores-predators, principal component analysis (PCA) was used to extract one axis to represent community changes, and the explanation rates were: 48.08%, 37.18%, 52.11% and 30.25% during different stages were used to construct linear models in the "relaimpo" package in R (3.6.0). We used AMOS (Analysis of Moment Structure) to develop a structural equation model (SEM) to analyze the energy channels in the

soil nematode communities.

3. Results

3.1. Nematode community composition and diversity

A total of 39 nematode genera were identified in the soil at five vegetation restoration stages (Table S1). The bacterivore abundance in 160 years was significantly higher than other restoration stages (Table S2, $P < 0.05$). The fungivores abundance were higher in 30 and 160 years than other stages. However, no differences in plant parasites and omnivore-predators were detected between stages (Table S2, $P < 0.05$).

The soil nematode Shannon's diversity index increased significantly with vegetation restoration (Fig. 2B, R2 = 0.83, $P < 0.05$). The Pielou index from 30 years to 160 years increased significantly (Fig. 2A, R2 = 0.99, $P < 0.001$). The soil nematode Shannon's diversity index in 160 years was significantly higher than 30 years. The Pielou index in 100 years was significantly higher than 30 years ($P < 0.05$). The PCoA analysis showed that nematode community composition was significantly different among different stages. The first two PCoA axes accounted for 34.3% of the total variance (Fig. 3, $P = 0.001$).

3.2. Soil microbial and nematode biomass carbon and metabolic footprints

Compared to the 0 years, the significant increases in biomass carbon of total microbes and fungi values in 30, 100, and 160 years. In 100 years of restoration, the biomass carbon of bacteria was significantly greater than that of others (Fig.S1, $P < 0.05$). The biomass carbon of bacterivores in 100 years was significantly higher than that in 30 and 60 years, while there was no significant difference between the other treatments (Fig. S2A, $P < 0.05$). The biomass carbon of fungivores showed an upward trend, except at 0 years (Fig. S2B). The biomass carbon of plant parasites increased with vegetation restoration, but not significant (Fig. S2C, $P < 0.05$). The biomass carbon of omnivore-predators was significantly increase in 160 years than that in 60 and 0 years (Fig. S2D, $P < 0.05$).

The enrichment footprint and structural footprint was significantly increase with restoration period, and achieved its highest value at 160 years. Compared to in 100 years, the significant decreases in fungivore footprint value in 0, 30, and 60 years. The bacterivore footprint was significantly greater in 160 years than that in 30 and 60 years. Except for in 160 years, omnivore-predator and plant parasite footprint exhibited no significant changes (Table 3, $P < 0.05$). The nematode functional metabolic footprint (total area) showed 160 years > 100 years > 60 years > 0 years > 30 years. Of these, 30, 60, and 160 years were in quadrant D, while 0 and 100 years were in quadrant B (Fig. 4). The connectance value of soil food web in 100 years and 160 years was significantly increase than that in 60 years (Fig. 5).

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

We used RDA to evaluate the relationship between soil environmental factors and nematode genera. The first two RDA axes accounted for 67.34% of the total variance (Fig. 6). The SOC, AP, pH, and NO– 3-N were significantly related to nematode distribution (Table S3, $P < 0.05$).

Constructing the SEM with different soil microbes and nematode components, we calculated the carbon flow at different nutrient levels in the soil food web ($\chi2 = 2.736$, df = 4, P = 0.603, CFI = 1.000, GFI = 0.961, RMSEA = 0.000). The vegetation restoration stages had a direct impact on the biomass carbon of bacteria and omnivores-predators. Moreover, the biomass carbon of bacterivores had a direct effect on that of omnivores-predators (Fig. 7, $P < 0.05$). The vegetation restoration time had a marginal effect on the biomass carbon of plant parasites
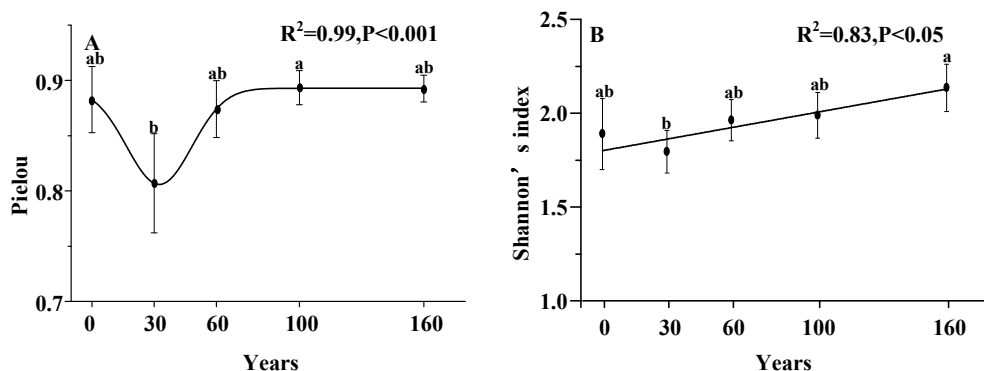
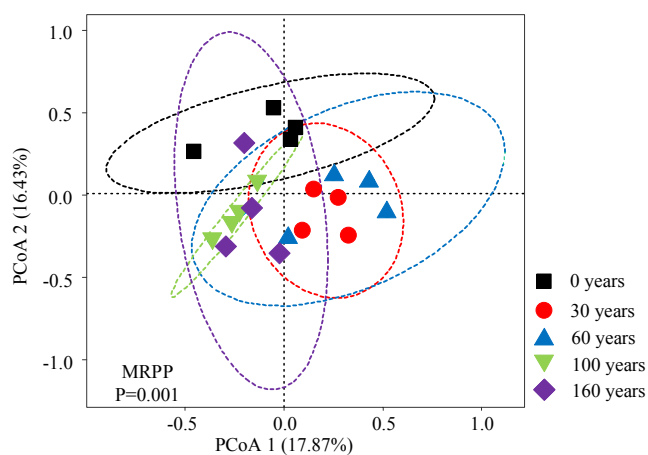**Fig. 2.** Soil nematode diversity index with vegetation restoration.

Fig. 3. PCoA of nematode genus composition with vegetation restoration.

and fungi. The biomass carbon of bacteria had a marginal effect on omnivores-predator nematodes (Fig. 7, *P* < 0.1). The model explained 76.6% of the variance in the biomass carbon of omnivores-predators, and 13.6%, 13.8%, and 14.1% of the variance in the biomass carbon of bacterivores, fungivores, and plant parasites, respectively. The variance in bacterial and fungal biomass carbon was explained by 17.6 and 16.2% by the model, respectively (Fig. 7).

4. Discussion

4.1. Effect on soil nematodes with vegetation restoration

Soil nematodes are important indicators of soil ecosystem function changes. Several studies showed that different vegetation types (Cesarz et al., 2013; Eisenhauer et al., 2013; Mejia-Madrid, 2018; Gu et al.,

2019; Olatunji et al., 2019; Sun et al., 2019) and different vegetation restoration time periods (Hu et al., 2016; Ciobanu et al., 2019; Coffey and Otfinowski, 2019; Jackson et al., 2019) significantly alter the diversity and abundance of soil nematode communities. In our study, soil nematode diversity increased significantly with vegetation restoration (Fig. 2), which indicated that 160 years of restoration on the Loess Plateau led to a more diverse and structured soil nematode community. The studies found vegetation restoration raise soil microbial diversity and below-aboveground biomass (Zhang et al., 2016; Zhang et al., 2018), resulting in an increase in soil resource input, improving the soil microenvironment (Cui et al., 2018), and promoting changes in soil nematode communities. In addition, the top-down (resource control) effect of different vegetation species influence soil nematode communities (Nico et al., 2013; Zhang et al., 2015), and caused changes in soil nematode diversity.

The principal component analysis showed that the nematode community composition significantly differed with vegetation restoration (Fig. 3). Several studies also confirmed our results that different vegetation types (Cesarz et al., 2013; Campos-Herrera et al., 2019) and the same species in different stages of restoration (Zhang et al., 2015) significantly affect the composition of soil nematode communities. Particularly, in our study, the bacterivore and fungivore nematode abundance and carbon content raised significantly with vegetation restoration, indicating that the top-down effect of vegetation not only significantly change the diversity and abundance of soil nematodes, but also has a significant impact on the composition of soil nematode communities (Scharroba et al., 2012; Shao et al., 2012; Eisenhauer et al., 2013). The vegetation restoration tends to change soil environment with causing soil nutrient accumulation, enhancing soil enzyme activities, and promoting soil microbe growth (Wu et al., 2020). The soil environment changed the abundance and carbon content of the bacterivore and fungivore nematode through bottom-up (resource control) effects (Eisenhauer et al., 2013). Similarly, the abundance and carbon content of plant parasites nematodes had an increase trend during natural

Table 3
Soil nematode metabolic footprints with vegetation restoration (µg C kg^{-1} soil).

	Enrichment footprint	Structure footprint	PP footprint	FF footprint	BF footprint	OP footprint
0 years	14.21± (6.17)ab	10.82± (5.12)c	5.39± (1.23)b	3.15± (0.67)bc	10.95± (6.86)ab	2.47± (0.90)b
30 years	3.37± (1.80)b	1.29± (0.42)c	8.38± (2.88)b	1.7± (0.44)c	4.52± (1.82)b	0±(0)
60 years	1.84± (0.36)b	29.69± (10.90)bc	5.2± (1.71)b	1.96± (0.51)ac	1.89± (1.12)b	28.73± (11.07)bc
100 years	11.27± (6.28)ab	54.57± (20.39)b	5.48± (1.46)b	5.12± (0.77)d	9.99± (5.66)ab	52.1± (19.67)bc
160 years	18.90± (7.18)a	72.10± (25.30)ab	40.50± (22.47)a	3.48± (0.52)abd	22.93± (7.67)a	68.48± (25.13)ac

Note: BF, bacterivores; FF, fungivores; OP, omnivores-predators; PP, plant parasites; The results are means ± (standard error) (n = 4). Different letters in table indicate significant difference (P < 0.05) by the ANOVA and LSD multiple test.
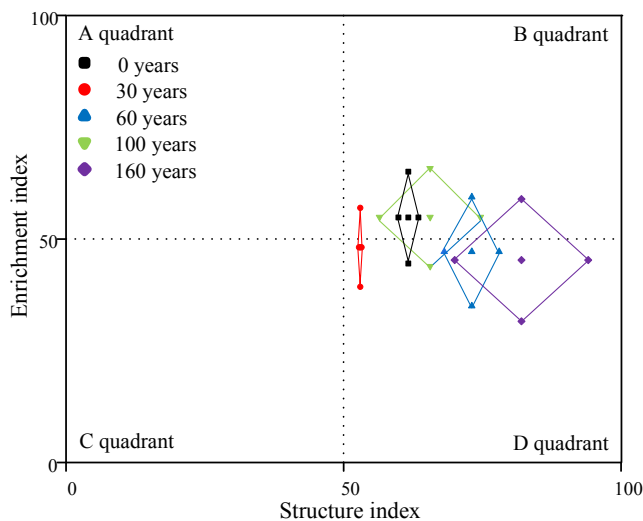
Fig. 4. Functional metabolic footprints of nematode communities with vegetation restoration. The functional metabolic footprint is depicted by the sequentially joining points: (SI-0.5sfoot/k, EI); (SI+0.5sfoot/k, EI); (SI, EI-0.5efoot/k); and (SI, EI+0.5efoot/k). The adjusted k value is 3.
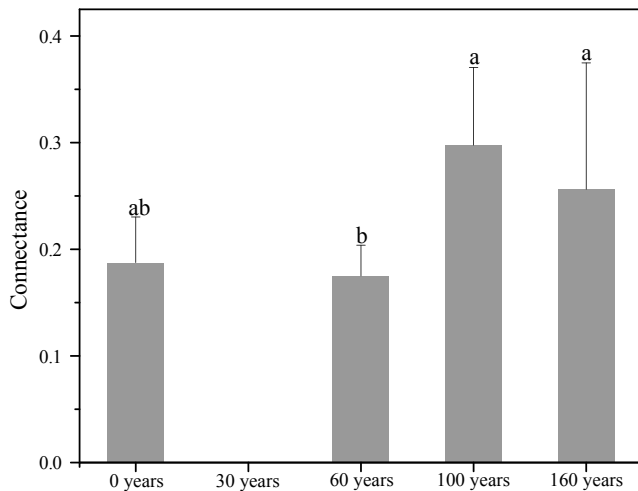

Fig. 5. Connectance of nematodes channels with vegetation restoration. Different letters indicate a significant difference (P < 0.05). The values are mean ± SE (n = 4).
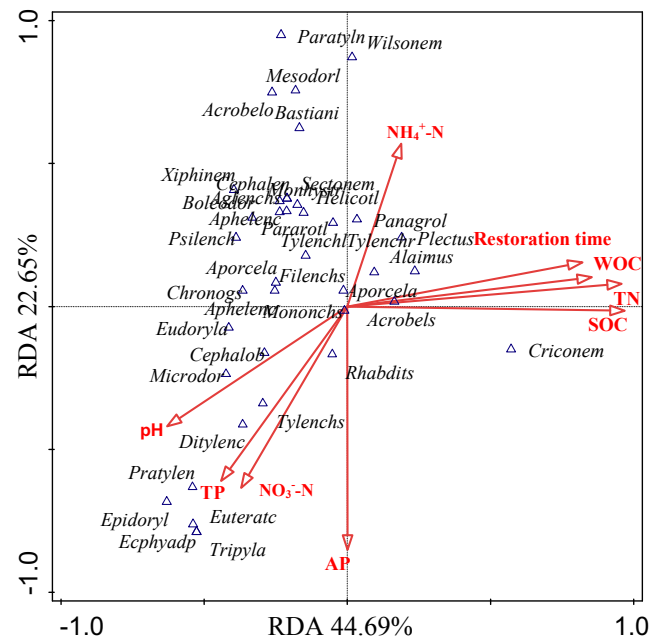

Fig. 6. Redundancy analysis (RDA) of nematode genera in relation to soil properties: SOC, total soil organic carbon; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; NO_3^--N; NH_4^+-N; pH and WOC, Water-soluble organic carbon.

carbon, as an energy source for soil bacteria and fungi, significantly positive correlation soil nematode communities through the bottom-up effects of predation. The N and P nutrients are limiting factors for soil microbial growth (Wu et al., 2020; Xiao et al., 2020) during vegetation restoration in the Loess Plateau. The study found that unduly high levels of NO– 3-N and AP has negative correlation the diversity and abundance of soil nematodes and inhibit their biomass growth (Zhao et al., 2014). Therefore, the NO– 3-N and AP changed soil nematode communities by affecting species with low nutrient levels in the soil micro-food web. In our result, the SOC, AP and NO– 3-N were an important driving factor in the soil micro-food web. In addition, previous studies suggested the pH was often used as an important environmental factor to drive to change in soil bacteria, and several researches also found that soil acidification is positively related with soil nematode communities (Chen et al., 2019; Xiao et al., 2020; Jiang et al., 2013). Therefore, soil pH can directly and indirectly effect soil nematode community change through the trophic cascade effects of food web (Guan et al., 2018).

4.2. Effect on nematode microbial food web metabolic activities with vegetation restoration

The enrichment metabolic footprint is used as an indicator of the external resources affecting micro-food web metabolic activity (Ferris et al., 2012). In our study, the enrichment metabolic footprint had significant increase trend from 30 years to 160 years, indicating that the external resource input changed during natural restoration. Liu et al. (2020) confirmed the result that vegetation restoration causes the litter accumulation and root biomass growth. The structural metabolic footprint generally reflects the net resource output of the food web and the metabolic activity of the higher trophic level nematodes (Ferris et al., 2012; Guan et al., 2018). The structural metabolic footprint in the present study tended to increase during the process of restoration, meaning a gradually strong in the metabolic activity of predators in the food web.

The functional metabolic footprint in the study is used to indicate the amount of carbon input soil food web in the process of the vegetation restoration (Ferris, 2010; Hodson et al., 2014). Our results showed that

vegetation restoration in our study, although not significant. Previous study found that the belowground biomass of vegetation increase significantly and reach its maximum value in 100 years during natural succession on abandoned farmland (Deng et al., 2014). Therefore, the trophic cascade effect of food web led to changes in carbon contents and abundance of plant parasites nematodes (Guan et al., 2018). Surprisingly, there was no significant change in the abundance of omnivores-predators. However, the omnivores-predators carbon content increased significantly with vegetation restoration. The reason was related to the increase in the number of the larger individual omnivores-predators nematodes during the natural restoration.

The natural vegetation restoration is not only the change of vegetation species and number, but also the continuous accumulation of SOC and other soil nutrients. Previous studies showed that the soil physicochemical and biotic environments can be strong driver of changes in the soil nematode communities (van den Hoogen et al., 2019; Zhang et al., 2015). The RDA showed that SOC, AP, pH, and NO₃-N significantly affected soil nematode communities (Fig. 6; Table S3). Soil organic
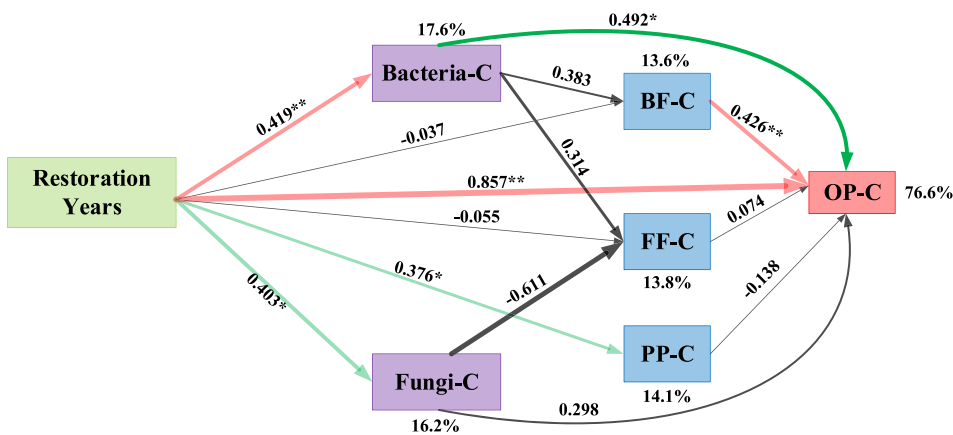
Fig. 7. SEM of the energy channels in soil nematode communities (χ2 = 2.736, df = 4, P = 0.603, CFI = 1.000, GFI = 0.961, RMSEA = 0.000). BF-C, bacterivores biomass carbon; FF-C, fungivores biomass carbon; OP-C, omnivores-predators biomass carbon; PP-C, plant parasites biomass carbon; Red solid arrows indicate a significant difference (P < 0.05); green solid arrows indicate a marginal difference (P < 0.1); yellow solid arrows indicate a non-significant difference (P > 0.1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the functional metabolic footprint increased with vegetation restoration, indicating higher amounts of carbon were input to the soil micro-food webs during restoration (Zhang et al., 2015). The process of vegetation restoration caused the continuous input of external resources into the soil food web, greatly enriching the resources in the soil ecosystem (Ferris, 2010). Resource enrichment provided an environment for the growth of soil microbes. As shown in Table 2, soil physicochemical properties such as SOC and TN reached a maximum in 160 years of vegetation restoration, which stimulated the growth of soil nematodes of lower nutrient levels and provided environment for the growth of OP. The soil ecosystem evolved a higher quality OP, a more balanced food-web metabolism, and a higher level of resource enrichment (Hodson et al., 2014). However, as their number in the ecosystem continued to grow, the OP reduced the number of nematodes at lower trophic levels through a trophic cascade effects between species (Guan et al., 2018). In our study, we found the biomass carbon of OP increased significantly, while that of other nematodes species decreased after 100 years (Fig. S1, S2). In addition, several researchers divide the functional metabolic footprint into four quadrants to reflect the stability of the soil food web (Ferris et al., 2001; Berkelmans et al., 2003; Ferris, 2010; Ferris et al., 2012). Our results indicated that the soil food web was more stable at 100 years of process of vegetation restoration. However, it showed degradation at 160 years of restoration. These results agree with those of Zhang et al. (2015), who also found that the soil food web in the mid-forest stages is more stable than that at the young and old forest stages. The reason is explained by the "intermediate disturbance hypothesis", meaning that the external disturbance intensity is maintained at a moderate level, the ecosystem is more stable (Connell, 1978; Martin et al., 2019). In addition, many studies suggested that various soil indicators experience a significant decline after the vegetation restoration completely (Zhang et al., 2015; Abbas et al., 2019; Wang et al., 2019; Yan et al., 2020a; Yan et al., 2020b). Therefore, we hypothesize that when the ecosystem recovers completely, the stronger surface vegetation obtains more soil nutrients, leading to the degradation of the soil ecosystem.

4.3. Effect on carbon flow through the soil food web with vegetation restoration

The connectance of soil nematode food-web values from 30 years to 160 years had an increase continuously, reaching the highest value at 100 and 160 years (Fig. 5). The connectance of the food web is used to response an indicator of the nutritional interactions in the carbon channel and is believed to reflect food web stability (Sánchez-Moreno et al., 2011; Guan et al., 2018). Our study indicated that, in the soil food web, consumers and resources would establish more complex interactions in the process of vegetation restoration, thereby promoting the carbon flow in the soil micro-food web (Guan et al., 2018).

Therefore, the food web had the strongest carbon flow at 100 years after vegetation restoration on the Loess Plateau, indirectly reflecting the stability of the food web. However, at 160 years after the process of vegetation restoration, the carbon flow intensity of the soil food web decreased, although the decrease was not significant, which meant degradation of food web.

We used PLFA to calculate the carbon content of fungi and bacteria in the soil. The carbon content of different nutrient components in nematodes was also estimated. By studying the relationship between the microbial community and carbon content among the nematode communities in the soil food web, we elucidated the carbon flow to improve our understanding of the soil food web. We used the above indicators to construct an SEM to reflect the carbon flow between microorganisms and nematodes (Sánchez-Moreno et al., 2011; Zhang et al., 2015). The SEM results showed that the bacterial and BF biomass carbon had significant effects on the OP biomass carbon, which indicated that bacteria played an important role in carbon flow through the food web on the Loess Plateau during vegetation restoration.

Previous study showed that bacteria play an important role in soil food webs in the process of restoration (Hu et al., 2016). Another study showed that fungi play an even greater role in vegetation restoration than bacteria (Zhang et al., 2015). The flow of carbon and energy through the soil food web is primarily driven by the feeding interactions between the communities in the soil biota (Derk et al., 2006; Lenoir et al., 2007). The bottom-up effects from plant communities also have an important impact on the soil microbial food web (Zhang et al., 2015). In addition, the impact of environmental and climatic conditions on the food web cannot be ignored. Therefore, the role of eubacteria in the food web during vegetation restoration requires further investigation.

5. Conclusions

In our study, the diversity and abundance of the soil nematode community increased continually during vegetation restoration. With time, vegetation restoration led to a significantly altered soil nematode community structure. During the process of vegetation restoration, external resources continually entered the soil food web, enhancing the growth of nutrient-rich nematodes, promoting carbon flow in the food web, increasing food web metabolic activity, and stabilizing the soil food web over time. The study provided a deeper understanding of the carbon flow through the soil food web in the process of vegetation restoration. The relationship between the soil micro-food web and the meso- and macrofauna should be considered in further studies. It is apparent that the best way to avoid soil degradation in the Loess Plateau region in North-west China is through abandoning agriculture and through the natural regeneration of the area.

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105293.

References

Abbas, S., Nichol, J.E., Zhang, J.L., Fischer, G.A., 2019. The accumulation of species and recovery of species composition along a 70 year succession in a tropical secondary forest. Ecol. Ind. 106, 10.

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, 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, 223–235.

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

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.

BRIAR, Shabeg, S., FONTE, Steven, J., PARK, Inmyoung, Johan, SCOW, Kate, 2011. The distribution of nematodes and soil microbial communities across soil aggregate fractions and farm management systems. Soil Biology & Biochemistry 43, 905-914.

Campos-Herrera, R., Blanco-Perez, R., Angel Bueno-Pallero, F., Duarte, A., Nolasco, G., Sommer, R.J., Rodriguez Martin, J.A., 2019. Vegetation drives assemblages of entomopathogenic nematodes and other soil organisms: Evidence from the Algarve, Portugal. Soil Biol. Biochem. 128, 150–163.

Cesarz, S., Ruess, L., Jacob, M., Jacob, A., Schaefer, M., Scheu, S., 2013. Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes. Soil Biol. Biochem. 62, 36–45.

Chen, C., 1954. The vegetation and its roles in soil and water conservation in the secondary forest area in the boundary of Shaanxi and Gansu provinces. Acta Phytoecologica et Geobotanica Sinica 2, 152–153.

Chen, D., Xing, W., Lan, Z., Saleem, M., Wu, Y., Hu, S., Bai, Y., 2019. Direct and indirect effects of nitrogen enrichment on soil organisms and carbon and nitrogen mineralization in a semi-arid grassland. Funct. Ecol. 33, 175–187.

Ciobanu, M., Eisenhauer, N., Stoica, I.-A., Cesarz, S., 2019. Natura 2000 priority and non-priority habitats do not differ in soil nematode diversity. Appl. Soil Ecol. 135, 166–173.

Coffey, V., Otfinowski, R., 2019. Legacies of afforestation on soil nematode community composition, structure, and diversity in a northern Canadian prairie. Plant Soil 435, 437–447.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science (New York N.Y.) 199, 1302–1310.

Cui, Y., Fang, L., Guo, X., Wang, X., Wang, Y., Li, P., Zhang, Y., Zhang, X., 2018. Responses of soil microbial communities to nutrient limitation in the desert-grassland ecological transition zone. Sci. Total Environ. 642, 45–55.

Dempsey, Mark, A., Fisk, Melany, C., Yavitt, Joseph, B., Fahey, Timothy, J., Balser, Teri, C., 2013. Exotic earthworms alter soil microbial community composition and function. Soil Biology & Biochemistry 67, 263-270.

Deng, L., Wang, K., Shangguan, Z., 2014. Long-term natural succession improves nitrogen storage capacity of soil on the Loess Plateau, China. Soil Res. 52, 262–270.

Derk, A., Matthias, S., Stefan, S., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. Ecology 87, 235–245.

Eisenhauer, N., Dobies, T., Cesarz, S., Hobbie, S.E., Meyer, R.J., Worm, K., Reich, P.B., 2013. Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. PNAS 110, 6889–6894.

Ekschmitt, K., Bakonyi, G., Bongers, M., Bongers, T., Boström, S., Dogan, H., Harrison, A., Nagy, P., O'Donnell, A.G., Papatheodorou, E.M., 2001. Nematode community structure as indicator of soil functioning in European grassland soils. European J. Soil Biol. 37, 263-268.

Ferris, H., 2010. Form and function: Metabolic footprints of nematodes in the soil food web. Eur. J. Soil Biol. 46.

Ferris, H., Bongers, T., Goede, R.G.M.D., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Ferris, H., Sánchez-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.

Frostegård, A., Bååth, E., 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. Biol. Fertil. Soils 22, 59–65.

Fu, X., Shao, M., Wei, X., Horton, R., 2010. Soil organic carbon and total nitrogen as affected by vegetation types in Northern Loess Plateau of China. Geoderma 155, 31–35.

Gu, L.-P., Kong, J.-J., Chen, K., Guo, Y.-Q., 2019a. Monitoring soil biological properties during the restoration of a phosphate mine under different tree species and plantation types. Ecotoxicol. Environ. Saf. 180, 130–138.

Gu, X., Fang, X., Xiang, W., Zeng, Y., Zhang, S., Lie, P., Peng, C., Kuzyakov, Y., 2019b. Vegetation restoration stimulates soil carbon sequestration and stabilization in a subtropical area of southern China. Catena 181.

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.

Hodson, A.K., Ferris, H., Hollander, A.D., Jackson, L.E., 2014. Nematode food webs associated with native perennial plant species and soil nutrient pools in California riparian oak woodlands. Geoderma 228, 182–191.

Hu, N., Li, H., Tang, Z., Li, Z., Tian, J., Lou, Y., Li, J., Li, G., Hu, X., 2016. Community diversity, structure and carbon footprint of nematode food web following reforestation on degraded Karst soil. Sci. Rep. 6.

Ingham, R.E., Santo, G.S., 1994. Extraction methods. Quantifying nematode control. Res. Rep. 149, 55–59.

Jackson, L.E., Bowles, T.M., Ferris, H., Margenot, A.J., Hollander, A., Garcia-Palacios, P., Daufresne, T., Sanchez-Moreno, S., 2019. Plant and soil microfaunal biodiversity across the borders between arable and forest ecosystems in a Mediterranean landscape. Appl. Soil Ecol. 136, 122–138.

Jiang, C., Sun, B., Li, H.X., Jiang, Y.J., 2013. Determinants for seasonal change of nematode community composition under long-term application of organic manure in an acid soil in subtropical China. Eur. J. Soil Biol. 55, 91–99.

Lenoir, L., Persson, T., Bengtsson, J., Wallander, H., Wirén, A., 2007. Bottom–up or top–down control in forest soil microcosms? Effects of soil fauna on fungal biomass and C/N mineralisation. Biol. Fertil. Soils 43, 281–294.

Liu, Y., Zhu, G., Hai, X., Li, J., Shangguan, Z., Peng, C., Deng, L., 2020. Long-term forest succession improves plant diversity and soil quality but not significantly increase soil microbial diversity: evidence from the Loess Plateau. Ecol. Eng. 142, 105631.

Liu, X., Zhang, W., Wu, M., Ye, Y., Wang, K., Li, D., 2019. Changes in soil nitrogen stocks following vegetation restoration in a typical karst catchment. Land Degrad. Dev. 30, 60–72.

Li, Y.-B., Wang, H., Fu, J., 2008. Regeneration niche of main tree species in Quercus liaotungensis forest gaps in Ziwuling Mountain. Shengtaixue Zazhi 27, 2062–2066.

Lozano, Y.M., Hortal, S., Armas, C., Pugnaire, F.I., 2014. Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. Soil Biol. Biochem. 78, 298–306.

Martin, M., Morin, H., Fenton, N.J., 2019. Secondary disturbances of low and moderate severity drive the dynamics of eastern Canadian boreal old-growth forests. Ann. For. Sci. 76, 16.

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.

Mejia-Madrid, H.H., 2018. Soil nematode abundance and diversity from four vegetation types in Central Mexico. Nematology 20, 15–32.

Nico, E., Tomasz, D., Simone, C., Hobbie, S.E., Meyer, R.J., Kally, W., Reich, P.B., 2013. Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. PNAS 110, 6889–6894.

Olatunji, O.A., Gong, S., Tariq, A., Pan, K., Sun, X., Chen, W., Zhang, L., Dakhil, M.A., Huang, D., Tan, X., 2019. The effect of phosphorus addition, soil moisture, and plant type on soil nematode abundance and community composition. J. Soils Sediments 19, 1139–1150.

Olsen, S., Sommers, L., Page, A., 1982. Methods of soil analysis. Part 2. Chemical and microbiological properties of Phosphorus. ASA Monograph 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, 623–629.

Pausch, J., Hofmann, S., Scharroba, A., Kuzyakov, Y., Ruess, L., 2016a. Fluxes of root-derived carbon into the nematode micro-food web of an arable soil. Food webs 9, 32–38.

Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen, O., Kandeler, E., Ruess, L., 2016b. Small but active–pool size does not matter for carbon incorporation in below-ground food webs. Funct. Ecol. 30 (3), 479–489.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144.

Sánchez-Moreno, S., Ferris, H., 2007. Suppressive service of the soil food web: effects of environmental management. Agric. Ecosyst. Environ. 119, 75–87.

Sánchez-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, 2374–2383.

Sánchez-Moreno, S., Nicola, N.L., Ferris, H., Zalom, F.G., 2009. Effects of agricultural management on nematode–mite assemblages: soil food web indices as predictors of mite community composition. Appl. Soil Ecol. 41, 107–117.

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.

Scharroba, A., Dibbern, D., Huenninghaus, M., Kramer, S., Moll, J., Butenschoen, O., Bonkowski, M., Buscot, F., Kandeler, E., Koller, R., Krueger, D., Lueders, T., Scheu, S., Ruess, L., 2012. Effects of resource availability and quality on the structure of the micro-food web of an arable soil across depth. Soil Biol. Biochem. 50, 1–11.

Sechi, V., Goede, R.G.M.D., Rutgers, M., Brussaard, L., Mulder, C., 2018. Functional diversity in nematode communities across terrestrial ecosystems. Basic & Applied Ecology In press, S1439179117304450-.

Shannon, C.E., Weaver, W., 1950. The mathematical theory of communication. Bell Labs Tech. J. 3, 31–32.

Sun, F., Pan, K., Olatunji, O.A., Li, Z., Chen, W., Zhang, A., Song, D., Sun, X., Huang, D., Tan, X., 2019. Specific legumes allay drought effects on soil microbial food web activities of the focal species in agroecosystem. Plant Soil 437, 455–471.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., Caixeta, L.d.B., Chen, X., Costa, S.R., Creamer, R., da Cunha Castro, J.M., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutierrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Rodriguez Martin, J.A., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Palomares Rius, J.E., Pan, K., Peneva, V., Pellissier, L., Pereira da Silva, J.C., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Sanchez Moreno, S., Scheu, S., Setala, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergard, M., Villenave, C., Waeyenberge, L., Wall, D. H., Wilschut, R., Wright, D.G., Yang, J.-i., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194-+.

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, 14296–14301.

Wang, K.B., Shao, R.X., Shangguan, Z.P., 2010a. Changes in species richness and community productivity during succession on the Loess Plateau (China). Polish J. Ecol. 58, 501–510.

Wang, Y.Q., Shao, M.A., Shao, H.B., 2010b. A preliminary investigation of the dynamic characteristics of dried soil layers on the Loess Plateau of China. J. Hydrol. 381, 9–17.

Wang, J., Liu, G.B., Zhang, C., Wang, G.L., Fang, L.C., Cui, Y.X., 2019. Higher temporal turnover of soil fungi than bacteria during long-term secondary succession in a semiarid abandoned farmland. Soil Tillage Res. 194, 11.

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.

Wu, Y., Chen, W., Li, Q., Guo, Z., Li, Y., Zhao, Z., Zhai, J., Liu, G., Xue, S., 2020. Ecoenzymatic stoichiometry and nutrient limitation under a natural secondary succession of vegetation on the Loess Plateau, China. Land Degrad. Develop. 32 (1), 399–409.

Xiao, H., Wang, B., Lu, S., Chen, D., Wu, Y., Zhu, Y., Hu, S., Bai, Y., 2020a. Soil acidification reduces the effects of short-term nutrient enrichment on plant and soil biota and their interactions in grasslands. Glob. Change Biol. 26, 4626–4637.

Xiao, L., Liu, G., Li, P., Li, Q., Xue, S., 2020b. Ecoenzymatic stoichiometry and microbial nutrient limitation during secondary succession of natural grassland on the Loess Plateau, China. Soil Tillage Res. 200, 104605.

Yan, B.S., Sun, L.P., Li, J.J., Liang, C.Q., Wei, F.R., Xue, S., Wang, G.L., 2020a. Change in composition and potential functional genes of soil bacterial and fungal communities with secondary succession in Quercus liaotwigensis forests of the Loess Plateau, western China. Geoderma 364, 11.

Yan, W.M., Zhong, Y.Q.W., Zhu, G.Y., Liu, W.Z., Shangguan, Z.P., 2020b. Nutrient limitation of litter decomposition with long-term secondary succession: evidence from controlled laboratory experiments. J. Soils Sediments 20, 1858–1868.

Yang, H., Wang, Z., Li, X., Gao, Y., 2019. Vegetation restoration drives the dynamics and distribution of nitrogen and phosphorous pools in a temperate desert soil-plant system. J. Environ. Manage. 245, 200–209.

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fertil. Soils 37, 199–210.

Yeates, G.W., 2007. Abundance, diversity, and resilience of nematode assemblages in forest soils. Canadian J. For. Res.-Revue Canadienne De Recherche Forestiere 37, 216–225.

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, 315-331.

Shao, Y., Zhang, W., Liu, Z., Sun, Y., Chen, D., Wu, J., Zhou, L., Xia, H., Neher, D.A., Fu, S., 2012. Responses of soil microbial and nematode communities to aluminum toxicity in vegetated oil-shale-waste lands. Ecotoxicology 21 (8), 2132–2142.

Zelles, L., 1999. Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biol. Fertil. Soils 29, 111–129.

Zhang, C., Liu, G., Xue, S., Wang, G., 2016. Soil bacterial community dynamics reflect changes in plant community and soil properties during the secondary succession of abandoned farmland in the Loess Plateau. Soil Biol. Biochem. 97, 40–49.

Zhang, J., Ai, Z., Liang, C., Wang, G., Xue, S., 2017a. Response of soil microbial communities and nitrogen thresholds of Bothriochloa ischaemum to short-term nitrogen addition on the Loess Plateau. Geoderma 308, 112–119.

Zhang, W., Qiao, W., Gao, D., Dai, Y., Deng, J., Yang, G., Han, X., Ren, G., 2018. Relationship between soil nutrient properties and biological activities along a restoration chronosequence of Pinus tabulaeformis plantation forests in the Ziwuling Mountains, China. Catena 161, 85–95.

Zhang, X., Ferris, H., Mitchell, J., Liang, W., 2017b. Ecosystem services of the soil food web after long-term application of agricultural management practices. Soil Biol. Biochem. 111, 36–43.

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.

Zhao, J., Wang, F., Li, J., Zou, B., Wang, X., Li, Z., Fu, S., 2014. Effects of experimental nitrogen and/or phosphorus additions on soil nematode communities in a secondary tropical forest. Soil Biol. Biochem. 75, 1–10.

Zou, H., Liu, G., Wang, H., 2002. The vegetation development in north Ziwulin forest region in last fifty years. Acta Botanica Boreali-occidentalia Sinica 22, 1–8.

Zhong, Y., Yan, W., Wang, R., Wang, W., Shangguan, Z., 2018. Decreased occurrence of carbon cycle functions in microbial communities along with long-term secondary succession. Soil Biol. Biochem. 123, 207–217.