Soil nematode diversity and network complexity mediate the impact of altered precipitation on dryland agroecosystem multifunctionality in the loess tableland area of China

1. Introduction

In recent decades, changes in precipitation patterns caused by global climate warming had significant impacts on terrestrial ecosystems (Eck et al., 2020; Li et al., 2021; Griffin-Nolan et al., 2021), particularly in dryland agroecosystems (Feng et al., 2022; Lu et al., 2018). Dryland agroecosystems cover a vast area globally and play a crucial role in world agriculture and food production (Javed et al., 2021). Previous studies have investigated the effects of altered precipitation on various ecosystem functions in dryland agroecosystems, such as crop productivity (Liu et al., 2011; Towa et al., 2013), organic matter decomposition (Cuevas et al., 2013; Meier and Leuschner, 2010; Wang et al., 2021b) and nutrient cycling (Liu et al., 2006). However, most of these studies have focused on individual functions without considering the multifunctionality of agroecosystems, which refers to their ability to provide multiple functions simultaneously (Cui et al., 2022a; Guo et al., 2023). Understanding how agroecosystems simultaneously provide multiple functions is essential for predicting their responses to altered precipitation and guiding sustainable development in the face of climate change.

Biodiversity plays a crucial role in maintaining ecosystem functions and connecting them with environmental change (Ali, 2023; Lefcheck et al., 2015). Previous research has shown that high biodiversity, both in terms of plant and microbial diversity, can alleviate the negative effects of altered precipitation on ecosystem multifunctionality (Lefcheck et al., 2015; Soliveres et al., 2016). However, most studies have focused on taxonomic diversity (Chen et al., 2021b; Walden et al., 2023; Wan et al., 2022), leaving other dimensions of biodiversity, such as functional and phylogenetic diversity, poorly understood (Walden et al., 2023). Functional diversity refers to the variety and range of functional traits (morphological, physiological, and ecological traits of species) within a biological community (Zhao et al., 2023; Zhou et al., 2020), while phylogenetic diversity represents the evolutionary relatedness of species (Wang et al., 2022). Additionally,
previous studies have mainly focused on single trophic level, such as plant or soil microbial communities (Berdugo et al., 2019; Kou et al., 2021; Li et al., 2023a; Lohmann et al., 2018), while ignoring the complex ecological networks that exist across multiple trophic levels (Schuldt et al., 2018; Soliveres et al., 2016; Zhang et al., 2021a). Recent evidence suggests that the complexity of soil multi-trophic networks play an important role in influencing the effects of altered precipitation on ecosystem multifunctionality (Dacal et al., 2022; McLean et al., 2022). Therefore, integrating different dimensions of biodiversity can considering multi-trophic interrelationships can enhance our understanding of how biodiversity responds to altered precipitation and contributes to ecosystem multifunctionality (Soliveres et al., 2016).

In agroecosystems, soil biodiversity plays a crucial role in maintaining ecosystem functions (Jiao et al., 2022c; Wu et al., 2023). Nemaotae, as the most abundant and diverse animals in soil, encompass multiple trophic groups such as bacterial feeders, fungal feeders, plant parasites and omnivores-predators (Yeates, 2003; Yeates, 2004). They have complex impacts on the functioning of agricultural ecosystems (Guo et al., 2021). Bacterial- and fungal- feeding nematodes are important consumers of soil microbes (Schuldt et al., 2018), and their predation activities can regulate soil microbial composition and diversity (Yeates and Wardle, 1996). This, in turn, promotes organic matter decomposition, nutrient cycling, and ultimately increases crop productivity (Pires et al., 2023; Yeates, 2004). Plant-parasitic nematodes are notorious belowground pests in agroecosystems (Bebber et al., 2014; Yeon et al., 2019), causing damage to plants through root feeding and negatively impacting crop growth and production (Liu et al., 2008; Taba et al., 2006). Omnivorous-predatory nematodes, at higher trophic levels, can capture and consume microbivorous and plant-parasitic nematodes, thus regulating the structure and complexity of the whole nematode community (Biederman et al., 2008; Ekschmitt et al., 2001; Li et al., 2023b). Nematodes have been widely used as bioindicators of soil biodiversity and general ecosystem conditions due to their presence at multiple trophic levels of soil food web and sensitivity to environmental disturbances, including climate change (Gingold et al., 2013; Pires et al., 2023). Therefore, soil nematode diversity is crucial for predicting and regulating the multifunctionality of agroecosystems under climate change (e.g., altered precipitation) (Siebert et al., 2020). However, further research is needed to provide concrete evidence and detailed information, particularly regarding the multiple dimensions of nematode diversity.
The Loess Plateau of China is a rainfed agricultural region where precipitation is a key factor influencing agroecosystem functioning (Li et al., 2016; Qiu et al., 2021; Xu et al., 2017). Numerous studies have been conducted in this region to explore the effects of altered precipitation on agroecosystems, including crop growth and yield, as well as soil moisture, organic matter and nutrient availability (Bai et al., 2008; Fang and Guo, 2015; Qiu et al., 2021; Wang et al., 2021b), and microbial properties (e.g. abundance, biomass and community characteristics) (Wang et al., 2023b; Wang et al., 2020). However, the responses of agroecosystem multifunctionality to altered precipitation are still not well understood. Moreover, despite the significant role of nematode communities in soil food webs, their responses to altered precipitation and their roles in maintaining agroecosystem functioning in the Loess Plateau region have received limited attention (Jiao et al., 2022c).

In this study, a manipulative field experiment was conducted in a typical dryland agroecosystem (grown with winter wheat) in the loess tableland region, which is the key agriculture area of the Loess Plateau. The experiment applied a fully factorial design to investigate the effects of altered precipitation and nematode inhibitor application on soil nematode diversity and agroecosystem multifunctionality. Three levels of precipitation (ambient, 1/3 decreased, and 1/3 increased) were simulated in situ based on historical precipitation data (Xu and Huang, 2023). Additionally, to clarify the importance of the soil nematode community in driving agroecosystem multifunctionality, two levels of nematode inhibitor treatment with or without the addition of 10% fosthiazate granules were applied under each precipitation level. Our preliminary results indicate that fosthiazate, a kind of broad-spectrum nematode inhibitor, effectively reduces the abundance and diversity of soil nematodes in the loess tableland region (data not published). High-throughput sequencing was used to analyze the composition and diversity (taxonomic, functional and phylogenetic diversity) of soil nematode communities under each treatment. Furthermore, we also analyzed the complexity of nematode co-occurrence networks to understand the complex interrelationships between different nematode groups. Agroecosystem multifunctionality was quantified based on key functions related to soil nematodes, including crop productivity, organic carbon decomposition, nutrient supply, and pathogen control. The objectives of this study are: (1) to address the effects of altered precipitation on agroecosystem multifunctionality, (2) to explore the responses of soil nematode diversity (different diversity dimensions) and co-occurrence
network complexity to altered precipitation, and (3) to clarify the importance of nematode responses in predicting and driving agroecosystem multifunctionality under altered precipitation.

2. Materials and Methods

2.1. Study area

This study was conducted at the Changwu agroecological experimental station, Institute of Soil and Water Conservation, Northwest A&F University, which is located in Changwu County, Xianyang City, Shaanxi Province, China (107°41′E, 35°14′N). This area is situated in the central south of the Loess Plateau, known for its loessial tableland landform characterized by a thick layer of loess exceeding 100 meters. The elevation of the area is approximately 1200 m. The climate in this region is classified as a warm-temperate continental monsoon climate, with an annual average temperature of 9.2˚C and the average annual precipitation of 542 mm over the past 22 years (1998-2019) (based on the meteorological data service system of Changwu experimental station). The annual sunshine duration was 1977 h and the frost-free period is 171 d. The underground water level ranges from 50 m to 80 m. The study area is representative of a rainfed agricultural region on the Loess Plateau, where winter wheat (Triticum aestivum L.) is a major staple crop. The soil type in this area is dark loessial soil (Heilutu), and the soil texture is silt loam, with a silt content of over 50%. The basic physicochemical properties of the soil at the study site at the begining of the field experiment were as follows: pH 8.17, moisture 13.48%, organic carbon 7.51 g·kg⁻¹, total nitrogen 1.06g·kg⁻¹, NO₃⁻-N 1.31mg·kg⁻¹, NH₄⁺-N 0.5 mg·kg⁻¹, available phosphorus 3.69 mg·kg⁻¹.

2.2. Experimental design and setup

A fully factorial field experiment (precipitation × nematode inhibitor) was conducted in a winter wheat field from August 2020 to July 2021. The experiment included sampling plots that three levels of precipitation (ambient precipitation (AP), decreased precipitation (DP, decreased by one-third below AP) and increased precipitation (IP, increased by one-third over AP). Additionally, one half of the sampling plots under each precipitation received the addition of nematode inhibitor (10% fosthiazate granules) (F) and the other half did not (NF). Thus, there were a total of six treatments, with six replicate sampling plots for each treatment (36 sampling plots in total). The selection of the three precipitation levels in our study was based on long-term annual precipitation data from the study area and the Chinese Loess Plateau region. . The data
collected spanned 22 years (1998-2019) for the study area (http://cwa.cern.ac.cn/meta/metaData) and 50 years (1957-2018) for the Chinese Loess Plateau area (Xu and Huang, 2023). During the specific experimental year of our study (August 2020 to July 2021), the total precipitation recorded in the study area was 537.8 mm (The monthly precipitation and average daily rainfall during this period are shown in Table S1), which is similar to the average annual precipitation over 1998-2019 (542 mm). These three levels of precipitation (DP, AP and IP) in our study were chosen to represent different precipitation conditions in various drought-prone regions of the Loess Plateau, including arid, semi-arid to semi-humid, and humid regions. Additionally, they can also reflect the variations in precipitation between different years, such as dry, average, and wet years.

In August 2020, all sampling plots (6 m × 3 m) were established, with a distance of 1m between two adjacent plots. A plastic sheet was inserted in the middle of the buffer zone for water isolation. The plastic sheets, with the height of 1.1m, were inserted at a depth of 1 m underground to restrict soil water movement. Additionally, 0.1 m of the sheets remained aboveground to prevent surface runoff. To create different precipitation levels, a manmade, real-time, precipitation allocation system was utilized, consisting of a precipitation shelter, a water tank, and auto-flowing drip irrigation equipment (14 polyvinyl chloride (PVC) pipes) (Fig. 1). For decreased precipitation (DP) treatment, a precipitation shelter was built in each plot. The shelter roofs were made of transparent plastic sheets (V-shaped strips), covering one-third of each plot area. As a result, the covered plots only received two-thirds of the ambient precipitation, while one-third of the precipitation was intercepted and collected in water tank. The collected precipitation was then transferred to an adjacent plot for increased precipitation (IP) treatment using auto-flowing drip irrigation pipes. These pipes, with a diameter of 2.5 cm, were evenly placed in the plot. The plots for AP treatment did not have a precipitation allocation system. The building of precipitation allocation systems was completed in August 2020. Shelters, tanks and PVC pipes were cleaned monthly to prevent any blockage caused by litter or other materials.

In mid-September 2020, the plots for nematode inhibitor (F) treatment were treated with the addition of 10% fosthiazate granules at the dosage of 30 kg/hm². The fosthiazate granules were uniformly sprinkled on the surface soil, and then ploughed to a depth of 20 cm. In the plots without nematode inhibitor (NF), the soil was also ploughed. Fosthiazate
((RS)-S-sec-butyl-O-ethyl-2-oxo-1,3-thiazolodin-3-ylphosphonothioate) is a widely-used organophosphate pesticide that functions as a broad-spectrum nematode inhibitor (Wada and Toyota, 2008). It inhibits the activity of acetylcholinesterase in root-feeding nematode upon contact and systemic translocation (Kimpinski et al., 2005). The results of our preliminary research has shown that the application of fosthiazate can effectively decrease soil nematode abundance and diversity in winter wheat fields in the loess tableland area (data not shown). The dosage of fosthiazate applied in our study was determined based on the recommended amount for optimal control of plant-parasitic nematodes (Gunjima et al., 2023; Kimpinski et al., 1997).

In late-September of 2020, a local variety of winter wheat, Changhang No.1, was sowed at a density of 150 kg/hm² in all plots. Prior to sowing, fertilizer consisting of urea (46% N) and calcium superphosphate (16% P₂O₅) was applied at a rate of 150 kg/hm² and 90 kg/hm², respectively. In March 2021, manual weeding was conducted in all the plots. All other field management followed local production practices during the entire growth period.

2.3 Plant and soil sampling

In early July of 2021, the wheat in all plots was harvested, and plant and soil samples were collected. Within each sampling plot, two random locations were selected, and approximately 10 wheat plants were manually cut at ground level in each location. These plant samples were collected to analyze shoot height and biomass. Root samples were obtained using a multi-point sampling method at the depth of 0–40 cm, using a 10-cm diameter root drilling sampler. The roots were then separated from the soil by washing them over a sieve of 0.15 mm mesh, and these samples were used to analyze root biomass. Additionally, a 1 m × 1 m quadrat was established in each plot to investigate wheat yield, in which all wheat plants were harvested at ground level, and spikes were collected. All plant samples were placed in paper bags and taken back to the laboratory immediately for further analysis.

In each plot, 12 soil samples were obtained along an S-shaped curve at the depth of 0–20 cm using a 5-cm diameter soil drilling sampler. To ensure representative results, these samples were homogenized together and combined into one composite sample. All soil samples were taken back to the laboratory immediately, and each sample was divided into three subsamples. One subsample was sieved through a 5-mm sieve and stored at 4°C for the analysis of soil nematode community, soil moisture, and microbial biomass carbon and nitrogen. Another subsample was
stored at -20°C for analyzing soil enzyme activities. The third subsample was air-dried for
analyzing other soil physicochemical properties.

2.4 Measurement of plant and soil properties

2.4.1 Wheat growth and yield

The shoot height (SH) of wheat plants were measured, and subsequently, all wheat samples
were oven-dried at 105°C for 30 min and then oven-dried at 75°C to constant weight. The dry
weight of aboveground plant and root samples were recored as shoot and root biomass (SB and
RB), respectively. In the case of wheat samples collected in 1m² squares, the number of spikes
(WSN) was counted, and the dry weight of all wheat grains in 1m² squares were measured to
calculate the grain yield of winter wheat (WY) (kg/hm²). Additionally, a random selection of one
thousand wheat grains was weighed to determine the thousand-grain weight (WTGW).

2.4.2 Soil physicochemical properties

Soil pH was determined using the potentiometric method (water-soil ratio: 2.5:1). Soil
moisture content (SMC) was measured using the gravimetric method at 105°C. Soil organic
carbon (SOC) was determined using concentrated sulfuric acid (H₂SO₄) hydrolysis and potassium
dichromate (K₂Cr₂O₇) oxidation external heating methods (D.L. Sparks, 1996). Soil total nitrogen
(TN) was determined using the semimicro-Kjeldahl method (Bremner and Keeney, 1965). Soil
total phosphorus (TP) was determined through the ammonium molybdate spectrophotometric
method. Soil available phosphorus (AP) was extracted from soil with 0.5 M NaHCO₃ and assayed
using spectrophotometry. Ammonium (NH₄⁺-N) and nitrate-nitrogen (NO₃⁻-N) in soil were
extracted with 0.01 M CaCl₂, and the concentrations in soil extracts were measured using a
Continuous Flowing Analytical System Auto Ana-lyzer 3-Continuous-Flow Analyzer (SAN++,
SKALAR, Breda, Holland). Readily oxidizable organic carbon (ROC) was determined by
potassium permanganate oxidation colorimetric method. Soil microbial biomass carbon (MBC)
and microbial biomass nitrogen (MBN) content were determined using the chloroformfumigation
extraction method (P.C. Brookes, 1985). The MBC concentrations in the soil extracts were
analyzed using an automated TOC (Total Organic Carbon) analyzer (Multi C/N 3000, Analytik,
Jena,Germany) (Vance et al., 1987), while the MBN concentrations were determined by the

2.4.3 Soil enzyme activities
Soil sample in each plot was used to analyze the enzyme activities associated with carbon, nitrogen and phosphorus cycles. The activities of β-1,4-glucosidase (β-GC) and alkaline phosphatase (AKP) were measured fluorometrically using 4-methylumb elliferone (MUB)-linked model substrates (DeForest, 2009). The urease activity (URE) was determined using the following procedure: 5 g of soil sample was mixed with 1 mL of methylbenzene and, after 15 min, the sample was mixed with 10 mL of 10% urea solution and 20 mL of citrate buffer (pH 6.7). The mixture was filtered after incubation at 37°C for 24 h, and 4 mL of sodium phenolate solution and 3 mL of sodium hypochlorite solution were added to 3 mL of the filtrate. After 20 min, the solution was diluted with distilled water to a final volume of 50 mL, and the released ammonium was assayed colorimetrically at 578 nm. The catalase activity (CAT) was determined as follows: 2 g of soil sample was mixed with 5 mL of 0.3% H₂O₂ and 40 mL distilled water and, after shaking for 20 min, the suspension was titrated with 0.1 N KMnO₄ (Stpniewska et al., 2009).

2.5. Analysis of soil nematode community

Nematodes were extracted from 100 g of fresh soil through a sequential extraction procedure involving Baermann extraction followed by centrifugal sugar flotation (Liu et al., 2008). This extraction procedure has been documented to perform a relative thorough extraction of soil nematodes (Liu et al., 2008). The extracted nematodes were transferred to a 5 ml centrifuge tube, fixed to 4 ml with sterilized water, mixed well and divided equally into two aliquots (2 ml per aliquots). One aliquot was used for counting nematodes under a microscope (40 × magnification) and calculating soil nematode abundance (individual numbers per 100 g of dry soil).

The other aliquot was used for high-throughput sequencing (HTS) to determine the composition of soil nematode community. DNA were isolated from this aliquot according to the instructions of PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA). The quality of the extracted DNA were determined by 1% agarose gel electrophoresis, and the concentration and purity of extracted DNA were determined by NanoDrop 2000 UV–vis spectrophotometer (Thermo Scientific, Wilmington, USA). The primers 3NDF (5′-GGCAAGTCTGGTGCCAG-3′) and 1132-rmodR (5′-TCCGTAATYCTTTAAGT-3′) were used to amplify the V4 variable region of 18S rDNA (Geisen et al., 2018). The amplification conditions were 98°C pre-deformation for 1 min, 98°C deformation for 10 s, 50°C annealing for 30 s, 72°C extension for 60 s, 30 cycles, and 72°C extension for 5 min. Sequencing was performed
on the Illumina HiSeq platform.

The raw data were spliced (FLASH, version 1.2.11), and the spliced sequences were filtered by Trimmomatic (Trimmomatic, version 0.33) and chimeras were removed (UCHIME, version 8.1) to obtain high-quality Tags sequences. Then the sequences were clustered with 97% similarity thresholds to identify operational taxonomic units (OTUs). The Ribosomal Database Project (RDP) Classifier Bayesian algorithm was used to classify all sequences into different taxonomic groups (USEARCH, version 10.0). The NCBI database and Blast algorithm were used to set a threshold value of $10^{-5}$ to obtain the taxonomic information of the species corresponding to each OTU, and to filter the OTUs that belong to Nematoda. Based on the OUT data of Nematoda, we analyzed the characteristics of the nematode community.

2.6. Data statistical analysis

Unless otherwise stated, all statistical analyses were conducted using the R statistical software v.4.2.3.

2.6.1 Analysis of agroecosystem multifunctionality

In this study, we collected 17 plant and soil variables that quantify four groups of key agroecosystem functions influenced by soil nematodes: (1) crop productivity (shoot biomass, root biomass, grain yield, thousand grain weight and spike number of wheat), (2) nutrient provisioning (STN, NH$_4^+$-N, NO$_3^-$-N, STP, AP, alkaline phosphatase activity, and urease activity), (3) organic carbon decomposition (SOC, ROC, β-1,4-glucosidase activity and catalase activity), and (4) resistance to plant pathogens (reduced relative abundance of fungal plant pathogens in soils) (Jiao et al., 2021). The relative abundance of potential fungal plant pathogens in soils was determined based on the HTS data of soil fungal communities (Appendix 1 in Supplementary Materials), and was inferred by parsing the soil phylotypes using FUNguild package in RStudio software 4.2.3. The inverse abundance (reduced relative abundance) of potential fungal plant pathogens was calculated by taking the inverse of the variable (total relative abundance of fungal plant pathogens $\times -1$)(Jiao et al., 2021). In total, to assess agroecosystem multifunctionality, a multifunctionality index was calculated for each sampling plot using an averaging approach (Maestre et al., 2012). To eliminate the effects of differences in measurement scale between variables representing different ecosystem functions, Z-scores were calculated for each variable and averaged to obtain the multifunctionality index (Maestre et al., 2012).
2.6.2 Analysis of soil nematode diversity

(1) Taxonomic diversity: To assess the taxonomic diversity of soil nematode communities, we calculated four diversity indexes based on the HTS data using the function `diversity` implemented in vegan package of R software. These indexes include the Shannon-Wiener diversity index ($H'$) (Shannon, 1948), the Chao1 index (Chao, 1984), the Pielou evenness index ($J'$) (Pielou, 1966) and the Simpson dominance index ($\lambda$) (Simpson, 1949). (2) Phylogenetic diversity: We constructed a phylogenetic tree using distance methods (Neighbour-Joining and Maximum Likelihood) and measured the phylogenetic diversity of nematodes using PD_whole_tree, This index represents the total branch lengths of the phylogenetic tree, and was calculated using the picante package of R software. (3) Functional diversity: We selected three trait categories to describe the functional characteristics of soil nematodes: diet: bacterivore, fungivore, herbivore, omnivore and predator (Yeates and Wardle, 1996), life history (c-p value that ranges from 1 to 5 and represents the position of the genus on a $r - K$ spectrum) (Bongers and Bongers, 1998); and (c) body mass (the mass averaged across species in a given genus). These traits are critical for nematodes to perform a variety of agroecosystem functions (Wang et al., 2023c), which can be obtained from the database of Nematode Ecophysiological Parameter (http://nemaplex.ucdavis.edu). We calculated three indexes to evaluate the functional diversity of soil nematodes, including the functional evenness index (FEve), the functional divergence index (FDiv) and the functional dispersion index (Fdis), using the mFD package of R software. (4) Multi-dimensional diversity: To obtained a comprehensive measure of nematode diversity, we calculated a multi-dimensional diversity index by averaging the standardized values (Z-scores) of nematode taxonomic, phylogenetic and functional diversity (Wagg et al., 2014).

2.6.3 Soil nematode co-occurrence networks analysis

The co-occurrence network analysis of soil nematodes was applied using the igraph package of R software based on Spearman correlation analysis. Firstly, a general co-occurrence network was constructed, consisting of soil nematodes indentified from all sampling plots. Then, the separate nematode networks were also constructed for different precipitation treatments (DP, AP and IP) or different nematode inhibitor treatments (F and NF). Finally, the topological parameters of all these networks were analyzed. Nematode genera with mean relative abundance greater than 0.1 % were selected for Spearman correlation analysis, and genera with Spearman correlation
coefficients ($\rho$) greater than 0.6 or statistical significance ($P < 0.05$) were used to construct the network (Guseva et al., 2022). Gephi software 0.9.6 was used to visualize the co-occurrence network. Additionally, sub-networks were extracted for each soil sample in each plot using the induced-subgraph function of the igraph package in R software. Topological parameters were calculated for each sub-network, including the number of nodes (NN) and edges (EN), graph density (GD), average degree (AD), average path length (APL), clustering coefficient (CC), betweenness centrality (BC), and positive (PCR) and negative correlation ratios (NCR). The nodes comprised in the network represent nematode genera and edges represent pairwise associations among nematode genera. Average degree denotes the average number of edges per node. Average path length is the mean length of all the shortest paths between all paired nodes. Graph density is the ratio of the number of edges observed in the network to the number of possible edges. Clustering coefficient is the sum of the proportion of nodes that are connected to other nodes. Betweenness centrality indicates the importance or centrality of a node in a network based on its position in the shortest paths between other nodes. These parameters provide insights into the complexity of nematode networks (Guseva et al., 2022; Yang et al., 2022).

2.6.4 Other statistical analysis

One-way ANOVA followed by the least significant difference (LSD) test was conducted to evaluate the significance of differences ($P < 0.05$) in plant and soil properties as well as nematode community characteristics (diversity and network parameters) among different precipitation and nematode inhibitor treatments, using the SPSS 21.0 (SPSS Inc., Chicago, IL, USA). Redundancy analysis (RDA) was performed to examine the relationships of soil nematode composition with plant and soil properties using CANOCO 5.0 (Microcomputer Power, Ithaca, NY, USA). Spearman correlation analysis was used to investigate the correlation between soil nematode community characteristics (diversity and network topological parameters) and the properties of plant and soil samples across different treatments using the linkET package of R software, and a heat map generated for visualization using the pheatmap package of R software (Mamet et al., 2019; Sunagawa et al., 2015). Ordinary Least Squares linear regression analysis was used to analyze the relationships between agroecosystem multifunctionality and soil nematode diversity/network complexity, using the gcookbook package of R software. Additionally, based on the results of RDA, correlation analysis and regression analysis, a
piecewise structural equation model (piecewise SEM) was constructed to assess the direct and indirect effects of altered precipitation, soil water content, nematode diversity (taxonomic, functional, and phylogenetic diversity) and network complexity on agroecosystem multifunctionality, using the package “piecewiseSEM” of R software. The goodness of model fit was evaluated using Akaike information criterion corrected (AICC) and Fisher's C statistics.

3. Results

3.1 Agroecosystem multifunctionality under altered precipitation and nematode inhibitor addition

Altered precipitation had significant effects on agroecosystem multifunctionality, while the application of nematode inhibitor induced changes in these effects (Fig. 3a). Agroecosystem multifunctionality generally increased with increasing precipitation when nematode inhibitor was not applied (Fig. 3a). However, the application of nematode inhibitor suppressed agroecosystem multifunctionality across all precipitation levels, and reduced the differences caused by altered precipitation (Fig. 3a).

The responses of different agroecosystem functions to altered precipitation and nematode inhibitor addition varied (Fig. 3b-e). Crop productivity function were higher in AP an IP treatments than in DP treatment when nematode inhibitor was not applied (Fig. 3b), attributed to the lower shoot biomass, grain yield and spike number of wheat in DP (Table S2), while it showed little variation under different precipitation levels when nematode inhibitor was applied (Fig. 3b). Nutrient supply function decreased with increasing precipitation when nematode inhibitor was not applied, but it was significantly suppressed by nematode inhibitor in all precipitation treatments, especially in DP (Fig. 3c). Soil total nitrogen content, nitrate-nitrogen content, alkaline phosphatase activity and urease activity all decreased to the lowest in DP treatment with nematode inhibitor addition (Fig. 3c, Table S2). In the absence of nematode inhibitor application, organic carbon decomposition function was significantly higher in IP treatment than in the other two treatments with lower precipitation, while it greatly decreased and did not differ with altered precipitation in the presence of nematode inhibitor application (Fig. 3d). Similar changes were observed in soil organic carbon and readily oxidizable carbon contents, as well as β-1,4-glucosidase activity (Table S2). Pathogen control function greatly increased with increasing precipitation when nematode inhibitor was not added (Fig. 3e). With the application of nematode
inhibitor, pathogen control function was significantly enhanced in DP and AP treatments, and did not differ among precipitation treatments (Fig. 3e).

3.2 Soil nematode community composition and structure under altered precipitation and nematode inhibitor addition

Altered precipitation had no significant effect on soil nematode abundance in the absence of nematode inhibitor, with an average abundance of 1003 ± 162 to 1360 ± 246 individuals per 100 g dry soil (Fig. 3a). The addition of nematode inhibitor resulted in substantial decreases in soil nematode abundance under all the three precipitation levels, ranging from 392 ± 44 to 703 ± 84 individuals per 100 g dry soil (Fig. 3a). However, the extent of decrease varied with precipitation, with a more slight decrease observed in decreased precipitation treatment (DP) (decreased by 26.25%) compared to the increased precipitation (IP) treatment (increased by 44.24%) and the ambient precipitation (AP) treatment (decreased by 69.63%) (Fig. 3a).

Both altered precipitation and nematode inhibitor had a significant impact on the composition of soil nematode communities ($P < 0.05$, Table 2). In this study, a total of 71,114 high-quality sequences were obtained from all soil samples, with 32,788 sequences belonging to Nematoda. These sequences were classified into 176 operational taxonomic units (OTUs), 35 genera, 26 families, 11 orders and 2 classes (Table 1). The number of nematode genera varied little among treatments (27-31), ranging from 27 to 31, with 21 genera common to all treatments (Table 1). In the absence of nematode inhibitor, the dominant nematode genus varied among treatments (Table 1). *Mesorhabditis* (bacterivore) was dominant in the DP treatment (the relative abundance of 39.79%), *Ecumenicus* (omnivore-predator) in the AP treatment (the relative abundance of 17.15%), and *Aphelenchoides* (fungivore) in the IP treatment (the relative abundance of 10.30%) (Table 1). However, when nematode inhibitor was added, two omnivorous-predatory genera, *Ecumenicus* and *Pristionchus*, had the highest dominance in nematode community in the DP (the relative abundance of 23.19%) and IP (the relative abundance of 27.90%) treatments, respectively (Table 1). *Prismatolaimus* (bacterivore) had the highest relative abundance (21.67%) in AP treatment (Table 1).

The trophic structure of soil nematode communities was also greatly affected by altered precipitation and nematode inhibitor (Fig. 3b). In the absence of the nematode inhibitor, bacterial-feeding nematodes dominated the nematode community in the DP treatment (the relative
abundance of 81.19% (Fig. 3b) and the IP treatment (the relative abundance of 50.21% (Fig. 3b), and omnivorous-predatory nematodes had higher relative abundance in the AP (39.20%) and IP (26.29%) treatments than in the DP treatments (5.05%) (Fig. 3b). When nematode inhibitor was applied, the relative abundance of fungal-feeding nematodes significantly decreased under all the three precipitation levels (decreasing from 11.77%-20.66% to 3.44%-5.52%) (Fig. 3b), while the relative abundance of omnivorous-predatory nematodes greatly increased in the DP and IP treatments (Fig. 3b).

3.3 Soil nematode diversity under altered precipitation and nematode inhibitor addition

In terms of taxonomic diversity, the Simpson diversity index ($\lambda$) (Fig. 4a), Pielou evenness index ($J'$) (Fig. 4b) and Shannon-Wiener diversity index ($H'$) (Fig. 4d) of soil nematode communities showed little variation among all treatments, except in the IP treatment with nematode inhibitor application, in which they all decreased obviously. The Chao1 index, which estimates species richness, increased significantly with increasing precipitation when nematode inhibitor was not added. However, it was not greatly affected by altered precipitation when nematode inhibitor was added (Fig. 4c). In terms of phylogenetic diversity, the PD\_whole\_tree diversity index of soil nematode communities slightly increased under increased precipitation (IP), regardless of the presence or absence of nematode inhibitor (Fig. 4e). Regarding functional diversity, the functional divergence index (FDiv) generally increased with increasing precipitation, regardless of nematode inhibitor application (Fig. 4f), while functional dispersion index (FDis) and functional evenness index (FEve) showed similar responses to altered precipitation when nematode inhibitor was added (Fig. 4j, h). Finally, the multidimensional diversity index of soil nematodes, based on the standardized taxonomic, phylogenetic and functional diversity indexes, increased significantly with increasing precipitation in the absence of nematode inhibitor application. However, it did not show significant changes with altered precipitation in the presence of nematode inhibitor (Fig. 4i).

3.4 Soil nematode co-occurrence network characteristics under altered precipitation and nematode inhibitor addition

Both altered precipitation and nematode inhibitor application had significant effects on soil nematode co-occurrence networks (Fig. 5, Table 2). The general co-occurrence network (Fig. 5a) was more complicated compared to the separate networks in different treatments (Fig. 5b-f) (Table
The application of nematode inhibitor had a significantly negative effect on the complexity of soil nematode co-occurrence network (Fig. 5b,c, Table 2), resulting in substantial decreases in the number of nodes (NN) and edges (EN), average degree (AD), graph density (GD) and clustering coefficient (CC) of nematode networks, while induced significant increases in average path length (APL) (Table 2). The positive correlation ratio was high in both the nematode networks of NF (72%) and F (74%) treatments (Table 2). Increased precipitation promoted the formation of more complicated nematode networks (Fig. 5d-f, Table 2), with increases in the number of nodes (NN) and edges (EN), betweenness centrality (BC) and clustering coefficient (CC) (Table 2). Although positive correlation remained dominant (positive correlation ratio > 50%) in nematode networks under altered precipitation, the negative correlation ratio gradually increased with increasing precipitation (from 0.39 to 0.45) (Table 2).

3.5 Relationships between soil nematode communities and agroecosystem multifunctionality

The results of Spearman correlation analysis showed significant correlations between the properties of wheat plant and soil and the parameters of soil nematode diversity and co-occurrence network complexity (Fig.S1). The Shannon-Wiener index of soil nematode community was positively correlated with wheat grain yield (P < 0.05) (Fig.S1). Chao1 index was also positively correlated with wheat grain yield, as well as soil microbial biomass nitrogen and catalase activity (P < 0.05) (Fig.S1). The PD_whole_tree index (PD) was positively correlated with the grain yield and thousand-grain weight of wheat (P < 0.01) (Fig.S1). The functional divergence index (FDiv) of soil nematode community was significantly positively correlated with soil microbial biomass nitrogen (P < 0.01) (Fig.S1), while functional evenness index (FEve) was negatively correlated with soil readily oxidizable organic carbon and available phosphorus (P < 0.05) (Fig.S1). The edge number (ED) of nematode network was positively correlated with soil microbial biomass nitrogen and wheat gain yield at harvest (P < 0.05) (Fig.S1), while the node number was positively correlated with soil catalase activity (P < 0.05) and wheat grain yield (P < 0.01) (Fig.S1).

The Mantel test results further indicated that nematode community composition (the abundance of four nematode trophic groups) was positively correlated with soil microbial biomass nitrogen (MBN) (P < 0.05) (Fig.6). The taxonomic and phylogenetic diversity of nematode communities, as well as the complexity of nematode co-occurrence network, were all positively
correlated with wheat grain yield ($P < 0.05$) (Fig.6). Nematode network complexity, nematode phylogenetic diversity and functional diversity were positively correlated with soil catalase activity (CAT) ($P < 0.05$) (Fig.6), and the latter one was also positively correlated with soil water content (SWC) and available phosphorus (AP) ($P < 0.05$) (Fig.6).

The results of ordinary least squares (OLS) regression showed that soil nematode multi-dimensional diversity was positively correlated with agroecosystem multifunctionality ($P < 0.05$) (Fig.7a), crop production function and organic carbon decomposition function ($P < 0.05$) (Fig.7b, c). The taxonomic (Chao1 index) and phylogenetic diversity (PD_whole_tree index) of soil nematode community also showed positive correlations with soil nematode multi-dimensional diversity ($P < 0.05$) (Fig.7d, g). Additionally, the Shannon-Wiener diversity index of soil nematodes was positively correlated with crop production function ($P < 0.05$) (Fig. 7e), while PD_whole_tree index was positively correlated with pathogen control function ($P < 0.05$) (Fig. 7f). In terms of nematode co-occurrence networks, the average path length (APL) and betweenness centralization (BC) were both positively correlated with organic carbon decomposition function ($P < 0.05$) (Fig. 7h, i).

Subsequently, we performed piecewise structural equation models (SEM) to infer the direct and indirect effects of altered precipitation, soil nematode diversity and network complexity on agroecosystem multifunctionality, in the absence (Fig.8a) and presence (Fig.8b) of nematode inhibitor. Since soil water content is highly sensitive to altered precipitation, it was also used as a predictor of agroecosystem multifunctionality in the models (Fig.8). The first SEM demonstrated that in the absence of nematode inhibitor application, the influence of altered precipitation on agroecosystem multifunctionality was mediated through soil water content, soil nematode diversity (multi-dimensional diversity) and nematode network complexity (Fig.8a). Specifically, in the absence of nematode inhibitor application, altered precipitation indirectly affected soil nematode diversity through soil water content ($\beta=0.81$, standardized coefficient), (Fig.8a). Then, soil nematode diversity had a significant positive influence on nematode co-occurrence network complexity ($\beta=0.84$, standardized coefficient), which further significantly impacted agroecosystem multifunctionality ($\beta=0.62$, standardized coefficient) (Fig.8a). There was also a weak and positive relationship between soil nematode diversity and agroecosystem multifunctionality ($\beta=0.35$, standardized coefficient). The second SEM demonstrated that when
nematode inhibitor was applied, altered precipitation only had a weak, direct influence on soil
nematode diversity ($\beta=0.54$, standardized coefficient). Although altered precipitation still had a
significant effect on soil water content ($\beta=0.54$, standardized coefficient), the relationship between
soil water content and soil nematode diversity was not strong ($\beta=-0.20$, standardized coefficient).
Finally, soil nematode diversity showed a significant and positive effect on agroecosystem
multifunctionality ($\beta=0.58$, standardized coefficient). Soil nematode network complexity had a
weak and positive correlation with soil nematode diversity ($\beta=0.43$, standardized coefficient), but
did not significantly affect agroecosystem multifunctionality ($\beta=-0.02$, standardized coefficient).

4. Discussion

Global climate change is inducing biodiversity decline across many trophic groups (Valencia
et al., 2018; Willis et al., 2015), potentially impacting multiple ecosystem functions and services
(Delgado-Baquerizo et al., 2016; Delgado-Baquerizo et al., 2020; Jing et al., 2015; Naeem et al.,
2012; Wagg et al., 2014). However, the relationship between altered precipitation, soil
biodiversity, and ecosystem multifunctionality, particularly in human-dominated agricultural
ecosystems, remains largely unexplored (Valencia et al., 2018; Wang et al., 2023a). Moreover,
previous research on the influence of belowground biodiversity on ecosystem multifunctionality
has mainly focused on soil microorganisms (Jiao et al., 2022b), while overlooking the significance
of other soil biota, such as nematodes, which occupy crucial positions across various trophic levels
of soil food webs (Jiao et al., 2022c). Therefore, our study investigates the effects of precipitation
variation (increased or decreased by one-third relative to ambient precipitation) on agroecosystem
multifunctionality and elucidates the underlying nematode-driven mechanism in a representative
rainfed agricultural region of China, specifically the loess tableland area.

4.1 Effects of altered precipitation on composition and structure of soil nematode communities

Altered precipitation can have significant effects on soil nematode abundance. Nematodes are
key components of soil food webs, and can provide valuable insights into soil biodiversity and
multitrophic interactions (Pires et al., 2023; Wan et al., 2022). It is widely recognized that most
soil nematodes inhabit water films or water-filled pore spaces in soils. Therefore, increased
precipitation, which leads to higher soil water content, can benefit the survival, growth and
reproduction of nematodes (Cui et al., 2022b; Guo et al., 2021). Consistent with previous research,
our study also found that soil water content increased gradually with precipitation. Consequently,
the treatment with decreased precipitation (DP) had fewer surviving nematodes compared to the

treatments with ambient precipitation (AP) and/or increased precipitation (IP).

Altered precipitation had complex effects on the composition and structure of soil nematode

communities, with changes in soil water content playing a significant mediating role (Ankrom et

al., 2022; Chen et al., 2021a). Different trophic groups of soil nematodes exhibited varying

responses to altered precipitation, with omnivorous-predatory and bacterial-feeding nematodes

showing more pronounced changes. Omnivorous-predatory nematodes, which have larger body

size and higher sensitivity to soil moisture (Guo et al., 2021; Zhou et al., 2021), were adversely

affected by decreased precipitation in the absence of nematode inhibitor application, leading to a

significant decrease in their relative abundance. In the presence of inhibitor addition, decreased

precipitation did not have significant effect, but increased precipitation resulted higher relative

abundance of omnivorous-predatory nematodes. Bacterial-feeding nematodes, on the other hand,

showed an opposite response, with drought not reducing or even increasing their relative

abundance. This could be attributed to the dominance of the bacterial-feeding genus,

*Mesorhabditis*, in the decreased precipitation treatment, as this genus has been reported to thrive

in dry soil environments (Martinez et al., 2023). Furthermore, we observed that the relative

abundance of fungal-feeding nematodes increased with increasing precipitation in the absence of

nematode inhibitor application. This finding can be attributed to the moisture requirement for the

germination and growth of fungal spores (Chen et al., 2023b; Cheng et al., 2022) and the

development of fungal hyphal networks (A’Bear et al., 2014; Chen et al., 2023a). Notably, altered

precipitation had a substantial impact on the *Aphelechoididae* genus, known for its high

sensitivity to drought (Guo et al., 2021; Martinez et al., 2023). However, with the application of

nematode inhibitor, the relative abundance of this genus significantly decreased, and their

differences caused by altered precipitation disappeared.

4.2 Effects of altered precipitation on soil nematode diversity and network complexity

To date, numerous studies have focused on the taxonomic diversity of soil nematode

communities under altered precipitation (Gong et al., 2023; Hu et al., 2022b; Ye et al., 2019), but

the responses of nematode phyllogenetic and functional diversity have received little attention. Our

study provides evidence that increased precipitation enhanced the taxonomic, phyllogenetic and

functional diversity of soil nematode communities to varying degrees. Specifically, as
precipitation increased, the Chao 1 index of soil nematodes gradually rose, indicating an increase in the species number of soil nematode community, including both observed species and unobserved/rare species (Roswell et al., 2021; van den Hoogen et al., 2019). This findings aligns with previous research suggesting that a moist soil environment, resulting from adequate precipitation, supports the survival of a greater number of nematode species (Cui et al., 2022b; Wang et al., 2021a). We also observed an increase in the PD_whole_tree index, which quantifies the evolutionary diversity within a community. This increase is likely due to the larger and more diverse soil nematode community that arises from increased precipitation, allowing for greater genetic variation and relatedness among nematode species (Ankrom et al., 2022; Fu et al., 2024). Furthermore, decreased precipitation had an adverse effect on the functional diversity of nematodes, as evidence by lower functional divergence and functional dispersion indexes in the DP treatment compared to the other two treatments. This decrease in functional diversity may be attributed to limited soil moisture under decreased precipitation, which favors the dominance of certain nematode species with functional traits that enable them to better tolerate drought. Consequently, this dominance leads to reduced diversity and a more homogenized distribution of functional traits within the soil nematode community (Ribeiro et al., 2023; Wu et al., 2024). Overall, our results indicate that increased precipitation stimulates multiple dimensions of soil nematode diversity simultaneously, as indicated by the multidimensional diversity index. However, these beneficial effects were eliminated when nematode inhibitor were applied, likely due to the high dominance of certain nematode genera, such as Pristionchus (27.9%), in the IP treatment with nematode inhibitor application.

The analysis of co-occurrence networks has been widely used in soil biodiversity research and provides mechanistic insights into complex community structure and ecological relationships within soil communities (Berry and Widder, 2014; Yang et al., 2023). Although co-occurrence networks may not always indicate true interactions between species (Li et al., 2023c), they contribute to our understanding of community complexity and its responses to climate change (Chen et al., 2022; Raffard et al., 2023). In our study, we found significant variations in the co-occurrence networks of soil nematodes among under different precipitation levels. Consistent with previous research (Chen et al., 2022), our results showed that increasing precipitation led to a more complex nematode network, characterized by a higher number of nodes and edges. This
could be attributed to soil water content acting as an important environmental filter in shaping nematode communities (Gong et al., 2023; Siebert et al., 2020). Additionally, we observed a higher negative correlation ratio in nematode network with increased precipitation, indicating intensified interspecific competition within the nematode community due to the increased number of nematode species (Han et al., 2022; Jing et al., 2023). Therefore, our findings suggest that increased precipitation promotes the formation of a more intricate nematode network with greater species diversity and increased competition. Furthermore, we found that the use of nematode inhibitor had a negative effect on the complexity of nematode network, as evident from changes in various network parameters (e.g. node number, edge number, average degree, graph density, clustering coefficient and average path length). This negative effect may counteract the positive impact of increased precipitation.

4.3 Contributions of soil nematode properties to agroecosystem multifunctionality under altered precipitation

A multitude of studies have shown a positive relationship between soil biodiversity and the functions and services provided by agroecosystems (Jiao et al., 2022a; Jiao et al., 2022c). In particular, soil nematodes play a crucial role in pest control, nutrient cycling, and organic matter decomposition (Jiao et al., 2022c). Despite this knowledge, the specific contributions of soil nematode diversity to agroecosystems multifunctionality are still being investigated and are not fully understood. Our study provides evidence that by improving different dimensions of nematode biodiversity, including taxonomic, phylogenetic and functional diversity, as well as the complexity of nematode co-occurrence network, increased precipitation can lead to higher crop productivity, better organic matter decomposition, and enhanced pathogen control. As a result, agroecosystems can experience an overall increase in multifunctionality. It is important to note that under decreased precipitation, the increased nutrient supply coincided with decreased nematode diversity. This could be caused by various factors, such as reduced microbial activity (Hu et al., 2022a; van Doan et al., 2021), increased mineralization of organic matter (Thakur et al., 2019; Wang et al., 2003) and decreased plant nutrient uptake (Hao et al., 2017; He et al., 2021; Torode et al., 2016).

Different dimensions of biodiversity in nematode communities showed varying associations with agroecosystem functions. The taxonomic diversity of soil nematodes was closely related to
factors associated with crop productivity, organic carbon decomposition and nutrient supply (e.g. wheat grain yield, MBC, ROC and CAT) (Ankrom et al., 2022; Chen et al., 2024; Feng et al., 2024), exhibiting a positive correlation with agroecosystem multifunctionality. Phylogenetic diversity of nematodes also positively related to agroecosystem multifunctionality, which had positive correlations with wheat grain yield, thousand-grain weight of wheat, and pathogen control. Nematode phylogenetic diversity provides insights into the evolutionary history and relationships among nematode species (Clarke and Warwick, 1999; Zhang et al., 2021b). Although nematode phylogenetic diversity was relatively insensitive to increased precipitation in our study, it is expected that over time, the increased nematode phylogenetic diversity resulting from increased precipitation may have a more significant impact on improving crop productivity and pathogen control in dryland agroecosystems. Functional diversity of soil nematodes, representing the variety of functional traits and ecological roles performed by nematode species (Bakonyi et al., 2007; Biederman et al., 2008), was closely related to factors such as soil available phosphorus, microbial biomass nitrogen and catalase activity. This is consistent with previous findings that nematode functional diversity plays an important role in regulating various ecosystem process, including nutrient cycling and organic matter decomposition (Cesarz et al., 2015; Ilieva-Makulec et al., 2016). Therefore, maintaining diverse ranges of nematode taxa, evolutionary relatedness and functional traits in agroecosystems can contribute to higher ecosystem multifunctionality under increased precipitation (de Jesus-Navarrete and Legorreta, 2022; Ilieva-Makulec et al., 2016).

Furthermore, the complexity of soil nematode network, as reflected by co-occurrence patterns among multitrophic-level nematodes, also play a crucial role in agroecosystem multifunctionality. Soil nematodes engage in integrated energy pathways carried out by interactions among nematode taxa, and these interactions are not necessarily captured by the sum of coexisting individuals (Young et al., 2023; Zhang et al., 2021c). Therefore, studying the role of nematode network complexity in predicting agroecosystem multifunctionality help us understand the importance of intricate soil biological interactions in enhancing and maintaining agroecosystem functioning. The results of our study indicated that certain topological parameters associated with nematode network complexity were positively related to wheat grain yield (node and edge number) and organic matter decomposition (average path length and betweenness centralization),
highlighting the contribution of complex and connected soil nematode networks to improved ecosystem multifunctionality (Jiao et al., 2022b; Wang et al., 2023a). Additionally, as precipitation increased, there was a higher negative correlation ratio in nematode networks, suggesting more competitive interactions between nematode taxa. This case, coupled with higher nematode diversity and lower nutrient supply function, may lead to the collapse of nematode communities (Becker et al., 2012; Maynard et al., 2017), which raises concerns about the stability of agroecosystem function under altered precipitation.

Finally, the SEM results revealed that the impact of altered precipitation on agroecosystem multifunctionality was mediated through several factors. Specifically, in the absence of nematode inhibitor, the influence of altered precipitation on agroecosystem multifunctionality was mediated through soil water content, soil nematode diversity (multidimensional diversity) and nematode network complexity (Fig.8a). However, when nematode inhibitor was applied, the correlation between precipitation variations and soil nematode diversity was weakened (Fig.8b), as the inhibitor significantly decreased the taxonomic diversity of soil nematodes under increased precipitation and the co-occurrence networks of nematodes was also significantly simplified. These findings emphasize the essential role of soil nematode multidimensional diversity and network complexity in mediating the effect of altered application on agroecosystem multifunctionality. Compared to the simplified nematode diversity metrics most previous studies applied, incorporating multiple dimensions of soil nematodes, such as taxonomic, phylogenetic and functional diversity and co-occurrence networks, can lead to more accurate predictions of agroecosystem multifunctionality under altered precipitation. Moreover, this study provides empirical evidence that chemical pesticides targeting belowground pests may negatively impact soil biodiversity and disrupt ecological networks, leading to the suppression of ecosystem functions (Berry and Widder, 2014; Han et al., 2022). Therefore, it is crucial to adopt sustainable agricultural practices that minimize the use of chemical pesticides and promote the conservation of soil biodiversity (Kovacs-Hostyanszki et al., 2017) for the sustainable development of agroecosystems.

Despite these important findings, there are three limitations to consider when interpreting the results and extrapolating conclusions from our study. Firstly, soil biodiversity is complex and distributed across various trophic levels. Although nematode communities serve as simplified
representations of multитrophic soil biota, incorporating information from other unassessed trophic
groups may further improve the predictions of agroecosystem function. For example, some
predators at higher trophic level have been found to be negatively correlated with agroecosystem
function (Buzhdygan and Petermann, 2023; Cardinale et al., 2003). Secondly, our study had a the
limited temporal scale, and conducting long-term field manipulation experiments in the future
would provide a better understanding of the ecological consequence of altered precipitation in
agroecosystems over extended periods. Lastly, it is important to note that co-occurrence network
analysis is based on observational taxa data, and the connection between two taxa in a network is
based on a correlation rather than causal effects. However, while inferring interactions between
organisms can be challenging, network analysis remains a valuable tool for identifying symmetric
correlations between taxa within biological communities, such as mutualism and competition(He
et al., 2023; Khatri-Chhetri et al., 2024).

5. Conclusion

The present study provides insights into the responses of soil nematode diversity and their
role in predicting and driving agroecosystem multifunctionality under altered precipitation in a
winter wheat field in the loess tableland region. The results demonstrate that increased
precipitation has a positive impact on soil water content, leading to greater diversity and network
complexity of soil nematode communities, and ultimately enhancing agroecosystem
multifunctionality. Importantly, this study highlights the importance of different dimensions of
nematode diversity, including taxonomic, functional, and phylogenetic diversity, as well as
co-occurrence network complexity, in linking nematode biodiversity with agroecosystem
multifunctionality under altered precipitation. Therefore, integrating these dimensions of
nematode biodiversity can contribute to a more comprehensive understanding of how soil
nematode communities regulate the effects of precipitation changes on agroecosystem
multifunctionality. It was also suggested that agricultural management practices, such as the use of
chemical pesticides, should consider the value of soil biodiversity in promoting and maintaining
agroecosystem multifunctionality under altered precipitation or other climate change scenarios.
Overall, this study has both empirical and theoretical significance in guiding the sustainable
development of dryland agroecosystems.

CRediT authorship contribution statement

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Jinghua Huang: Conceptualization, Methodology, Visualization, Funding acquisition, Project administration, Validation, Writing – original draft, Writing – review & editing. Jing Chen: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft. Tianyuan Huang: Investigation, Formal analysis, Resources, Writing – review & editing. Guoqing Li: Investigation, Validation, Supervision, Writing – review & editing. Jinshi Jian: Formal analysis, Resources, Writing – review & editing. Zijun Wang: Formal analysis, Resources, Writing – review & editing.

**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.

**Data availability**

Data will be made available on request.

**Acknowledgments**

This work was supported by the National Natural Science Foundation of China (No. U2243225, No.31500449) and the QinChuangyuan project of Shaanxi Province (QCYRCXM-2022-361).

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