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Precipitation regulated soil nematode community and footprint in cropland ecosystems

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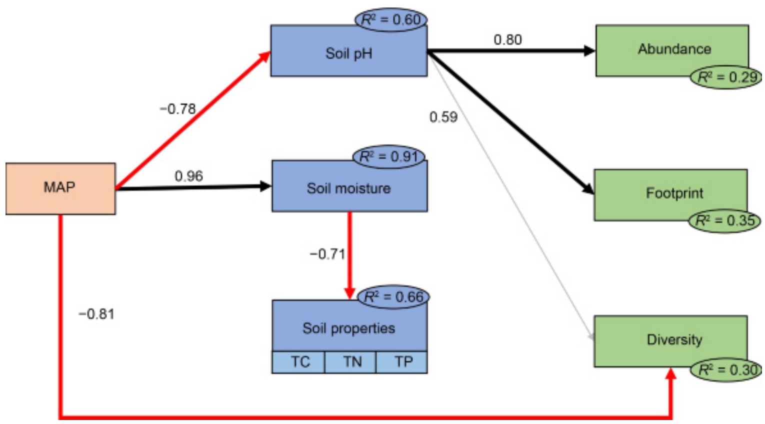
ABSTRACT

- Nematode abundance and footprint show unimodal patterns with precipitation levels.
- MAP governed nematode diversity along the precipitation gradient of agroecosystem.
- Soil pH determined nematode abundance and footprint in low precipitation levels.



Precipitation plays a crucial role in global biodiversity change across terrestrial ecosystems. Precipitation is proven to affect soil organism diversity in natural ecosystems. However, how precipitation change affects the function of the soil nematode community remains unclear in cropland ecosystems. Here, we tested soil nematode communities from different precipitation sites (300 mm to 900 mm) of the agricultural ecosystem. The abundance of total nematodes, fungivores, and plant parasites, together with the footprint of fungivores was significantly affected by mean annual precipitation (MAP) in cropland ecosystem. Plant parasites diversity and footprint showed negative relationships with MAP. The random forest suggested plant parasite footprint was the most responsive to MAP. The structural equation model revealed that MAP affected nematode abundance and footprint indirectly via soil pH; nematode diversity was affected by MAP directly. We conclude that precipitation could act as the main selection stress for nematode diversity among the large gradient of agricultural ecosystems. However, the soil pH may act as a stress factor in determining nematode community and carbon flow in the soil food web. Our study emphasized that using nematode value by trophic group would provide a deep understanding of nematode response to precipitation in cropland ecosystems.

Keywords soil nematode community, nematode carbon flux, the Northeast China Transect, agricultural ecosystem, precipitation

1 Introduction

Precipitation is one of the key drivers of biodiversity from the local to global scale in terrestrial ecosystems (Bellard et al., 2012). Precipitation has been widely recognized as one of the most important factors regulating soil carbon and nitrogen cycling, and hence, influences soil biological communities (Andrés et al., 2017; Feyissa et al., 2021). Precipitation can trigger soil biological communities by causing a transition from alkaline to acidic soils across climate gradients (Shen et al., 2019). It also can directly affect the soil biological community by regulating resource availability and behaviors (Kardol et al., 2010). Even though the impacts of precipitation on soil organisms are documented for some natural ecosystems (Liu et al., 2020; Franco et al., 2022), the responses of belowground communities to the precipitation changes in

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agricultural ecosystems, especially on a large scale, are still poorly understood. Notably, concurring agricultural ecosystems with precipitation may impact soil biological communities with dramatically uncertain processes. This knowledge gap may cause an underestimation of climate change on biological communities.

Agricultural management could cause important changes on the soil biota community, such as changing soil biota community structure, reducing biodiversity and limiting the carbon flow in the soil food web (Sánchez–Moreno and Ferris, 2007; Zhang et al., 2017; Yang et al., 2021). It could weaken top-down control by decreasing the abundance of predators which are sensitive to disturbances (Köhl et al., 2014; Murrell and Barton, 2017). The limited resource supply could cause nematode diversity and footprint reduction in agricultural habitats, compared with natural ecosystems (Gong et al., 2021; Zhang et al., 2017). Simultaneously, monoculture could stimulate the plant parasitic nematodes which is a potential threat to agriculture (Decraemer and Hunt, 2006). Besides, given that the strength of agriculture effects also associates with climate change, such as altered precipitation, this could add additional pressure or release the effect on soil nematodes (Siebert et al., 2020). Therefore, it is important to understand the functional roles of soil nematodes in the agricultural ecosystem.

Soil nematodes are aquatic organisms inhabiting soil water films that depend upon soil moisture in the soil to move and migrate to their feeding sources (Demeure et al., 1979), and their activities are closely tied to moisture availability (Nielsen et al., 2014). They cover all major trophic groups (from bacterivore, fungivore to herbivores and predators) of the soil food web, which show vastly different responses to environmental disturbances and global change (van der Hoogen et al., 2019). Precipitation can control the nematode community by directly controlling moisture availability and indirectly regulating resource availability (Franco et al., 2020). A global-scale study showed that the composition of the nematode community was influenced by precipitation, which could have implications for ecosystem function (Nielsen et al., 2014). Soil nematode community can be used as a bioindicator for gaining a comprehensive understanding of the functional status of soils with precipitation (Cesarz et al., 2015; Song et al., 2016; Cesarz et al., 2017). Moreover, nematode metabolic footprint is proposed to be used to calculate carbon flow in the soil food web by combining the function of nematode biomass and carbon (Ferris et al., 2012; Luo et al., 2021). The nematode metabolic footprint could provide effective information for monitoring resource availability and estimating nematode functions (Ferris, 2010; Barnes et al., 2018). The precipitation effects on soil nematode footprint vary with climate zones and their relationship provides quantification information of precipitation–nematode function to climate change (Franco et al., 2022). Besides, climate change, such as altered precipitation, is highly exposed to agricultural ecosystems (Montgomery, 2007). Since the composition of nematode communities is closely tied to nutrient cycling and decomposition, they also can well reflect the soil condition of the agriculture ecosystem (Crotty et al., 2015). Therefore, understanding the responses of soil nematode community to environmental changes (e.g., precipitation gradient) is critical for guiding soil management in agricultural ecosystems.

The Northeast China Transect (NECT), belonging to the International Geosphere-Biosphere Programme (IGBP), is an effective platform for global change research (Gao and Zhang, 1997; Ni and Zhang 2000), since it is mainly driven by precipitation (Nie et al., 2012; Wang et al., 2015). Meanwhile, NECT is part of the base of agricultural production in China (Ni and Zhang, 2000). This agricultural region is in one climate zone and has a relatively long cultivation history. Therefore, NECT provides an ideal experimental transect for studying the responses of precipitation gradients in agriculture at a wide spatial scale. Previous study has reported how the aboveground processes responded to precipitation in this region (Li et al., 2020). However, the knowledge of how the belowground organisms change with the precipitation gradient along the NECT is still limited.

In this study, soil nematodes were studied to explore how soil organism communities change with precipitation at regional scales of the typical agricultural ecosystems. We hypothesized that nematode abundance, diversity, and carbon flow would increase with precipitation increase since nematode life cycling is closely dependent on water. Furthermore, the nematode diversity and carbon flow analysis based on the trophic group would be more sensitive and provide more detailed information than the whole community-based analysis with precipitation change because different trophic groups responded differently to precipitation. Finally, precipitation would shape nematode diversity and carbon flow via multiple environmental factors, particularly climate and soil factors, in an agricultural ecosystem.

2 Materials and methods

2.1 Study site

The study sites were from 42°N, 128°E to 44°N, 123°E belonging to part of the Northeast China Transect (NECT) which was an important component of the International Geosphere-Biosphere Programme (IGBP) transects. It was a typical transect of middle-high latitude. It spans a wide large range of precipitation gradients with mean annual precipitation (MAP) varying from 300 mm to 900 mm west to east in Northeast China, and MAP is the main driver of this transect (Ni and Zhang, 2000). It is dominated by the temperate continental monsoon climate. The main cropland in this region is planted with maize that is managed conventionally. The maize monoculture has been in practice for over 50-years. In the present study, conventional tillage included fall plowing, spring cultivation, planting with about 20 cm depth of agricultural tillage (commonly referred to as plough sole) (Yan et al., 2017). The base fertilizer of N, P and K was 200, 70, and 90 kg ha^{-1}, respectively. The weeds are handled with a combination of broad-spectrum herbicides and manual hoeing when needed (Guo et al., 2020). The basic properties of the study sites are listed in Table 1.

2.2 Experiment design and soil sampling

The field sampling work was done during the growing season of September 2018 from 6 representative sites of different precipitation levels (from 300 to 900 mm) in the agricultural ecosystem. The 6 sites were Changling (CL), Sijianfang (SJ), Changchun (CC), Dongliao (DL), Longwan (LW) and Baihe (BH) (sites information was listed in Table 1). At each site, three 50 m × 50 m subplots (50 m apart from each other) were randomly established as replicates. At each subplot, 10 soil cores (diameter 5.5 cm) were collected and mixed thoroughly to form as one soil sample. To explore the agricultural effect in these sited, soil depth was chosen as 0−10 cm. Totally, 18 soil samples (6 MAP gradients × 3 replicates) were collected from the maize field. Debris and large roots were removed manually. All of the samples were placed in individual plastic bags and stored at 4°C for further analysis.

2.3 Analysis of soil physicochemical properties

For soil moisture (SM), 10 g of fresh soil was measured by oven-drying at 105°C for 48 h. Soil pH was evaluated in 1:5 soil–water suspension with a pH meter (Mettler Toledo, FE28, Switzerland). The soil samples were grounded to pass through a 0.16 mm mesh. Then, the total soil carbon (TC) and total nitrogen (TN) were combusted by the automatic elemental analyzer (Elemental Analyzer System Vario MACRO cube, Germany), and HCl was used to preprocess alkaline soil. The total soil phosphorus (TP) was digested with H_2SO_4-$HClO_4$ and detected using the continuous flow analyzer (Skalar 5000, the Netherlands).

2.4 Nematode extraction and identification

A modified cotton-wool filter method was used to extract nematodes from 50 g of fresh soil from each replicate and stored in formalin for identification (Oostenbrink, 1960; Townshend, 1963). A light compound microscope was used to count the total number of nematodes and identify the nematode (100 for each sample) to the genus level (Nikon Eclipse Ni-U, 100× magnification). Based on the feeding habits, the nematodes were assigned to bacterivores (BF), fungivores (FF), omnivores-predators (OP) and plant parasites (PP) (Yeates et al., 1993) (Table S1). The Shannon diversity index, maturity index, enrichment index, structure index and nematode metabolic footprint were calculated (Ikoyi et al., 2021).

Formula for calculating the Shannon diversity index (*H*) was as follows (Yeates and Bongers, 1999):

$$H = -\Sigma P_{\mathrm{i}} \ln P_{\mathrm{i}},$$

P_{i} is the proportion of genera i in the sample.

The nematode metabolic footprint (F) was calculated as per the following formula (Ferris, 2010):

$$F = \Sigma(N_{\mathrm{t}}(0.1W_{\mathrm{t}}/m_{\mathrm{t}} + 0.273(W_{0.75})))$$

N_{t}, the nematode abundance; W_{t}, the nematode fresh bodyweight of genera t; *W*, the average each nematode genus was estimated based on the database available online at the website Nemaplex; m_{t}, cp value of t genus. The nematode Shannon diversity and metabolic footprint were divided into the bacterivorous, fungivorous, plant parasite and omnivore-predator based on the nematode trophic group.

2.5 Statistical analysis

A Mantel test was used to determine which environmental properties (MAP, MAT, soil pH, SM, TC, TN and TP) correlated with soil nematode community. Redundancy analysis (RDA) was applied to examine the effect of environmental properties on soil nematodes using vegan packages of R.

Table 1 Study sites information.

Site	Location	Altitude (m)	MAT (°C)	MAP (mm)	Soil type
Changling (CL)	44°35′N, 123°30′E	140	6.2	381	Salt-alkali
Sijianfang (SJ)	44°18′N, 124°07′E	190	6.2	416	Light chernozem
Changchun (CC)	43°54′N, 125°13′E	232	6.3	586	Black soil
Dongliao (DL)	42°54′N, 125°25′E	310	5.9	688	Dark brown soil
Longwan (LW)	42°22′N, 126°26′E	670	5.9	756	Dark brown soil
Baihe (BH)	42°23′N, 127°05′E	780	4.1	840	Dark brown soil

The relationship between MAP and nematode parameters was investigated using linear regression and curvilinear regression analysis. The Random Forest was performed to create models that describe the relationship of MAP with abundance, diversity and footprint of nematode using the rfPermute and A3 package. They were performed in R 4.0.3 (Legendre and Legendre, 2012). Differences at the $P < 0.05$ levels were considered to be statistically significant. Structural equation modeling (SEM) was performed to examine the causal relations between environmental factors and nematode communities (Grace, 2006). A priori structural equation model was constructed on the relationship of MAP, edaphic factors (TC, TN, TP, SM and pH), and soil nematode based on the literature review and the predictions. The SEM was developed by the full conceptual model using maximum likelihood estimation. The index of Chi-square (χ^2), *P* value, degrees of freedom (*df*), comparative fit index (*CFI*), root mean square error of approximation (*RMSEA*) and akaike information criterion (*AIC*) were used to judge the model. The SEM analysis was conducted by using the Amos 17.0 software (Arbuckle, 2006).

3 Results

3.1 The effect of precipitation on soil nematode community

The Mantel test showed that there were significant correlations between nematode community and environmental properties ($r = 0.44$, $P < 0.01$) (Table 2). Of all the environmental properties, MAP showed the highest correlation with soil nematode communities ($r = 0.44$, $P < 0.01$). The RDA analysis also showed that MAP had the strongest effect on the nematode community ($P < 0.05$) (Fig. 1). Thus, MAP was the fundamental factor that controlled the soil nematode community. Meanwhile, among the soil properties we tested, soil pH mainly affected soil nematodes in SJ and CL sites whose MAP levels were lower than 450 mm. MAP was positively correlated with the soil nematode community in high MAP sites of BH, LW and DL, and negatively correlated with the soil nematode community in low MAP sites of SJ and CL.

Table 2 The Mantel test of soil nematode community and environmental properties.

Variable	Mantel	
	r	*P*
MAP	0.44	<0.01
SM	0.39	<0.01
pH	0.38	<0.01
TN	0.23	<0.05
TC	0.21	0.43
MAT	0.21	0.07
TP	0.15	0.13

3.2 Soil nematode abundance and indices

The abundance of total nematode, FF and PP were significantly affected by precipitation which formed a unimodal relationship with increasing precipitation ($P < 0.05$) (Fig. 2, Fig. 3A). There were no clear variations in the abundance of BF and OP with increasing precipitation. For nematode diversity, precipitation significantly affected total diversity and PP diversity which showed negative relationships with increasing precipitation ($P < 0.05$) (Fig. 2, Fig. 3B). The footprint of FF and OP, as indicated by a unimodal trend in FF footprint and a decrease in OP footprint, changed significantly with increasing precipitation ($P < 0.01$) (Fig. 3C).

3.3 The linkage of environmental properties and soil nematode

The structural equation model of soil nematode with precipitation ($P = 0.99$, $\chi^2 = 1.87$, $df = 8$, $CFI = 1.00$, $RMSEA = 0.00$, $AIC = 41.87$) provided a good match for the data (Fig. 4). MAP affected nematode abundance and footprint through soil pH. Soil pH had direct effects on abundance and footprint. MAP was negatively related to nematode diversity. Soil moisture was strongly affected by MAP and then negatively correlated with soil properties of TC, TN and TP. But there was no significant correlation among soil moisture, soil properties and nematode indices.

The random forest analysis was used to evaluate the importance of soil nematode factor correlated with MAP. It was shown that footprints based on the whole nematode

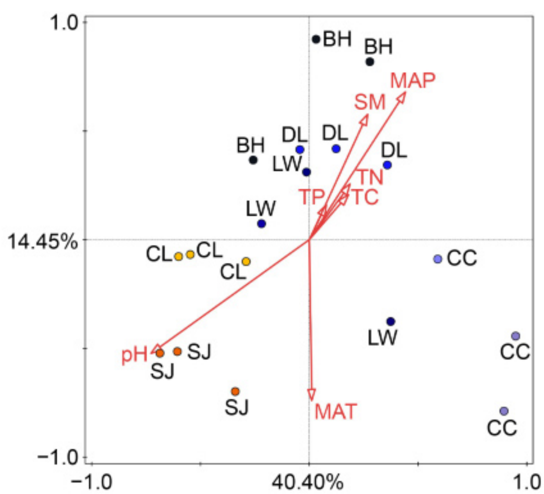

Fig. 1 Redundancy analysis (RDA) of soil nematode indices with environmental variables. The significance of RDA results was tested by the Monte Carlo permutation test.

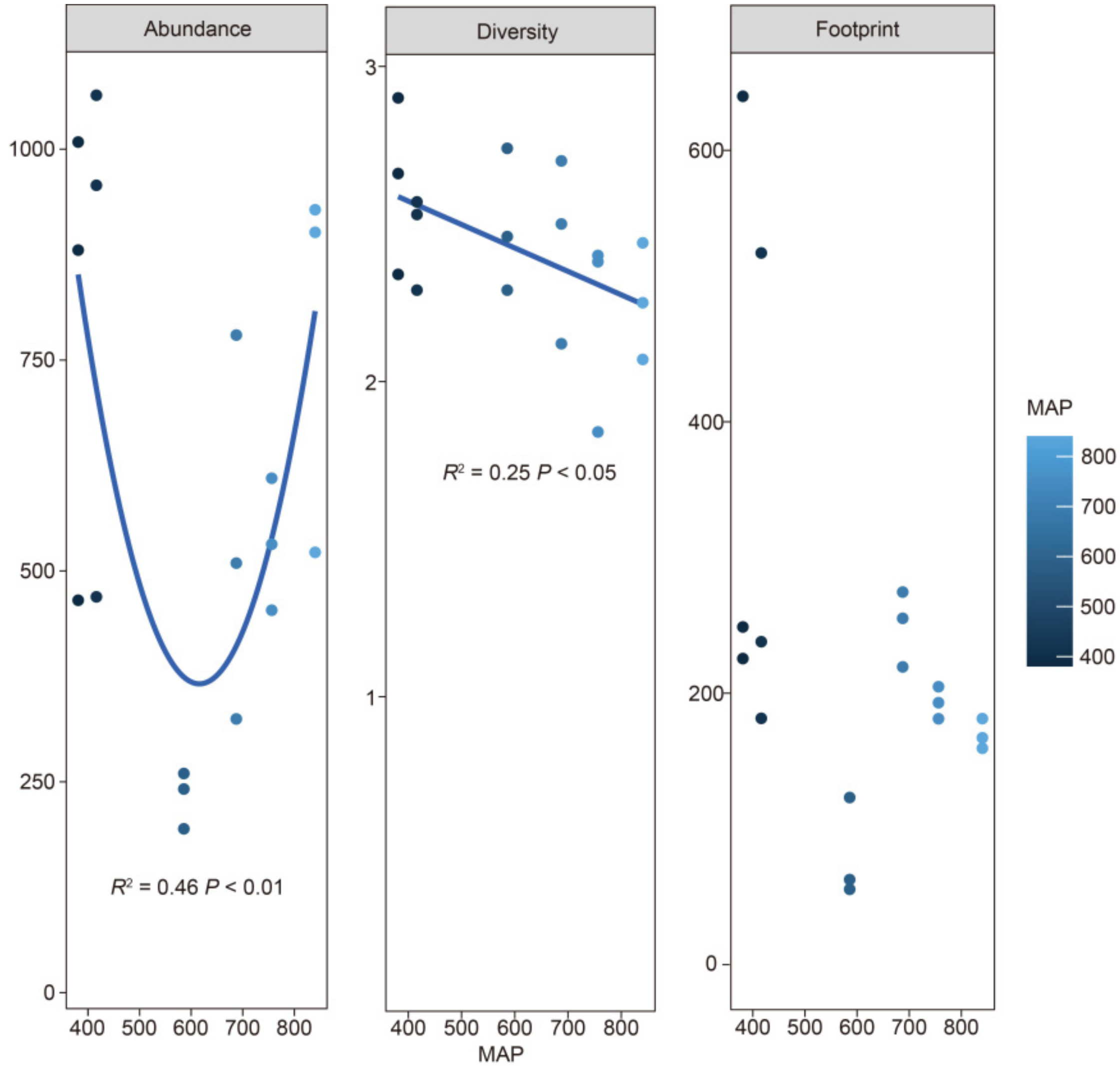

Fig. 2 The total abundance, diversity, and footprint index of nematode community with precipitation levels. Lines indicate regression model fits with statistically supported by R^2 and P values.

community and the footprint of PP were significantly related with MAP ($P < 0.05$) (Fig. 5).

4 Discussion

4.1 The effects of precipitation on soil nematode abundance and diversity

In our study, total abundance of soil nematode, together with the trophic group of fungivores and plant parasites, showed significant changes with MAP. Other studies suggested that precipitation would change the associated nematode community in a large region (Franco et al., 2019; Xiong et al., 2020; Zhang et al., 2020; Ankrom et al., 2022; Cui et al., 2022). And these studies were conducted in the grassland ecosystem. In our study, the nematode community was also found to be severely affected by precipitation, even though they were under agricultural management. Precipitation was directly related to water parameters like soil moisture and water holding capacity (Knapp et al., 2002; Lauenroth and Bradford, 2012). And water availability in the soil matrix was already proven as one of the most important parameters in controlling nematode activity (Landesman et al., 2011). Therefore, water availability, which mainly depended on precipitation, acted as one of the most important triggers that determined nematode community adaptations. It was also found happening in agricultural ecosystems. Besides, changes in precipitation could cause species heterogeneity via spatial variation in terrestrial habitats and their food resources, thereby further leading to different nematode community composition structures at the regional scale (Xiong et al., 2020). However, no significant change was found in omnivore-predators with precipitation. The agricultural ecosystem drove multiple resource stresses that disadvantaged sensitive nematodes such as omnivore-predators.

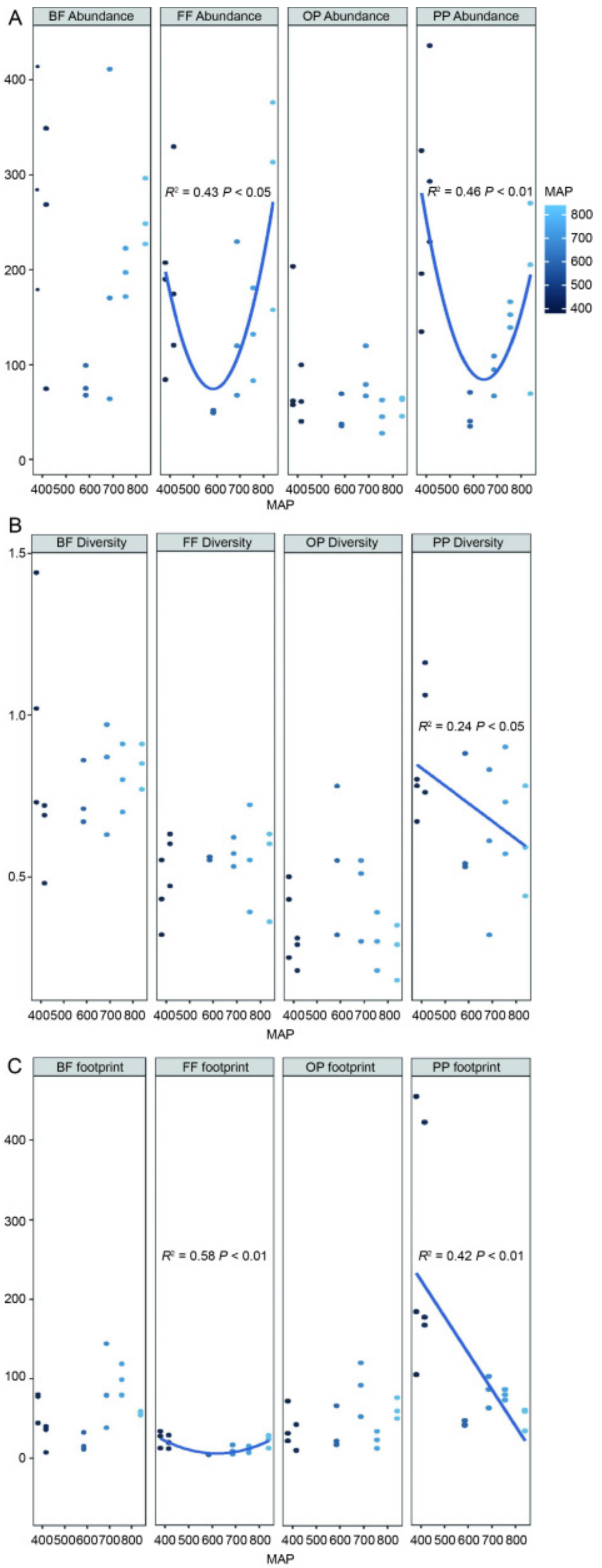

Fig. 3 The abundance (A), diversity (B) and footprint (C) index of each nematode trophic group with precipitation levels. Lines indicate regression model fits with statistically supported by R^2 and P values. BF, bacterivores; FF, fungivores; OP, omnivores-predators; PP, plant parasites.

It could be possible that the agricultural ecosystem was no essentially benefit to high trophic levels, such as omnivore-predators which were sensitive to disturbances (Bongers, 1999; Ferris et al., 2001). Also, the low abundance of omnivore-predators in the whole nematode community might have made it hard to find obvious changes. Taking all these factors together, it seems to suggest that environmental filtering by precipitation probably also occurred for the soil nematode community mainly through its impacts on low trophic levels of fungivores and plant parasites at a regional scale of the agriculture ecosystem.

The relationship of nematode diversity with MAP may imply the passive effect of MAP on the nematode. While taking a deeper look at the nematode trophic groups, we found that the high nematode diversity values were probably driven by the high diversity of plant parasites with slow growth rates and longer life cycles in low precipitation sites (Rehman et al., 2016). Plant parasites normally caused damage to plant growth by feeding plant roots (Williamson and Hussey, 1996; Nicol et al., 2011). The decrease in the diversity of plant parasites demonstrated that the precipitation negatively affected the plant parasites and probably weakened top-down control in the root channel (from plant parasites to root). And this would potentially benefit the health of the agricultural ecosystem. Therefore, total diversity may be not good enough for soil nematodes in implying climate change; combining the trophic group diversity could provide more information on valuing the response of nematode community to changes in precipitation in agricultural ecosystems.

4.2 The effects of precipitation on soil nematode metabolic footprint

Precipitation could not only regulate the associated nematode abundance and diversity, but also affected metabolic footprint which was suggested contributions of nematodes to carbon cycling. By evaluating all the nematode factors with MAP, we found that footprint had important contributions in explaining the MAP change. Compared with regular values, like nematode abundance and diversity, footprint provided additional information of the metabolic activity and carbon flow in soil food webs. It was an effective method for estimating the contribution of nematodes to ecosystem functioning (Ferris et al., 1997; Ferris, 2010). Our results suggested that the precipitation change not only impacted nematode community composition, but importantly also changed the nematode carbon turnover in the agricultural ecosystem. Our study highlighted the importance of using footprint to predict the soil nematode response to precipitation.

The high footprint value in low precipitation regions suggested that nematodes maintained greater parts of soil

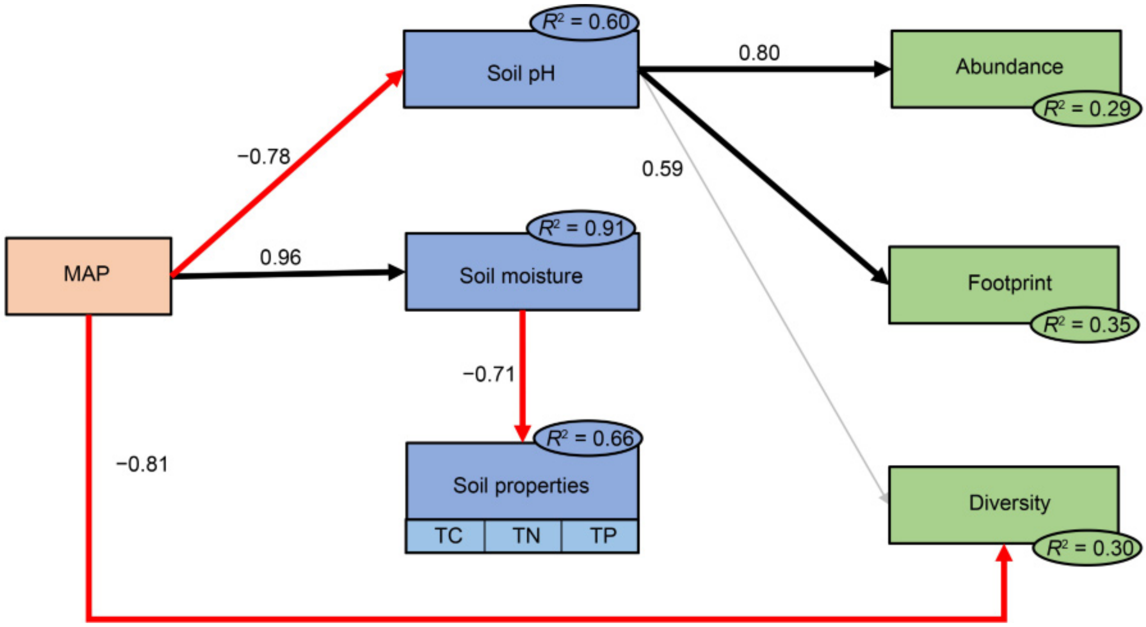

Fig. 4 Structural equation model (SEM) describing environmental factors on nematode community. R^2 is the endogenous variable of the model. The arrows indicate causal relationships among all the variables (gray continuous arrows, non-significant effects; black continuous arrows, positive effects; red continuous arrows, negative effects). The arrow widths indicate the strength of the causal influence. The numbers beside the arrows are the standardized regression coefficients.

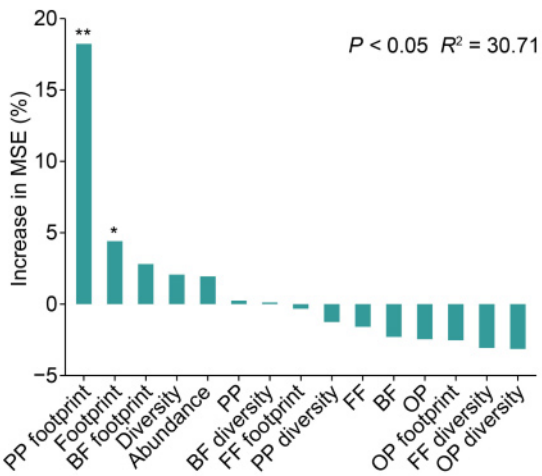

Fig. 5 Random forest describing the MAP relation with the abundance, diversity and footprint of nematode. BF, bacterivores; FF, fungivores; OP, omnivores-predators; PP, plant parasites.

carbon flow in low precipitation levels. However, the changes in microhabitats caused by precipitation triggered soil nematode variations and further differently impacted the carbon fluxes in different food channels (Kergunteuil et al., 2016). The change in fungivore footprint may suggest the potential change of carbon sequestration in the fungal channel by precipitation. The fungal channel was characterized as a slow carbon turnover channel that decomposed the recalcitrant nutrient, e.g., nutrients from the residue, probably resulting in low rates of carbon and nutrient mineralization (Moore et al., 2005). The consistent responses of abundance and footprint of fungivores with precipitation were observed stronger than those of bacterivores communities, which indicated that the resource flow into the soil food web via the fungal channel was more susceptible to climate disturbance. A previous study documented that climate restriction on the soil nematode community would be eliminated by agriculture (Li et al., 2020). But its study sites were in upland double-cropping areas from central to south of China, which had milder weather and relatively high temperature. Our study was single cropping areas in the North-east of China with colder temperatures and it was more susceptible to climate change. The change in plant parasites' footprint suggested that the carbon flow through root channel was reduced by precipitation. This also supported the plant parasites' diversity results. The stepwise regression analysis also showed that plant parasites' footprint was the important value in response to MAP change. Both of these implications indicated that increased precipitation would mitigate the damage through both reducing the structure of plant parasites and carbon flow in root channel. It was particularly important for the agricultural ecosystem which would refer to guide agricultural production. Therefore, our study suggested that precipitation gradient would still affect differently on soil nematode trophic groups and carbon assimilation in the soil food channels in agricultural ecosystems of middle-high latitude. By detecting trophic group footprint, our findings provided the idea that nematode community changes with precipitation which could further facilitate carbon flow among soil food channels in the agricultural ecosystem.

4.3 The precipitation effects on the linkage of soil properties and soil nematode

Based on the SEM model, nematode diversity was directly affected by precipitation. Precipitation reflected the long-term effects of climate change were water balance and wetness. Whereas, soil moisture, as a short-term effect of water availability, did not show a significant effect on nematode communities. It suggested that nematode diversity was more determined by long-term climatic factors rather than an instantaneous change in soil water availability (Papatheodorou et al., 2004; Bakonyi et al., 2007). And as we discussed above, the effects of precipitation on nematode diversity were mainly visible in the plant parasites. These results supported the idea of direct regulation by precipitation on nematode diversity and emphasized the sensitive role of plant parasites to precipitation (Zhang et al., 2020).

Even though precipitation could affect edaphic factors, only soil pH affected the soil nematode community. And the soil pH mainly determined nematode abundance and footprint. At the global scale, the climate is proven to be the single most critical factor that affected soil pH (Global Soil Data Task Group, 2000). Precipitation may affect soil pH through its effects on the aboveground process, and also via its effect on soil carbon cycling (Laganiãre et al., 2010; Deng et al., 2014). Based on RDA, soil pH was closely related to SJ and CL sites. So, it was possible that the soil nematode community was primarily structured by soil pH in regions with lower than 450 mm of precipitation. The high pH which was because of high concentrations of ions in soil solution could unbalance osmotic pressure in the soil nematode body (van Gundy, 1965). Therefore, in these regions, high soil pH levels might act as stress conditions, which were more suitable for plant parasites than other nematode groups.

5 Conclusion

In our study, not only the total values of abundance and diversity changed with MAP, but also the values of abundance, diversity and footprint based on trophic group also changed, especially fungivores and plant parasites, suggesting that the community and C fluxes of the fungal and root channels are more susceptible to precipitation change in the agricultural ecosystem. Among all the nematode values, the plant parasites footprint showed the greatest response to precipitation Therefore, simple detection of the total change may not provide the primary cause of nematode communities to precipitation change, and hence, information on trophic groups which provided the trophic cascade effect needed to be studied further. Overall, the abiotic effects on the nematode community were mainly caused by the change of precipitation. The precipitation could regulate soil pH, and then affect nematode diversity and footprint. Therefore, regional scale precipitation could act as a selection stress for the functional composition of nematode communities by indirectly manipulating soil pH, and possibly further influencing C allocation in the soil food web in the agricultural ecosystem. By providing the quantification of spatial precipitation with nematode diversity and functional relationships, our study highlights the importance of footprint in response to precipitation, and evaluating soil nematode values into trophic groups would contribute to a deeper understanding of soil biodiversity responses to climate change in cropland ecosystems. Future studies should test whether interannual precipitation would affect the soil nematode community with the transect.

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Electronic supplementary material

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