Neutral effect of nitrogen addition and negative effect of precipitation reduction on the soil faunal community in a temperate forest

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Abstract Nitrogen deposition can promote belowground soil carbon pools, and precipitation reduction can eliminate this positive effect. Soil fauna play crucial roles in regulating dynamics of organic matter and maintaining biodiversity in ecosystems. However, it is not clear whether belowground soil fauna have similar responses to changes after long-term nitrogen deposition and drought. We simulated nitrogen deposition by applying nitrogen fertilizer, simulated drought by excluding 30% of the ambient precipitation in a temperate forest from 2009. Our results showed that experimental precipitation reduction alone significantly changed the composition and decreased the abundance of soil faunal community. Precipitation reduction could also promote soil food web in a fungal dominated pathway through decreasing trophic group of Isotomidae abundance. In contrast, although nitrogen addition treatment increased soil available nitrogen content, it had a neutral effect on soil faunal community. Soil faunal community showed strong temporal variations in response to nitrogen deposition or precipitation reduction. Precipitation reduction and nitrogen addition had significant interactions with sampling time for trophic groups such as saprozoites and omnivores. Shannon-Weiner diversity was not sensitive to nitrogen addition and/or precipitation reduction treatment. Our results suggest that the driving factors of global change may directly and indirectly regulate soil faunal community.

Keywords Nitrogen addition, precipitation reduction, biodiversity, soil food web, temperate forest

Introduction

Temperate forests cover approximately 5.3 million square kilometers globally, accounting for 16% of the world's forest area (Hansen et al., 2010). The biodiversity and ecosystem functioning of temperate forests are maintained and shaped by multi-trophic soil organism interactions (Bardgett and van der Putten, 2014; Wu et al., 2021). Soil faunal community maintains the biodiversity of ecosystems and decomposes organic matter through the feeding processes (Beaumelle et al., 2021). In turn, the temperate forest belowground ecosystem can also provide food resources and habitats for different soil faunal trophic groups such as omnivores, predators, saprozoites and phytophages (Digel et al., 2014). However, research on biodiversity and its feedback to ecosystem functioning studies have focused on aboveground vegetation or belowground microbial community, often neglecting belowground soil faunal community (Lladó et al., 2017; Landuyt et al., 2019). There are many kinds of soil fauna, occupying different trophic niches. The influence of external disturbance on the groups may be related to different ecological processes through the food webs. However, in the context of global change, there is still a limited understanding in our research on how soil faunal community responds to external disturbances.

Precipitation is often the most important factor determining the ecological function in different ecosystems (Clark et al., 2016; Konapala et al., 2021). Human activities induced global change driven factors such as climate warming and nitrogen deposition are altering the biotic and abiotic conditions of terrestrial ecosystems, with a series of consequences for its structure and functioning (Leuzinger et al., 2011; Zhang et al., 2018). Climate warming causes increased evaporation and less precipitation, leading to significantly higher levels of drought in many regions of the world (Naumann et al., 2018). Changes in the intensity and frequency of precipitation (droughts) are projected to increase substantially in some regions, such as northeast China (Dai, 2012; Fischer and Knutti, 2015). Soil fauna have adapted to a constant soil microenvironment for reproduction and distribution, and field experiments suggested that soil faunal abundance and diversity negatively respond to precipitation reduction (Waagner et al., 2011; Flórián et al., 2019). Precipitation reduction inhibits soil water availability and increase soil stress on faunal community, directly reduces soil faunal diversity (Nielsen and Ball, 2015; Konapala et al., 2020). Precipitation reduction can also promote the saprophytic community by increasing the proportion of soil fungal community (Hågvar and Klanderud, 2009). However, these effects may be influenced by the intensity of drought and the frequency of drought. In addition, after long-term drought conditions, whether soil faunal community will form adaptability, so that the response to drought remains relatively stable, we do not know.

Nitrogen is the basic element for all organisms on earth. Nitrogen deposition rates are increasing rapidly in many parts of the world, including northeast China (Galloway et al., 2008; Liu et al., 2013). There are no consistent results on the effects of nitrogen addition on the soil faunal community. Ochoa-Hueso et al. (2014) found that nitrogen deposition significantly increased the abundance of soil fauna community in the Mediterranean semi-arid ecosystem. Similarly, a global meta-analysis showed that nitrogen fertilization increased the average abundance of soil faunal community by 27.9% (Corredor et al., 2021). However, some studies also showed that nitrogen addition did not significantly alter the abundance and diversity of soil fauna in a mature subtropical forest, but decreased abundance and diversity in a Mediterranean forest (Tian et al., 2020; Peguero et al., 2021).

In the context of global change, soil fauna may be affected by a variety of driving factors of global change, and ultimately feedback to the change of ecosystem function. Both precipitation reduction and nitrogen deposition can directly regulate the soil faunal community by changing soil environmental conditions, such as by decreasing soil water content and soil pH value. In addition, precipitation reduction can reduce the absorption of nutrients in the roots of belowground plants and the input of aboveground photosynthetic productions, resulting in decrease of phytophagous soil faunal community (Thakur et al., 2019; Peguero et al., 2021). On the other hand, temperate forest ecosystems are generally considered to be nitrogen-limited. Nitrogen deposition can increase the nitrogen available to plants in the soil, improve plant nutrient transport and photosynthetic products, and thus promote phytophages (Cole et al., 2008). Nitrogen addition may also lead to light limitation and subsequent competitive exclusion of understory herbs while promoting plant growth, resulting in a large amount of evaporation and soil moisture loss, and ultimately reducing herbivores by reducing the input of food resources (Simkin et al., 2016). These various results demonstrate the complexity of the responses of soil faunal community with multiple trophic community levels to nitrogen deposition and precipitation reduction. Temperate forest is the main ecosystem for human survival, providing a variety of ecological services for human survival and development. Changes in temperate forest area and ecosystem biodiversity may affect the normal function of ecosystems and ultimately affect human material acquisition. Therefore, it is necessary to study the effects of global change such as nitrogen deposition and precipitation reduction for soil faunal community.

Here, a field experiment was conducted to simulated nitrogen deposition and drought scenario in a temperate forest ecosystem in Changbai Mountains, Northeast China during growing season. Temperate forest in Changbai Mountains is the most typical and well-preserved temperate mountain forest ecosystem with high biodiversity in eastern Asia. The region has also faced persistently high nitrogen deposition and extreme drought in the last three decades (Zheng et al., 2017). This study aimed to investigate the single and additive effects of long-term nitrogen addition and precipitation reduction treatments on the abundance, diversity, and composition of soil faunal community. Based on previous studies, we hypothesized that (1) nitrogen addition will increase the abundance and diversity, and also change the compositional structure of soil faunal community, whereas (2) precipitation reduction would have the opposite effect on above variables. We further hypothesized that (3) precipitation reduction will counteract the positive effects of nitrogen addition on soil faunal community, and show interactive effects on soil faunal community.

Materials and methods

Study site description

The experiment was carried out in a temperate forest ecosystem at Changbai Mountains experimental station in Northeast China at approximately 738 m a.s.l. (42°24' N, 128°06' E). This forest belongs to the primitive broad-leaved Korean pine forest with a history of more than 300 years. The dominant tree species in the region are *Pinus koraiensis*, *Acer mono*, *Tilia amurensis*, *Fraxinus mandshurica* and *Quercus mongolica*; the dominant shrubs are *Philadelphus schrenkii* and *Corylus mandshurica*; the dominant herbs are *Dryopteris coreano-Montana*, *Filipendula palmata,* and *Carex pilosa*. The local soil is formed by volcanic ash and belongs to Eutric Cambisol (based on FAO classification). The study area has a temperate continental climate with the mean annual temperature of 3.6 °C, and the average temperature in the growing season is 15 °C. The mean annual precipitation is 740 mm, and the total precipitation from May to September reaches 80 % of the total annual precipitation. After a long-term field simulation experiment, the basic characteristics of the plot are listed in Table S1and Table S2.

Experimental setup and sampling

The study site was established in 2009 using a split-plot design. Six experiment plots (50 m × 50 m) with a 20-meter buffer distance were located in three blocks, each block including one undisturbed field and another precipitation reduction field (CK and P treatment, respectively). Four treatments (precipitation reduction, P; nitrogen addition, N; nitrogen addition combined with precipitation reduction, NP), and control (with ambient condition, CK) were assigned to six plots. The 6 plots were separated by a 50-meter-long iron sheet. The depth of the iron sheet embedded in the plot was 50 cm. Hence, 12 subplots (50 m × 25 m) were established. V shape polycarbonate plastic plates with 95% light transmittance were used as rainout shelters to simulate precipitation reduction events (Fig. 1). In order to reduce the impact on the microenvironment of the plot, the distance between the polycarbonate plastic plate and the ground was set to 1 m. According to the data of China ecosystem research network, the precipitation in dry years is 30% less than that in normal years (about 200 mm). The way to reduce the total precipitation by 30% is to set the total area of the polycarbonate plastic plates to cover 30% of the total plot surface. To accurately measure the precipitation received by rainout shelters, at the edge of the plot, plastic plates perpendicular to other plates were set up to channel the collected precipitation into a well. To investigate the effects of nitrogen deposition, one of the two subplots was treated with nitrogen fertilizer, and the other was not. $NH_4NO_3$was used as the nitrogen source, and 50 kg $N{\cdot}ha^{-1}{\cdot}yr^{-1}$ was applied (approximately two times the natural nitrogen deposition rate in this area). NH_4NO_3 solution was sprayed monthly from May to October since 2009. The control and precipitation reduction plots were sprayed with the same volume of deionized water.

Soil faunal community sampling and identification

The growing season in the area is from May to October, and samples were collected in spring (May), summer (July) and autumn (September) of 2018. Considering that the forest litter layer is unstable, and the organic matter content in the deep soil is low, which is not conducive to the survival of soil faunal community, we only sampled in the soil layer of 0-10 cm. After removing litter on the soil surface, 0-10 cm soil cores were collected with a 20 cm diameter cutting ring. Six soil fauna samples were collected from each subplot and then randomly mixed into two composite samples. Soil faunal samples were stored in black plastic bags and extracted within 24 h. Additional soil samples were extracted by the soil drill and frozen to determine soil physicochemical parameters (n=3). Ten squares of 1m × 1m area were selected, and plant species in the area were counted as plant richness.

Macrofauna (body length >2 cm) were manually counted, and mesofauna (body length <2cm) were extracted using a modified Tullgren funnel method for a separation time of 48 h (Lefors et al., 2018). During the separation process, the soil was sprayed with an appropriate amount of water to prevent the temperature of the soil sample from rising too fast and causing compaction and affecting the separation effects. Soil faunal samples were preserved in 75% ethanol and subsequently counted under a dissecting microscope. After counting, the number of soil faunal community was characterized to determine the abundance (individuals per square meter). Soil fauna were identified using a compound light microscope to family (few to suborder level) level according to *China Pictorial Keys to Soil Animals* (Yin, 1998).

Soil physicochemical measurements

Soil water content (SWC) was determined by mass loss method, that is; i.e. 10 g of soil was dried at 105℃ for 24 h to constant weight (Noborio, 2001). Soil pH was to mix air-dried soil and distilled water in a ratio of 1:2.5, shaken for 30 minutes, and then measured the supernatant with a pH meter (Sartorius PB-10) (Sonmez et al., 2008). Soil organic carbon (SOC) and total nitrogen (TN) contents were analyzed using an element analyzer (Multi N/C 3000, Analytik Jena, Germany). Soil NH_4^+-N and NO_3^--N were determined using a continuous flow analyzer (Skalar, Netherlands) after extraction using 2M KCl.

Data analysis

After the extraction and identification, the Shannon-Weiner index (H') (Shannon, 1948) was used to describe soil faunal community diversity. The abundance of soil fauna was ln-transformed to improve homogeneity of variances. Percentage variables such as soil water content (%) were arcsin transformed. Generalized Linear Mixed Model (GLMM) analysis was performed to analyze changes in soil physicochemical characteristics, soil faunal abundance, H' under nitrogen addition and/or precipitation reduction treatment at different sampling times. The GLMM analysis used different treatments and sampling time as fixed effects, and blocks as random factors. The GLMM was performed using "lme4" package (Bates et al., 2014). Post-hoc tests (LSD) were used to examine the differences of above variables among the control, nitrogen addition, precipitation reduction and nitrogen addition combined with precipitation reduction treatments. Principal coordinate analysis (PCoA) based on Bray-Curtis distance was applied to visualize shifts in the composition of soil faunal community under nitrogen and/or precipitation reduction treatment (Legendre and Anderson, 1999). Permutation multivariate analysis of variance (PERMANOVA) was performed to detect the significance differences of Bray-Curtis distance. Principal response curves (PRC) analysis was applied to investigate treatment effects over time in terms of main groups of soil fauna under nitrogen addition and/or precipitation reduction treatment (Van den Brink et al., 2009). PRC is a special method based on Redundancy Analysis method (RDA), and is applied to investigate the changes of observation variables under different treatment over time. On the PRC diagram, the first principal component of variance, explained by the control, nitrogen addition and/or precipitation reduction treatment in different sampling time is displayed on the y-axis, while (sampling) time factor is on the x-axis. After the PRC analysis, a Monte Carlo permutations test (with 999 permutations) was performed to test whether the PRC analysis results were credible. The analysis mentioned above was conducted by the "vegan" package in R 4.2.0 (Oksanen et al., 2018). After Mantel test analysis, Spearman's rank correlation analysis was applied to detect the relationship between total abundance and plant richness or soil physicochemical characteristics.

Results

Responses of soil faunal community to nitrogen addition and/or precipitation reduction treatment

Neither nitrogen addition nor precipitation reduction treatment significantly affected the soil faunal Shannon diversity index (Fig. 2b, $p>0.05$). Overall, statistical results showed that soil faunal abundance, Shannon-Weiner diversity index (H') and trophic taxonomic abundance showed significant temporal variations throughout the sampling period (Fig. 2-4, $p<0.05$). The highest abundance occurred in May, while the lowest occurred in July (Fig. S1). Compared to the control treatment, precipitation reduction significantly decreased the total soil faunal abundance as well as trophic abundance of Isotomidae (Fig. 2 and Fig. 4, $p<0.05$). In contrast, nitrogen addition alone had no significant effect on the soil faunal community (Fig. 2, $p>0.05$). Precipitation reduction combined with nitrogen addition decreased the total abundance of soil faunal community (Fig.S1 $p<0.05$). Precipitation reduction treatment, nitrogen addition treatment and sampling time had significant interaction effects on the abundance of decomposers and omnivorous abundance (Fig. 3, $p<0.05$).

PRC tests showed that the model was an acceptable method to analyses the changes of main soil faunal groups (Fig.5, F=6.83, P=0.026). Specifically, statistical analysis revealed that 32.73% of total variance variation, of which 29.59% was explained by different treatments, the remaining 13.88% was sampling time. In addition, since the nitrogen addition treatment was closer to the control baseline, the impact of precipitation reduction treatment on the soil faunal community was greater than that of the nitrogen addition treatment. The importance of Chironomidae larvae, Hypogastruridae, Isotomidae, Entomobryidae and Onychiuridae, Oribatida and Mesostigmata significantly increased after nitrogen addition and/or precipitation reduction treatment.

Compositional changes of the soil faunal community

A total of 8208 soil faunal individuals were captured and identified throughout the sampling period. Oribatida and Isotomidae accounted for 44.99% of the total populations. More specific information about different soil faunal groups was listed in Table S3.

Our results from the PCoA analysis showed that different treatments explained 43.63% of the variation in soil faunal community composition (Fig. 6, F=1.68, p=0.027). PCoA analysis separated soil faunal community from the control in the precipitation reduction treatment (Table S4, F=3.081, p=0.045). The same pattern was also observed in precipitation reduction combined with the nitrogen addition treatment (Table S4, F=2.753, p=0.036). Contrary to above results, soil faunal community composition did not change under the nitrogen addition treatment (Table S4, F=1.180, p=0.344).

Soil faunal community related to plant richness and soil properties

Mantel test showed that soil NH_4^+, NO_3^-, SWC and plant richness were main factors that significantly correlated to the composition of soil faunal community (p<0.015). Regression analysis showed that soil water content (SWC) and plant richness were significantly positively correlated with Isotomidae and total community abundance (Fig. 7, $p<0.05$).

Discussion

Influence of nitrogen addition on soil faunal community

This study explored the response of soil faunal community to simulated nitrogen deposition in a temperate forest. Contrary to our initial hypothesis, we did not detect significant changes in the composition, total abundance or diversity of soil faunal community. The results are similar to the observations in grasslands and arable land that nitrogen addition had no significant effect on soil faunal community (Reeleder et al., 2006; Cole et al., 2008). The lack of significant changes in the abundance of soil faunal community may be due to the offset of the positive and negative effects of nitrogen addition. Previous studies revealed that soil faunal community is closely related to environmental factors, and had limited adaptability to the environment changes (Wang et al., 2015; Yin et al., 2018). In this study, although we did not detect changes in soil pH under nitrogen addition treatment, the contents of NO_3^- and NH_4^+ changed significantly throughout the sampling period. Studies have demonstrated that NO_3^- and NH_4^+ are the two main forms of soil inorganic nitrogen, and these two ions with higher content in soil can cause obvious toxic inhibition effects on soil organisms (Shao et al., 2018). However, we did not detect significant differences in soil faunal community between nitrogen addition treatment and the control, and we speculated that the level of nitrogen addition might be an important factor that we have overlooked. A study in a temperate forest also demonstrated that soil faunal community was less affected at low nitrogen addition levels (20-50 kg $N \cdot ha^{-1} \cdot yr^{-1}$) than those at higher levels (80 kg-100 kg $N \cdot ha^{-1} \cdot yr^{-1}$) (Liu et al., 2020). The possible reason is that in this study, the low level of nitrogen addition will change the soil characteristics, such as TN, NO_3^-, and NH_4^+ contents, but cause less stress to the soil faunal community.

On the other hand, nitrogen addition can enhance the amount of available nitrogen in the soil, thereby increasing plant biomass and altering the internal histochemical properties of plants (higher foliar nitrogen and protein content and C:N ratios), leading to an increase in available food resources for the soil faunal community (Stevens et al., 2018). On the other hand, nitrogen addition significantly reduced plant richness in our current study. Many studies have shown that soil fauna are regulated by plant richness, and our linear regression results also showed that soil faunal community and total abundance are significantly correlated with Isotomidae abundance (Villanueva-Lopez et al., 2019). Therefore, these contradictory results may indicate that the negative effect of nitrogen addition on soil fauna will be offset by the positive effect, thus maintaining the stability of faunal community.

Influence of precipitation reduction on soil faunal community

Consistent with our second hypothesis, the precipitation reduction treatment reduced the abundance and changed the composition of soil faunal community. Our results are similar to previous studies of Mediterranean pine forest and temperate forest ecosystem (Lindberg et al., 2002; Tsiafouli et al., 2005). The negative impact of precipitation reduction on the soil faunal community is shown by the shifts of soil faunal abundance. In particular, we found that the abundance of Isotomidae (Collembola) decreased significantly under the precipitation reduction treatment. Hence, our findings on the negative effect of precipitation reduction on soil faunal community mainly focus on Isotomidae. A previous study demonstrated that soil water availability was a direct factor affecting the microhabitat and reproduction of soil faunal community (Waagner et al., 2011). Soil Isotomidae lacks a true tracheal system and breathes through its outer skin, so it needs to be able to function properly in a higher soil humidity microenvironment (Nickerl et al., 2013; Holmstrup, 2019). Declines in soil moisture can directly alter soil osmotic pressure, thus affecting the hatching of Isotomidae larvae. Another possible explanation is that different groups of soil Collembola are different in body size; Isotomidae is a typical larger-size group, which is susceptible to soil desiccation, and is more sensitive to disturbance than smaller-size Collembola groups (Yin et al., 2018). This explanation is also supported by our PRC analysis.

Soil fauna are interconnected through belowground food webs, and the precipitation reduction treatment may lead to changes in food resources and thus affect faunal communities. Aboveground photosynthetic products and belowground root exudates of plants are the main food sources for soil organisms. Long-term drought can accelerate soil carbon loss by altering soil microbial communities and aggregates, leading to a decline in plant rhizosphere nutrient exchange, weakening plant carbon capture capacity, and ultimately reducing plant primary productivity (Su et al., 2020). Our results suggested that the precipitation reduction treatment suppressed plant richness, which reduced the input of aboveground food to the belowground, ultimately reducing the abundance of Isotomidae. In the belowground soil food web, Isotomidae is an omnivorous group mainly fed by soil nematodes, protozoa, fungi and bacteria (Sanaullah et al., 2011; Xue et al., 2017). The distribution of soil nematodes requires high water conditions, and the growth of soil fungal hyphae between soil pores also requires high water. Our previous studies in this ecosystem have demonstrated that precipitation reduction reduced nematode abundance and fungal composition (Wang et al., 2021). For above populations are less active in soil and more dependent on available water than Isotomidae. Therefore, precipitation reduction can inhibit above communities, and this negative legacy effect may regulate the activity of Isotomidae through the 'bottom-up' process of the soil food web.

Influence of nitrogen addition and precipitation reduction on soil faunal community

Nitrogen deposition and precipitation reduction, as two major drivers of global change, often play crucial roles in different ecosystems. Consistent with our third hypothesis, PCoA analysis showed that the composition of soil faunal community changed after nitrogen addition combined with the precipitation reduction treatment. However, unlike our third hypothesis, our results showed a negative effect on soil faunal regardless of precipitation reduction or nitrogen addition (although the effect of nitrogen deposition was not statistically significant). Studies on the responses of soil faunal community to nitrogen addition combined with precipitation reduction (drought) are relatively rare. A previous study at a secondary successional grassland BioCON experiment site in

USA concluded that summer drought and nitrogen fertilizer exerted no effects on the abundance of soil Collembola community (Eisenhauer et al., 2012). Similarly, our results also showed that the total abundance of the Collembola remained stable. On the other hand, GLMM results showed a significant interaction between nitrogen addition and precipitation reduction on the abundance of saprozoites and omnivores. Mantel test showed that soil NO_3^-, NH_4^+, SWC and plant richness jointly contributed to the changes of soil faunal composition. The decline in abundance of some trophic groups suggested that soil faunal community was more sensitively assessed by trophic level than by taxonomic level to nitrogen addition and precipitation reduction treatments. Compared with soil phytophages, predators and saprozoites are located in lower trophic niches and have a wider spectrum of food resources (Potapov et al., 2019). The saprophytic groups mainly consume the soil bacterial community. Precipitation reduction can inhibit the mineralization of nitrogen and significantly reduced the biomass of soil bacterial community with low drought resistance. Nitrogen addition can accelerate the leaching of organic matter and reduce the proportion of C and N in the soil, which is more suitable for soil fungal community, resulting in the transformation of soil food web decomposition channels to fungal channels with stronger stress resistance. Nitrogen addition can accelerate the leaching of organic matter, reduce the ratio of C and N in the soil, make it more suitable for soil fungal community, resulting in the transformation of soil food web decomposition pathways to slower and stress-resistant fungal energy pathways (Seddon et al., 2016; Adams et al., 2021). Consequently, nitrogen deposition and precipitation reduction reduced the abundance of saprophagous community. Omnivores group mainly depends on the environment to determine whether the main available food is plant or prey source, and plant source uptake is positively correlated with prey source. The feeding of omnivores on plants is affected by both nitrogen and water in plants (Han et al., 2015). When the nitrogen content in soil is high and the water content is low, the ability of omnivores to intake plant-derived and prey-derived food will decrease, which will affect omnivores abundance. In addition, we found no significant changes in the diversity index of soil faunal community under different treatments. This suggested that the diversity index is not sensitive to nitrogen addition and/or precipitation reduction when assessing changes in soil faunal community.

Temporal changes of the soil faunal community under nitrogen addition and/or precipitation reduction treatment

Temporal changes under global change drivers such as nitrogen deposition or drought have been documented in different ecosystems (Wiwatwitaya and Takeda, 2005; Tian et al., 2020). Our study also found that nitrogen deposition interacted with precipitation reduction and sampling time, suggesting temporal differences in the regulation of nitrogen addition by precipitation reduction. Overall, soil faunal abundance showed a high-low-moderate variation across our three sampling times. Considering that the main food of soil faunal community is originally derived from the input of aboveground litter. In May, litter is more conducive to the feeding of soil faunal community after experiencing physical fragmentation of non-growing season freeze-thaw. In addition, lower soil moisture and higher nitrogen can even supplement the growth of vegetation in the growing season, while lower soil moisture can promote the decomposition of aerobic microorganisms, thereby minimizing the negative effects of nitrogen addition and precipitation reduction treatment. The lowest abundance was observed in July, mainly because the precipitation of the ecosystem is mainly concentrated in summer. Precipitation can alleviate the drought stress caused by precipitation reduction, but at the same time it will also reduce the permeability of soil voids, resulting in a decrease in soil oxygen content. At the same time, precipitation can also lead to the loss of litter and other organic matter in the food web, resulting in inhibited growth of soil faunal community. Compared with July, the soil faunal increased in September, likely because the input of fresh litter on the ground provided sufficient food sources for the belowground food web (Doblas-Miranda et al., 2009; Szanser et al., 2011). Therefore, if the response of future soil biodiversity to global change is to be fully predicted, the indirect effects of aboveground resources need to be considered.

Conclusions

Our findings showed that precipitation reduction significantly changed soil faunal community composition and reduced abundance. Compared to the control, Isotomidae is the most sensitive taxon in its response to the precipitation reduction treatment. In contrast, soil faunal community composition and abundance were unaffected under the nitrogen addition treatment. Nitrogen addition and precipitation reduction showed interactive effects on saprozoites and omnivores. Moreover, soil faunal abundance, trophic groups abundance, diversity and dominant community abundance are subjected to temporal variations. Soil water content and plant richness are two driving factors that may directly and indirectly determine soil faunal abundance. Our findings highlight that long-term precipitation reduction in the growing season is a stronger determinant than nitrogen addition in shaping soil faunal community in a temperate forest. Our research also provides data support for exploring the effects of long-term nitrogen deposition and drought on belowground soil faunal community under global change.

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Declarations

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest.

Availability of data and material

Data are available from the corresponding author on reasonable request.

Code availability

Not applicable.

Author contributions

QW and YX designed the study, were awarded funding, supervised data and edited manuscript. YX and HW contributed equally to this work. QW, HW, YX, GY, GL, BH and YF contributed the whole manuscript preparation and design and wrote the main manuscript text. QW, HW, YX, GY, GL, BH and YF prepared all Figures, HW, YX, GL, YF, BH, GY and QW prepared field experiments, prepared tables and collected literatures. All authors read and approved the final manuscript.

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Figures 1-7

Fig. 1 Rainshelter is used as a precipitation reduction treatment device in broadleaved pine forests in the forest ecosystem of Changbai mountain, China.(Photo credit: Hong L. Wang)

Fig. 2 Results of Generalized Linear Mixed Model (GLMM) performed on the soil faunal total abundance and Shannon-Wiener diversity for the effects of nitrogen addition (N), precipitation reduction (P), sampling time (T), and their interactions. May, (May); Jul, (July); Sep, (September). The values are bold if $p<0.05$.

Fig. 3 Results of Generalized Linear Mixed Model (GLMM) performed on the soil faunal trophic groups abundance for the effects of nitrogen addition (N), precipitation reduction (P), sampling time (T), and their interactions. May, (May); Jul, (July); Sep, (September). The values are bold if $p<0.05$.

Fig. 4 Results of Generalized Linear Mixed Model (GLMM) performed on Oribatida and Isotomidae for the effects of nitrogen addition (N), precipitation reduction (P), sampling time (T), and their interactions. May, (May); Jul, (July); Sep, (September). The values are bold if $p<0.05$.

Fig. 5 Principal Response Curves (PRC) diagram indicating temporal changes in the abundance of main soil faunal groups under different treatments (the control, CK; nitrogen addition, N; precipitation reduction, P; nitrogen addition combined with precipitation reduction, NP). May,

(May); Jul, (July); Sep, (September). The zero baseline (horizontal line) indicates the control.

Fig. 6 Principal coordinates analysis (PCoA) using Bray-Curtis dissimilarity generated from main soil faunal communities abundance. Each dot denotes one sample. Samples are colored according to different treatments (the control, CK; nitrogen addition, N; precipitation reduction, P; nitrogen addition combined with precipitation reduction, NP).

Fig. 7 Linear relationships of Isotomidae abundance, total faunal abundance and soil water content (SWC) and plant richness.

Fig. 1.

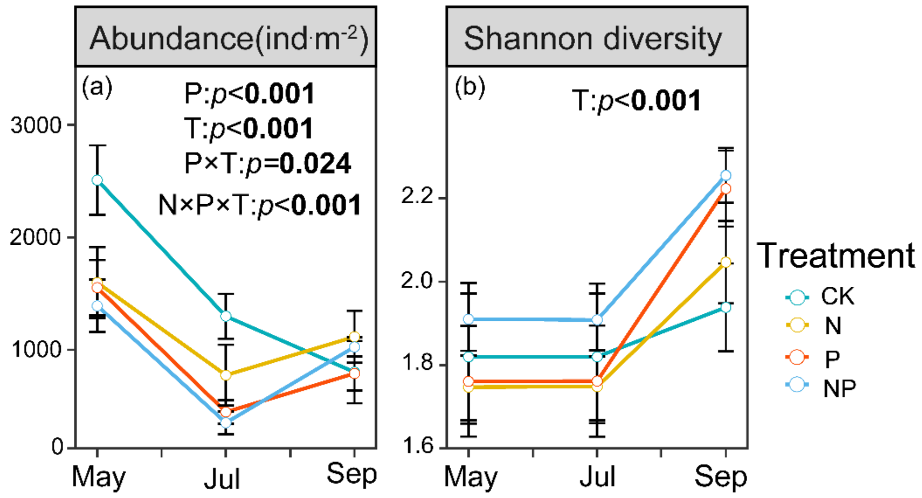
Abundance(ind·m-2)
(a)
P:p<0.001
T:p<0.001
P×T:p=0.024
N×P×T:p<0.001
3000
2000
1000
0
May
Jul
Sep
Shannon diversity
(b)
T:p<0.001
2.2
2.0
1.8
1.6
May
Jul
Sep
Treatment
CK
N
P
NP

Fig. 2.

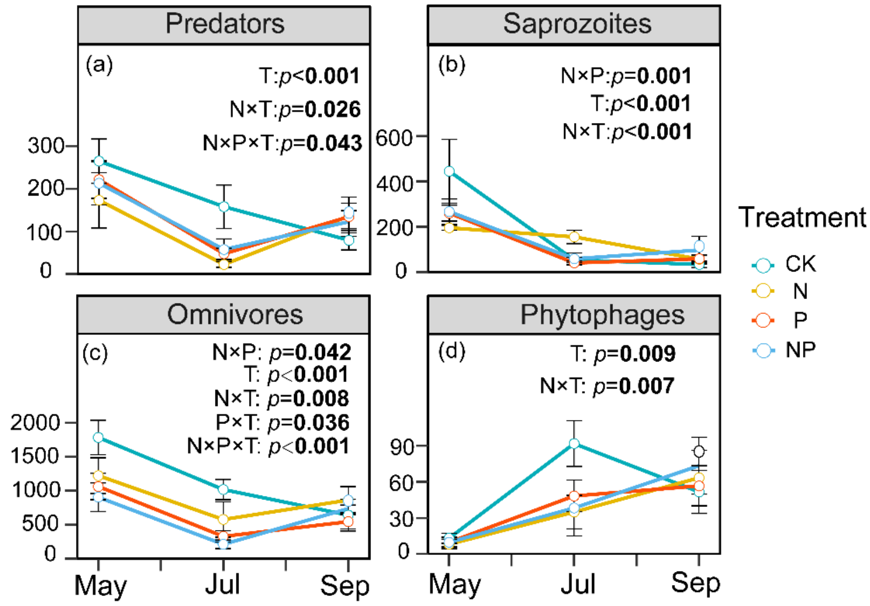
Predators
(a)
T:p<0.001
N×T:p=0.026
N×P×T:p=0.043
Saprozoites
(b)
N×P:p=0.001
T:p<0.001
N×T:p<0.001
Treatment
CK
N
P
NP
Omnivores
(c)
N×P: p=0.042
T: p<0.001
N×T: p=0.008
P×T: p=0.036
N×P×T: p<0.001
Phytophages
(d)
T: p=0.009
N×T: p=0.007
May
Jul
Sep

Fig. 3.

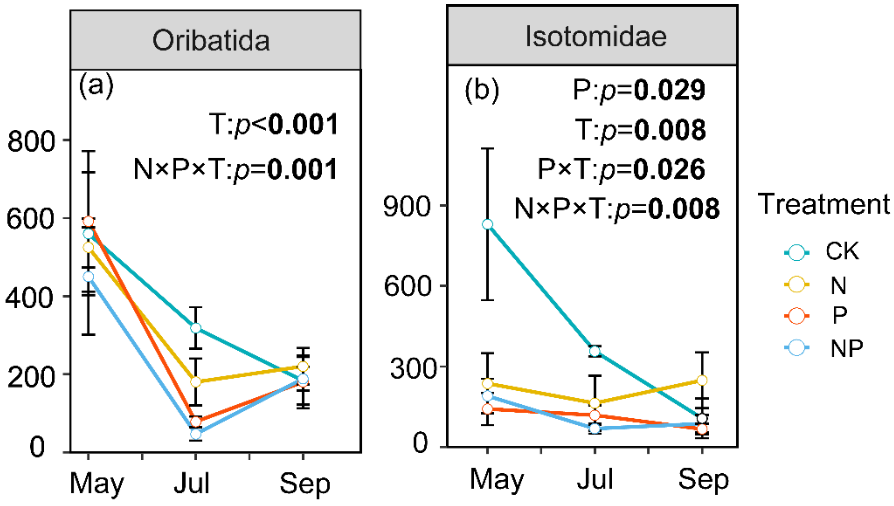
Oribatida
(a)
T:p<0.001
N×P×T:p=0.001
800
600
400
200
0
May
Jul
Sep
Isotomidae
(b)
P:p=0.029
T:p=0.008
P×T:p=0.026
N×P×T:p=0.008
900
600
300
0
May
Jul
Sep
Treatment
CK
N
P
NP

Fig. 4.

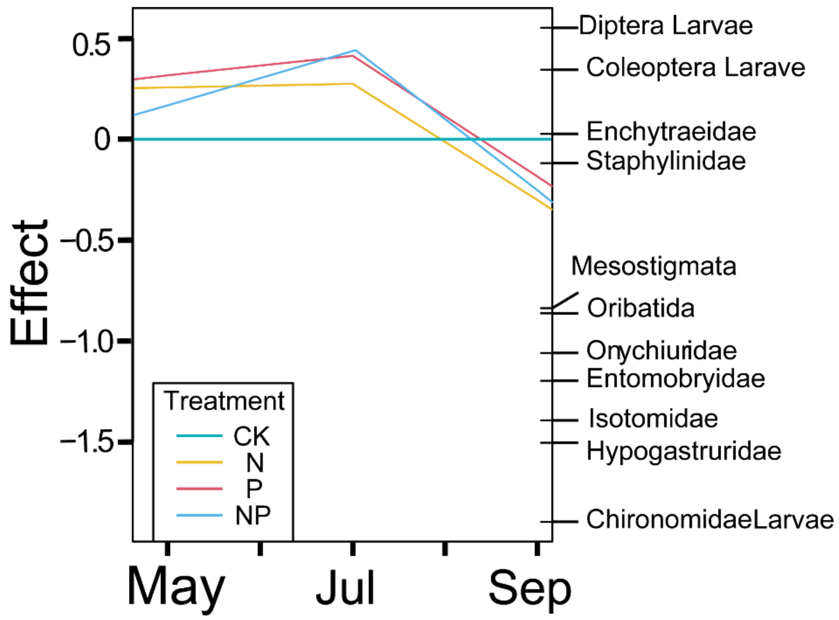
0.5
0
−0.5
−1.0
−1.5
Effect
Treatment
CK
N
P
NP
May
Jul
Sep
Diptera Larvae
Coleoptera Larave
Enchytraeidae
Staphylinidae
Mesostigmata
Oribatida
Onychiuridae
Entomobryidae
Isotomidae
Hypogastruridae
ChironomidaeLarvae

Fig. 5.

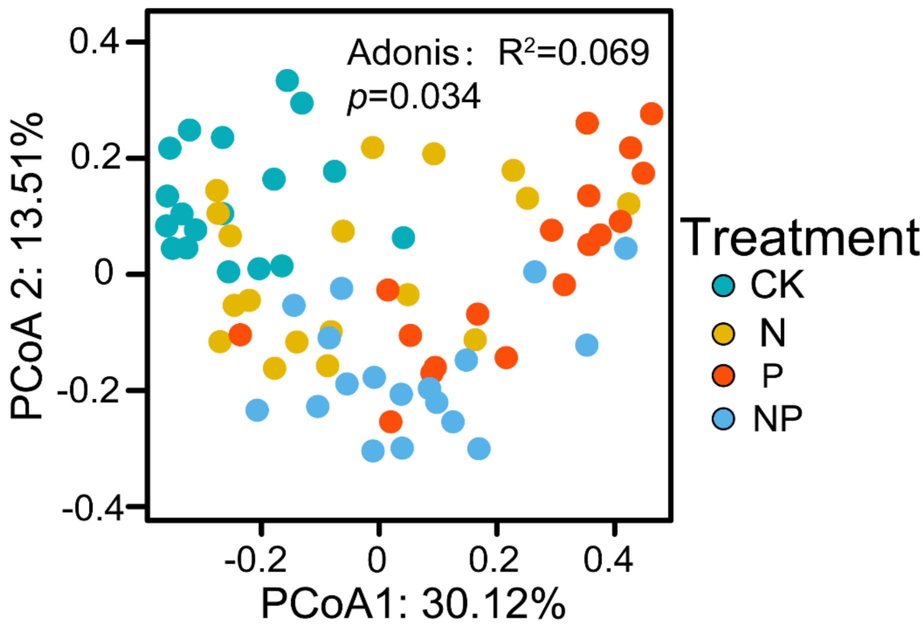
Adonis: R^2=0.069
p=0.034
0.4
0.2
0
-0.2
-0.4
PCoA 2: 13.51%
-0.2
0
0.2
0.4
PCoA1: 30.12%
Treatment
CK
N
P
NP

Fig. 6.

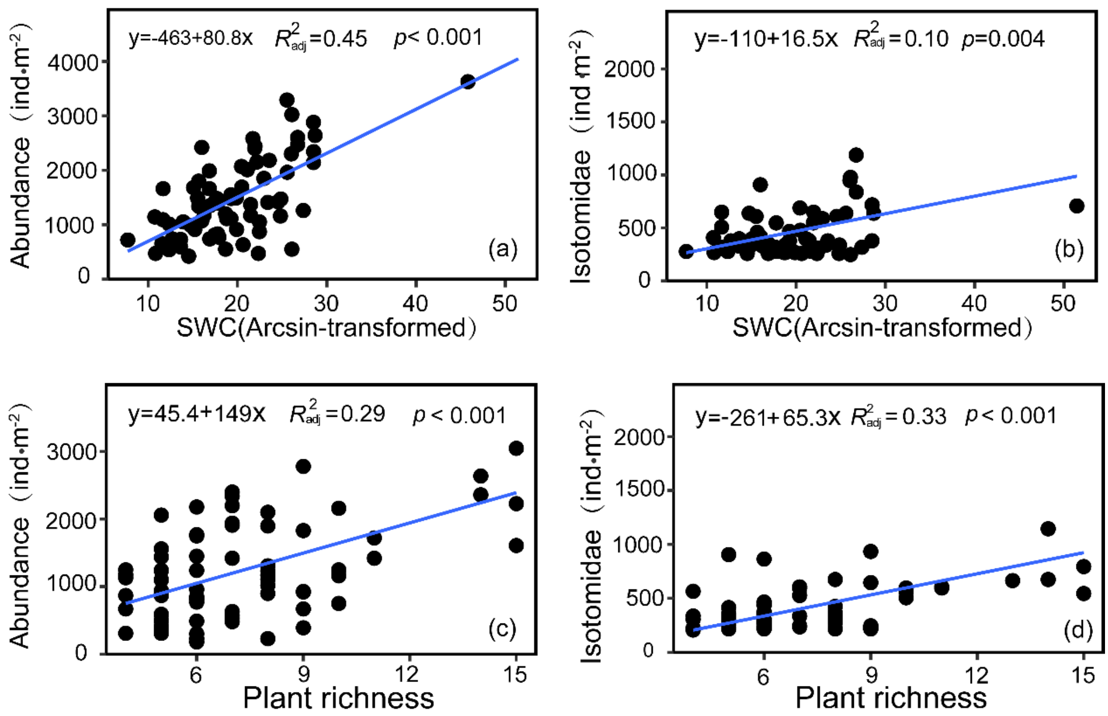
y=-463+80.8x R^2_{adj}=0.45 p< 0.001
Abundance（ind·m^{-2}）
SWC(Arcsin-transformed）
(a)
y=-110+16.5x R^2_{adj}=0.10 p=0.004
Isotomidae（ind·m^{-2}）
SWC(Arcsin-transformed）
(b)
y=45.4+149x R^2_{adj}=0.29 p < 0.001
Abundance（ind·m^{-2}）
Plant richness
(c)
y=-261+65.3x R^2_{adj}=0.33 p < 0.001
Isotomidae（ind·m^{-2}）
Plant richness
(d)

Fig. 7.