

Nitrogen addition and experimental drought simplified arthropod network in temperate grassland

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Abstract

Changes in species interactions due to species loss are threatening ecological networks. To explore the responses of arthropod networks to global changes, we conducted a multifactorial field experiment in temperate grassland, in which nitrogen (N) deposition, drought and snowmelt timing were manipulated. We constructed modular networks for arthropod functional groups and assessed their complexity by connectance, interaction diversity and interaction strength. Specifically, the pattern of reduction of network complexity was different in N and drought conditions: (a) increased foliar N strengthened single pathway and weakened the net effect of other pathways in N treatment; (b) filtered plant species and changed micro-habitats in drought conditions. Whereas delayed snowmelt increased arthropod abundance only in early spring, but its interaction with N treatment or drought showed various impacts on functional groups. Therefore, it is suggested that the co-effect of multiple global change factors, occurring in different seasons, should be considered as a panorama.

1 Introduction

In natural ecosystems, the complex interactions among arthropods play a key role in maintaining ecosystem functions, but the current situation of arthropod diversity is worrying (Cardoso et al., 2020; Eggleton, 2020; Wagner, 2020; Wagner et al., 2021). The key point of maintaining biodiversity has shifted from the protection of individual species to that of their interactions (Harvey et al., 2017). To understand the strength and complexity of arthropod interactions, it is necessary to expand the focus from single interactions to the network analysis for all the interactions. More importantly, the ecosystem complexity embodied in the interaction networks is declining rapidly (Pocock et al., 2012; Moreno-Mateos et al., 2020). Considering the sensitivity of interactions among arthropods to multiple global drivers (Tylianakis et al., 2008; Rosenblatt & Smith-Ramesh, 2017; Hamann et al., 2020), ecological networks may be facing more serious challenges than biodiversity *per se* (Valiente-Banuet et al., 2014).

Arthropods are encountering novel suites of biotic and abiotic conditions as a result of rising N deposition, more frequent drought events and warming-induced snowmelt advancement (Bobbink et al., 2010; Huang et al., 2015; Zhu et al., 2019). As a dimension of food web-based cascading process, the bottom-up effects of plant communities have been demonstrated to have a strong impact on most arthropods (Abrams, 1995; Scherber et al., 2010). In fact, it is practically impossible for us to observe all interactions of multi-trophic communities at the same time. The interaction between consumers and resources may be regulated by the characteristics of resources (variety, quality and quantity), and arthropods also have to adapt to new habitats due to global change. Thus, it is urgent to understand the process of bottom-up effects of plant communities that affected arthropods under the scenarios of global change (Hortal et al., 2015; Sage, 2020).

First, changes in plant richness had been demonstrated to have a strong positive bottom-up effect on arthropods (Scherber et al., 2010; Castagneyrol & Jactel, 2012; Wan et al., 2020), and thus it is crucial to maintain the complexity and stability of multi-trophic interactions (Rzanny & Voigt, 2012). N deposition and drought filtered out plant species in different ways and then cascaded up to the loss of species at higher trophic levels (Dunne & Williams, 2009; Stevens et al., 2010; Pocock, Evans & Memmott, 2012; Craven et al., 2016). Second, plant nutrient quality is also the major factor to influence arthropod communities. The N concentration in host-plant tissue can consistently serve as one of the best predictors for insect herbivores (Throop & Lerdau, 2004). The elevated plant N concentration due to N deposition could significantly improve individual herbivore performance, and induce changes in plant-herbivore relationship through decreased plant defenses (Mattson, 1980; Throop & Lerdau, 2004). Drought can also weaken plant defense and increase the concentration of nutrients (Luo et al., 2018), and ultimately result in the increase of chewing herbivory (e.g. grasshopper, but toxic in higher N) (Franzke & Reinhold, 2011; Gutbrodt et al., 2011). Earlier snowmelt can reduce herbivore abundance by shaping plants of low nutrient and water content, even cascade up to affect the predation and mutualism of higher trophic levels (Wipf & Rixen, 2016; Mooney et al., 2020). Third, the enhanced primary productivity could increase consumer abundance and diversity, especially in low plant diversity communities (Srivastava & Lawton, 1998; McCary et al., 2021). However, such positive correlation has been reversed under experimental drought (Prather et al., 2020) and N addition (Haddad et al., 2000). Delayed snowmelt could decrease primary productivity (van Wijk et al., 2003; Gamon et al., 2013; Kelsey et al., 2021), and therefore potentially affect arthropod communities (Wirta et al., 2015; Penczykowski et al., 2017). Finally, the changes of microhabitat, such as the soil moisture and vegetation structure, especially induced by N deposition, drought and advanced snowmelt, could directly impact arthropods (Rosenblatt, 2016; Hamann et al., 2020). For example, drought can reduce soil moisture and increase water loss from arthropods, thus filter out drought intolerant species (Jamieson et al., 2012; Barnett & Facey, 2016; Torode et al., 2016). N deposition is found to have negligible direct impacts on arthropods (Throop & Lerdau, 2004; Johnson & Jones, 2017). Moreover, drought and N deposition may alter the microenvironments for arthropods by changing vegetation height, and ultimately affect the performance of arthropods. For arthropods, the type of predation risk was modulated by vegetation height, i.e., short or tall vegetation structure provide different abiotic conditions and predation risk (Langellotto, 2004; van Klink et al., 2015). Compared with low-vegetation environments, high-vegetation environments can assure arthropod development and survival by maintaining more stable soil temperature and reducing extreme climate events (Cherrill & Brown, 1992; Bourn & Thomas, 2002; Bourn & Thomas, 2002; Roy & Thomas, 2003). On the contrary, some arthropods (e.g., beetles) hunt more efficiently in low-vegetation ground, while there are more traps (e.g. Thomisidae and Araneidae) and parasitic (e.g. Hymenoptera) risk in high-vegetation habitat (Gibson et al., 1992; Morris, 2000; Langellotto & Denno, 2004).

In the last decade, the importance of ecological networks was recognized again, and was proposed that the strength and complexity of interactions were determinants of the topological properties of the networks (Ings et al., 2009; Tylianakis et al., 2010; Tylianakis & Morris, 2017). With the increasing awareness of ecological networks, the analysis of species-based and functional group-based interaction networks had greatly improved our understanding of ecosystem processes (Ings et al., 2009; Tylianakis et al., 2010; Rzanny & Voigt, 2012; Giling et al., 2019). Compared with species-based method, functional group-based approach allows the comparison between communities composed of different species and further help us better understand the niche changes under global changes. In addition, most studies of global changes focused on single factors, but recent meta-analysis clearly indicated that the consequences of multiple global change agents may be better understood if studied in concert (Hamann et al., 2020; Wilson & Fox, 2020). Thus, we conducted a field experiment in the natural grassland of northeast China with the intention to detect the effects of N addition, simulated drought, and delayed snowmelt on grassland arthropod ecological network. We modularized the whole arthropod communities and characterized them as an interaction network. We attempt to answer the following questions: (1) how does the network complexity change under different global changes? (2) how does the global change factor modify the interaction pattern of arthropod functional groups?

2 Materials and methods

Study site & Experimental design

The study site is located at the field base of Erguna Forest-Steppe Ecotone Research Station, Inner Mongolia, China (N50°10'46.1", E119deg22'56.4"). This site has a temperate continental steppe climate. The mean annual precipitation is 361 mm and the mean annual temperature is -2.45 (1972-2018). More than 85% of precipitation falls during growing season from May to September. The main vegetation type is meadow steppe, and the dominant species are *Leymus chinensis*, *Stipa baicalensis*, *Cleistogenes squarrosa*, *Thermopsis lanceolata*, *Cymbaria dahurica*, and *Carex duriuscula* (Yang et al., 2019). The site is topographically flat and had been fenced since 2013 to avoid livestock grazing.

To explore the response of ecological network to global climate changes, we (1) used rain shelters to simulate the drought condition, (2) added N fertilizer to simulate N deposition and (3) used black shade mesh covers to delay snowmelt. The experiment was a complete factorial design of Drought (drought and ambient) x N addition (N addition and control) x snowmelt timing (with and without delaying manipulation) following randomized block arrangement with six replicates for each treatment. Each plot was 6 m x 6 m in size, and every two adjacent plots were separated by 2 m wide buffer. The drought was simulated by excluding 66% natural rainfall with passive rainout shelters (light transmittance >95%) from May to August, and watertight aluminum plates were buried around the plots to prevent the external subsurface water permeation into the drought plots. N addition was implemented in mid-May by adding NH_4NO_3 (dissolved in purified water for even spraying) to the due plots with the rate of 10 g N per square meter, while in non-N addition plots equal amount purified water was sprayed to simulate the effects of water added in the N addition plots. Snowmelt was postponed by covering the due plots with shade cloth that reduced the amount of solar radiation reaching the snow surface at the end of winter (Wipf & Rixen, 2016).

Plant & Soil sample methods

Prior to the sample collection, all the plots were spatially zoned for the sake of long-term monitoring for them. In August 2019 and 2020, plant heights were measured for all the species within each plot, and plant biomass was measured by harvesting all the aboveground live plant material in the two randomly selected 0.5m x 0.5m quadrats within each plot. Biomass of two sub-quadrats were combined, and sorted to species and dried to constant weight at 65. Three soil samples (0-10 cm layer) in each plot were collected by using a stain-steel cylinder (5 cm in diameter) and were mixed into a composite sample for the plot and passed through 2 mm sieve before measured. Gravimetric soil water content [%] was measured after the soil subsamples were dried at 105 degC for 48 h. The N concentration in plants was analyzed by an automatic element analyzer (Vario MACRO cube, Elementar Analysensysteme GmbH).

Arthropod sampling methods & Classification

The sampling of arthropods was conducted from 2019 to 2020 during the peak of plant growth in each growing season. A randomly removable subplot (1 m x 1 m) was selected in the center of each experimental plot, and arthropods therein were collected by using an electric suction sampler connected with a long gauze bag (Brook et al., 2008). Samples were taken from August to September in 2019 and 2020. The following taxa were collected and identified in 2019 and 2020: Diptera, Hymenoptera, Coleoptera, Araneae, Opiliones, Heteroptera, Orthoptera, Thysanoptera, Odonata, Collembola, Lepidoptera, Corrodentia, Neuroptera and Collembola. All of the taxa listed above represent all the arthropods we collected and mostly identified to species or genus level, but Hymenoptera (mainly parasitic wasp), Collembola and minority of Heteroptera (leafhopper) were identified to family or superfamily. The arthropod samples were preserved in 95% ethyl alcohol. We distinguished all arthropods into eight functional groups, including herbivores (plant suckers and plant chewers), carnivores (parasitoids, web spiders, ground hunters and vegetation-associated hunters), omnivores and detritivores to evaluate the difference of their responses to climate changes. We calculated the arthropod richness and abundance as the number of taxa and individuals in each sampling plot, respectively.

Statistical analysis

Firstly, the effects of N addition, drought, delaying snowmelt and their interactions on plant community

features (plant biomass, plant richness, plant foliar N), environmental factors (plant height, CV_{height} and soil moisture) and the diversity and abundance of total arthropod and each functional group were analyzed using repeated-measures ANOVA, with plot and year as random factors. The species diversity of arthropod communities was estimated using cumulative effective diversity index, calculated as e^H , where H is the Shannon-Wiener index of arthropod community. Compared with Shannon-Wiener index, cumulative effective diversity could reduce errors by controlling the difference in species richness caused by differences in sampled insect individuals (Ricklefs & Miller, 2000).

Next, we used Mantel test to analyze the correlation of two paired arthropod functional groups and build interaction networks. Plant community, environmental features and each arthropod functional group are represented as a matrix. Dependent parameters mentioned above has been partitioned into 5 parts: (1) plant biomass; (2) the presence/absence of plant species in the matrix (coded as 1 and 0 respectively); (3) N content of plant species under all the treatments; (4) soil moisture, plant height and CV_{height} displayed as a matrix; (5) each arthropod functional group. Bray-Curtis dissimilarity was calculated for each plant community character, environmental features and arthropod functional groups across all plots of a same treatment. Then, Mantel tests were used in turn for all pairs of functional groups from different trophic levels and from the same trophic level, respectively. We also calculated the relationship between environmental features and each arthropod functional group by Mantel tests, and the link between the two groups existed whenever r (correlation index) was significant ($p < 0.05$). In the condition of vertical interactions, the indirect biotic effects of non-adjacent trophic levels are mediated by correlated functional groups, so we did not analyse the relationship between non-adjacent trophic levels. Considering the modest effect of delaying snowmelt in the peak of growing season, the network webs were plotted for ambient, N addition, drought and their interaction for two years.

To characterize the interaction network, we calculated three indices, including connectance (C_{FG}), interaction diversity (ID) and interaction strength (IS) (Rzanny & Voigt, 2012). These indices can be used to predict community stability and ecosystem functioning and were found to be sensitive to multiple global change factors in interaction networks (Tylianakis et al., 2008; Tylianakis et al., 2010; Ebeling et al., 2011). IS and ID were calculated by the r value of above-mentioned Mantel tests. C_{FG} and ID were explained as different aspects of ecosystem complexity, which is the diversity of interactions among different functional groups. We took omnivores and detritivores as herbivores when calculating C_{FG} , ID and IS. The validity of so doing lied in the following facts: (1) Most of omnivorous beetles feed on plant stems, roots and litters and the rest omnivores, mainly ants, were significantly correlated with plant chewers ($r^2=0.46$, $p < 0.01$); (2) Detritivore species (mainly Diptera) feed mainly at larval stage on plant litter, stage, which was significantly correlated with plant communities (biomass: $r^2 = 0.52$, $p < 0.01$; richness: $r^2 = 0.28$, $p < 0.01$; N content: $r^2 = -0.17$, $0.05 < p < 0.1$).

C_{FG} was calculated as the number of realized links between two arthropod functional groups in each pair (L) divided by the number of potential interactions (L_{Max}).

$$C_{FG} = L / L_{\text{Max}}$$

ID was calculated using the Shannon index: where p_i is the proportion of interaction i to the total sum of n observed interactions (i.e. each significant Mantel test was divided by the total number of all significant Mantel tests):

$$ID = \sum_{i=0}^n p_i \log_2 p_i$$

Mean IS is the arithmetic mean of number of all significant interactions:

$$IS = \frac{1}{n} \sum_{i=0}^n p_i$$

In addition, the IS of environmental factors with all the arthropod functional groups was assessed and Duncan's test was used to analyze the significance of difference of IS between all the experimental treatments including ambient.

Finally, we explored the driving factors of the effect of plant communities on arthropod network in β -diversity level. The variation of plant richness (including species turnover and nest) and biomass (including balanced-variation and abundance-gradients components) could strongly impact arthropod networks. We followed the additive taxonomic β -diversity partitioning method on plant absence-presence matrix (Baselga, 2010) and plant biomass matrix (Baselga & Chao, 2017). In plant biomass matrix, the total β -diversity (β_{bc}) has been partitioned into β_{bal} (balanced-variation) and β_{gra} (abundance-gradients components). In plant absence-presence matrix, the total β -diversity (β_{sor}) has been partitioned into β_{sim} (species turnover) and β_{sne} (nestedness). To compare the direction and magnitude of responses to experimental treatments, we calculated the response ratio $[\ln(RR)]$ and the 95% confidence interval of plant β -diversity under N addition, drought and their interactions.

All statistical analyses were performed using the statistical software R 1.2.5033 by ‘vegan’ (version 2.5-6), ‘betapart’ (version 1.5-4) package.

3 Result

N addition and drought significantly changed the relationship between herbivore and plant communities. For instance, the relationship between plant community and plant suckers was found to be significant, and it was driven primarily by plant biomass under natural condition ($\beta_{bal}/\beta_{gra} = 168\%$) (Fig.1a) but by plant species turnover under experimental drought ($\beta_{sim}/\beta_{sne} = 188\%$) (Fig.1b&4). Moreover, omnivores were subject to both species turnover and plant N content under drought condition but not to them under any other experimental treatment. Drought engendered significant effects of plant species turnover on herbivores regardless of N addition, and N addition stimulated the significant effects of plant N content on herbivores (plant suckers and detritivores) whether with or without drought.

There were three remarkable points in the interaction of arthropod functional groups in networks (Fig.1): (a) the interacting functional group pairs (i.e., plant suckers vs. vegetation hunters, plant suckers vs. parasitoids, detritivores vs. parasitoids) were observed in all the treatments including ambient condition. Both web spiders and ground hunters were strongly correlated with herbivore/detritivores (including both plant suckers and detritivores) under ambient condition and N addition, yet part of links of web spiders and ground hunters has been lost under experimental drought; (b) Under N addition, further application of experimental drought did not impact the relative abundance of vegetation hunters, but exerted a negative effect on the interaction between plant chewers and vegetation hunters, and a positive effect on the interaction between vegetation hunters and parasitoids. (c) omnivores appeared a key functional group as both its relative abundance and number of interactions with other arthropod functional groups increased by experimental drought regardless of N addition.

Finally, by quantifying ecological network properties, we found that both experimental drought and N addition decreased C_{FG} , ID and IS of the interactions between arthropod functional groups and their sum except for increased ID and IS of carnivores-carnivores and ID of herbivores-carnivores (Fig.2). The IS of environmental factors on arthropod functional groups has been significantly increased by experimental drought, and the change of micro-habitat exerted significant effects on much more arthropod functional groups under experimental drought than ambient condition (Fig.1&3). Our manipulation of snowmelt effectively maintained snow cover for 1.7 days (in 2019) and 10.8 days (in 2020) longer. Compared with drought and N addition, delaying snowmelt only exerted a modest impact on plant and arthropod communities in the peak of growing season (Table.1&2&3; but see Fig.S1). Thus, we ignored the influence of delaying snowmelt when analyzing the ecological network at the peak of the growing season.

4 Discussion

Our results declared that both N addition and drought reduced the complexity of interaction network *via* reducing C_{FG} , ID and IS (Figure 2). The decreasing C_{FG} and ID of arthropod networks suggested that some species have been lost (Eklof & Ebenman, 2006; Tylianakis et al., 2010) and the decreasing IS suggested that the interdependence among functional groups was weakened (Rzanny & Voigt, 2012). Notably, N addition reinforced partial relationships between some herbivores and carnivores, which broke the balance of the

network and reduced its complexity, while drought eliminated some relationships among functional groups by filtering out some plant species that were related to arthropods. Compared with the ever-lasting effect of N addition and drought on arthropod communities in the peak of growing season, delayed snowmelt had a direct effect on arthropods only in the early growing season (Figure.S1); although delayed snowmelt had no direct effect on arthropod community in the peak growing season, it had significant interactive effects with N addition and/or drought on partial arthropod functional groups (Table.1&2).

Specifically, the effect of plant N could be cascaded up to higher trophic levels in N addition plots (Fig.1c&2), and foliar N was widely believed to have profound influence on arthropod's interaction both within and among trophic levels (Ilić et al., 2021). Changes in foliar N affect network complexity by interacting with foraging behavior of herbivores, and such effect could also be cascaded up (Bukovinszky et al., 2008). In our experiment, the relative abundance of plant suckers, detritivores and vegetation hunters was increased by N addition (Fig.1c). Generally, abundance of nitrophilous consumers increased due to elevated N content of primary producers when they were relieved from N restriction (Haddad et al., 2000; Elser et al., 2007; Wimp et al., 2010). For instance, aphids or leafhoppers (plant suckers) fed by piercing the phloem of their food plant and thus they are sensitive to changes in plant quality (Muller et al., 1999); In particular, a significant increase in relative abundance of plant suckers and detritivores resulted in reinforcement of partial relationships (e.g., plant suckers vs. web spiders, detritivores vs. parasitoids) under N addition treatment; however, plant chewers (e.g. grasshopper) were insensitive to N addition (Ritchie, 2000) (Table.3). The changes of different functional groups could be attributed to the specific responses of their N-related traits to N addition. Thus, N addition could weaken the net effect of other interactions thereby reducing ecosystem network complexity by strengthening trophic chains in single pathway (Fig.1&2).

Drought and its interaction with N addition both decreased the network complexity as indicated by declined connectance, ID and IS (Fig.2). Our results showed such decrease was realized not only through increasing foliar N, but also via reducing plant species richness (Fig.1b&2). Generally, more diverse producer communities could support more diverse primary consumers, which could be cascaded up to secondary consumers (Scherber et al., 2010; Rzanny & Voigt, 2012). Indeed, our results highlighted the negative effect of reduced plant richness on arthropod network features under drought conditions (Fig.1&2). Many network properties had been changed due to species loss and especially its resulted loss of relationship among arthropods within the networks under drought conditions. For example, omnivores (e.g. ants and beetles) had been transformed into the core of networks under drought conditions because they are better adapted to dry environments with low plant diversity. Such dry habitats are less attractive to most other arthropods, and are thus difficult to maintain stable interactions among arthropods and between arthropods and plants. More importantly, omnivores were found to be linked with many more other functional groups under experimental drought (Fig.1b&1d), suggesting that omnivores may play a critical role in maintaining the arthropod networks (Fig.1b&1d). Although some species could still adapt to the dry habitats, the change of microhabitat structure significantly impact arthropod functional groups and could not offer a suitable environment for predation (Fig.3). For instance, experimental drought decreased the relative abundance of web spiders and their links with other functional groups due to decreased vegetation height and uniformity (Figure.1). Weaving webs requires appropriate two-dimensional or complex three-dimensional environment (Gibson et al., 1992), but drought-induced high structural heterogeneity and low vegetation height are disadvantageous for predation of web spiders, leading to the disappearance of links of web spiders with plant suckers and parasitoids. Similar results had been obtained by different ecosystem studies measuring structure of food webs both qualitatively and quantitatively (Ledger et al., 2012; Woodward et al., 2012; Rosenblatt & Smith-Ramesh, 2017; Amundrud & Srivastava, 2019). However, several researches demonstrated that plant biomass is the key driver of arthropod community under multiple global changes in grassland, but the plant species richness of their study sites was much lower than ours (Wimp et al., 2010; Prather et al., 2020). Although drought strongly impacted plant biomass in the present study (Table.1), the spatial structure (β_{bal} and β_{bal}) of plant communities did not change significantly (Fig.4). Therefore, compared to the variation of plant biomass in grassland, the existence of plant species under climate changes is more important and thus appears the key factor for the arthropod ecological network stability and complexity (Brodersen et al., 2018).

Delayed snowmelt enhanced abundance of arthropod community in June, but showed little effect during the rest of the growing season (Fig.S1), despite that, delayed snowmelt showed significant interactive effects with drought or N addition on part of functional groups (Table.2&3; Fig.S1). For example, the interaction of delayed snowmelt with drought or N addition significantly influenced parts of carnivorous functional groups, including web spiders and parasitoids, which suggests that the global change events occurring in different seasons may interact (Table.2&3). It is conceivable that the effects of multiple global change factors on plants may be amplified and cascaded up to partial functional groups at higher trophic levels, ultimately leading to the mismatch between trophic levels (Post & Forchhammer, 2008; Rosenblatt & Smith-Ramesh, 2017), which will undoubtedly affect ecosystem stability (Baert et al., 2018; De Laendera et al., 2016; De Laender, 2018). The responses of carnivores as a whole to the interaction of snowmelt delay with drought or with N addition were modest, but significant changes did occur to its finer functional groups (including decreasing ground hunters and parasitoids). Especially, the diversity of parasitoids and web spiders differed in the responses to the interaction of snowmelt delay with drought (Table.2&3). It means that the responses of arthropods to multiple global change factors might be dependent on their specific traits (Voigt et al., 2003). Even now the reason for the responses of these functional groups remains unclear, but our study suggests that it is necessary to examine more complete taxa or functional groups in future researches, with the purpose of capturing the panorama of the responses of entire ecosystems. Meanwhile, long-term and slow global changes such as snowmelt can cause subtle biases in ecosystems that need to be taken into account in global change studies (Kroel-Dulay et al., 2015).

Author contribution

B Zhang, W Ma and Z Wang jointly conceived the study. B Zhang, W Ma, L Song and X Liang collected data. B Zhang analyzed output data and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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- Table 1** ANOVA table of F values on the effect of drought, nitrogen addition, delaying snowmelt, and their interactions on the plant community characters (including Plant biomass, plant richness and foliar N content, plant height and CV_{height}) and soil moisture.

	D	N	S	D×N	D×S	N×S	D×N×S
Plant biomass	77.7*** —	101.4*** —	1.0	26.2*** —	0.4	0.2	2.4
Plant richness	61.0*** —	30.1*** —	1.9	8.1** —	<0.1	6.4* —	2.5
Foliar N	37.4*** —	102.0*** —	1.6	2.8	0.6	2.6	4.1* —
Height	147.7*** —	2.7	<0.1	1.7	<0.1	0.8	5.8* —

	D	N	S	D×N	D×S	N×S	D×N×S
CV _{height}	9.5** —	4.4* —	0.1	3.4	1.6	2.0	0.1
Moisture	20.2*** —	0.2	<0.1	<0.1	1.1	0.4	0.8

Notes: Significant effects ($p < 0.05$) are given in bold; asterisks denote significant levels: *, $p < 0.05$; **, $p < 0.01$; and ***, $p < 0.001$, respectively. — & — represent the upward and downward trend of indicators. — & — represent the upward and downward trend of indicators.

Table 2 ANOVA table of F values on the effect of drought, nitrogen addition, delaying snowmelt, and their interactions on the effective diversity of arthropod functional groups, including herbivores (plant suckers and plant chewers), carnivores (parasitoids, web spiders, ground hunters, vegetation hunters), omnivores, detritivores.

	D	N	S	D×N	D×S	N×S	D×N×S
Total	34.6*** —	0.9	0.1	1.0	0.1	4.1*	<0.1
Herbivores							
Total	5.1* —	2.7	0.8	2.6	1.2	<0.1	1.3
Plant suckers	<0.1	7.2** —	1.9	0.3	<0.1	0.9	3.7
Plant chewers	19.7*** —	1.1	<0.1	12.9*** —	0.1	<0.1	<0.1
Carnivores							
Total	27.2*** —	<0.1	<0.1	<0.1	1.5	<0.1	1.9
Parasitoids	2.8	<0.1	<0.1	1.3	6.2* —	<0.1	0.1
Web spiders	3.7	2.0	1.2	1.7	9.4** —	2.5	<0.1
Ground hunters	3.4	<0.1	7.9** —	<0.1	1.7	<0.1	<0.1
Vegetation hunters	0.4	3.0	0.5	0.6	<0.1	<0.1	2.8
Omnivores	4.7* —	5.0* —	<0.1	4.0* —	1.9	0.4	3.2
Detritivores	11.9*** —	10.0** —	3.7	9.9** —	<0.1	<0.1	1.1

Notes: Significant effects ($p < 0.05$) are given in bold; asterisks denote significant levels: *, $p < 0.05$; **, $p < 0.01$; and ***, $p < 0.001$, respectively. — & — represent the upward and downward trend of indicators. — & — represent the upward and downward trend of indicators.

Table 3 ANOVA table of F values on the effect of drought, nitrogen addition, delaying snowmelt, and their interactions on the abundance of arthropod functional groups, including herbivores (plant suckers and plant chewers), carnivores (parasitoids, web spiders, ground hunters, vegetation hunters), omnivores, detritivores.

	D	N	S	D×N	D×S	N×S	D×N×S
Total	5.8* —	36.7*** —	<0.1	12.0*** —	4.9* —	2.1	1.0
Herbivores							
Total	2.2	21.3*** —	<0.1	3.6	1.0	<0.1	0.9
Plant suckers	14.4*** —	23.0*** —	<0.1	9.8** —	0.2	<0.1	0.3
Plant chewers	9.2** —	2.0	0.2	1.6	1.5	<0.1	1.1
Carnivores							
Total	27.2*** —	<0.1	<0.1	<0.1	1.5	<0.1	1.9
Parasitoids	11.4** —	0.6	0.6	<0.1	0.3	<0.1	2.7
Web spiders	64.9*** —	3.3	0.5	4.7* —	0.3	1.5	<0.1
Ground hunters	31.9*** —	1.6	1.3	0.3	5.1* —	<0.1	0.8
Vegetation hunters	<0.1	20.7*** —	<0.1	0.7	1.4	<0.1	<0.1
Omnivores	29.9*** —	<0.1	2.3	0.8	0.2	4.5* —	0.1

	D	N	S	D×N	D×S	N×S	D×N×S
Detritivores	20.1*** —	20.7*** —	0.4	13.4*** —	3.6	0.6	0.5

Notes: Significant effects ($p < 0.05$) are given in bold; asterisks denote significant levels: *, $p < 0.05$; **, $p < 0.01$; and ***, $p < 0.001$, respectively. — & — represent the upward and downward trend of indicators.

Figure legends

Figure 1 Functional group network webs in (a) Ambient, (b) Drought, (c) Nitrogen and (d) Drought * Nitrogen. Blue lines represent trophic interactions; Red lines represent biotic non-trophic interactions; Gray lines represent abiotic non-trophic interactions. The diameter of the circle under ambient is taken as the standard abundance, and the diameter of the circle under treatment changed according to the change of relative abundance (PS: plant suckers; PC: plant chewers; OM: omnivores; DE: detritivores; WS: web spiders; GH: ground hunters; VH: vegetation hunters; PA: parasite; PN: plant N content; EF: environmental factors).

Figure 2 Networks properties (connectance, interaction diversity and interaction strength) for the arthropod functional groups for ambient vs. treatment (including drought, nitrogen and their interaction) for 2 years. The Carnivores (C)-C value refer to network descriptors of the interaction of secondary consumer (a-c, horizontal interactions); C-Herbivores (H), the interaction between primary and secondary consumer (d-f, vertical interaction); H-H, the interaction of primary consumer (g-i, horizontal interactions); Total, the complete web of consumer (j-l).

Figure 3 Interaction strength of environmental factors to arthropod functional groups.

Figure 4 Response ratio of six β -diversity to N addition, drought and their interaction in grassland. The response ratio is data (treatment)/data (control), the horizontal error bars represent the 95% confidence interval. β_{sor} : overall pairwise dissimilarity of Sørensen, β_{sim} : turnover, β_{sne} : nestedness; β_{bc} : overall pairwise dissimilarity of Bray-Curtis; β_{bal} : balanced variation in abundance; β_{gra} : abundance gradients. Solid squares represent significant response of β -diversity to treatments, while hollow squares represent no significant responses.

Figure 1

Figure 2

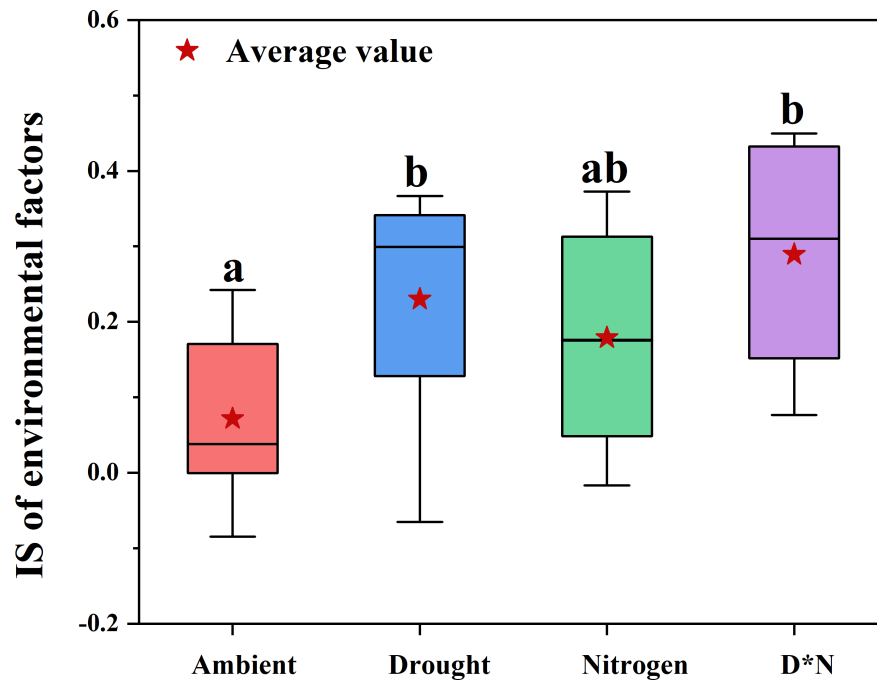


Figure 3

Figure 4