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Effects of altered precipitation on insect community composition and structure in a meadow steppe

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Abstract. 1. Precipitation can be a key driver of ecosystem functioning in semi-arid and arid grasslands. Altered precipitation patterns had significant impacts on plant community dynamics, which in turn influenced the community composition and structure of higher trophic levels, especially insects, in grasslands.

2. A field experiment was conducted by manipulating the amount of natural precipitation (control, +30% rainfall, and −30% rainfall) to examine the effects of altered precipitation patterns on insect diversity, abundance, and trophic structure in a meadow steppe over 3 years (2007–2009).

3. The results showed that the increased precipitation treatment significantly enhanced above-ground biomass of the entire plant community and particularly grasses, whereas the decreased precipitation treatment significantly reduced them. There were year-to-year changes in species richness, Shannon–Wiener index, and abundance of the whole insect community. Both increased and decreased precipitation caused declines in insect species richness and abundance owing to potentially complex vegetation-mediated effects and direct habitat effects. The abundance of each trophic guild in the insect community responded differently to altered precipitation patterns, with lower herbivore abundance and unchanged abundance of predators and parasitoids. Thus changes in precipitation may generate an insect community that is increasingly dominated by secondary consumers.

4. The present results suggest that altered precipitation causes a declines in insect diversity and shifts in trophic structure, potentially influencing ecosystem functioning in grasslands. Additionally, the inter-annual variation in the insect community under altered precipitation highlights the importance of long-term experiments for drawing correct conclusions about the impacts of climate change on grassland ecosystems.

Key words. Changes in rainfall, climate change, insect abundance, insect species richness, insect trophic composition, plant biomass, plant community composition.

Introduction

The increasing concentration of atmospheric CO_2 is predicted to increase the global mean temperature, which is closely associated with changes in precipitation patterns, including the intensity and frequency of rainfall (IPCC, 2007). Altered precipitation patterns have been shown to affect ecosystem functioning and processes, such as primary production and nutrient cycling (Knapp *et al.*, 2002; Wu *et al.*, 2011), especially in semi-arid and arid areas where water is the primary limiting factor to primary production. As future precipitation patterns are predicted to be highly variable (Meehl *et al.*, 2007), this causes a great deal of uncertainty about potential ecosystem responses to climate change (Knapp *et al.*, 2008). Therefore, a better understanding of the consequences of altered precipitation patterns has important implications for conservation planning and ecosystem management (Beier *et al.*, 2012).

The influence of variation in precipitation on the dynamics of plants and animals is a key issue in global change ecology (Fay *et al.*, 2003; Staley *et al.*, 2006; Engelbrecht *et al.*,

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2007). Previous studies on the impacts of variation in precipitation on the plant community suggest that altered precipitation could influence species richness (Zavaleta *et al.*, 2003; Adler & Levine, 2007), shape community composition (Sandel *et al.*, 2010; Yang *et al.*, 2011) and alter primary productivity (Heisler-White *et al.*, 2008; Thomey *et al.*, 2011). Additionally, organisms at higher trophic levels have also been proposed to be sensitive to altered precipitation, as water availability exerts strong controls over the structure and dynamics of their community through direct and indirect effects (Masters *et al.*, 1998; Suttle *et al.*, 2007). However, only a few studies have considered the responses to altered precipitation of trophic levels above plants and particularly the insects (Frampton *et al.*, 2000; Huberty & Denno, 2004). Altered insect community dynamics associated with precipitation are likely to have consequential influences on ecosystem functioning, particularly by affecting insect productivity (Gamfeldt *et al.*, 2005; Borer *et al.*, 2012), altering plant diversity and community composition (Mulder *et al.*, 1999), and even influencing nutrient cycling in soil (Belovsky & Slade, 2000; Matt & Charlton, 2006). Thus there is a compelling need for studies that consider the responses of the insect community to altered precipitation in terrestrial ecosystems.

Compared with primary producers (plants), the effects of altered precipitation patterns on insect diversity and composition are more difficult to predict. On the one hand, changes in precipitation are associated with variation in other abiotic environmental conditions, which could alter the phenology and performance of insects (Morecroft *et al.*, 2002; Guo *et al.*, 2009), consequently influencing insect community dynamics directly. For instance, altered precipitation may affect the temperature and humidity of the habitat where the overwhelming majority of insects live, so that many insects cannot maintain an optimal body temperature in their surrounding environment, inhibiting the completion of lifecycle development (Battisti *et al.*, 2005), and thereby affecting insect species richness and abundance in the entire community. On the other hand, altered precipitation may indirectly influence the insect community via trophic cascade effects (Menéndez *et al.*, 2007; Warne *et al.*, 2010). As the insect community is closely related to that of the plants altered precipitation may indirectly affect insects by changing plant community. For example, Suttle *et al.* (2007) observed that supplementary water during the spring period resulted in a decline in insect species richness via decreases in plant biomass and species richness. In addition, spring irrigation enhanced vegetation height and ground cover, which led to increases in the abundance and diversity of insects (Frampton *et al.*, 2000). Thus, the effects of altered precipitation on the insect community may be more complex than previously thought.

Both decreased and increased precipitation may occur after global climate change (IPCC, 2007). For northeastern China, spring precipitation is predicted to decrease by 35%, and summer precipitation to increase by 31% (Liu *et al.*, 2005). We conducted a field experiment by manipulating the rainfall to examine how altered precipitation patterns affect the diversity and trophic structure of the insect community. We hypothesised that decreased rainfall will cause declines in the diversity and abundance of herbivorous insects because the lower precipitation will induce reductions in plant biomass and species richness (Pfisterer & Schmid, 2002; Wang *et al.*, 2007). In contrast, we hypothesised that increased rainfall will increase the diversity and abundance of herbivorous insects owing to increased plant biomass and species richness (Zavaleta *et al.*, 2003; Robertson *et al.*, 2009; Wu *et al.*, 2011). Such changes in plants and herbivorous insects may strongly affect the species richness and abundance of higher trophic levels by decreasing the abundance of insect predators in the decreased precipitation treatments, and increasing their abundance in the increased precipitation treatments. Furthermore, altering the rainfall will have different effects on each insect functional guild owing to their different sensitivities to climate change (Voigt *et al.*, 2003), which will influence insect trophic structure. Owing to the greater dominance of herbivores in terms of abundance in the insect community in the experimental area (Zhu *et al.*, 2012), the dynamics of the insect community may be similar to that of just the herbivores.

Materials and methods

Study site

The experiment was conducted at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, P. R. China (44°45′N, 123°45′E) where the climate is classified as semi-arid, continental and monsoon with a frost-free period of about 140 days. The annual mean temperature and precipitation ranged from 4.6 to 6.4 °C and from 280 to 400 mm during 1999–2011, respectively. More than half of the annual precipitation is received during the growing season (from April to September), with most falling between June and August. Soils are mixed saline and alkaline (pH 8.5–10.0). The plant community in the study site is dominated by *Leymus chinensis* (Trin.) Tzvel. and *Stipa baicalensis* Roshev. (Wang & Ba, 2008). Other species are also abundant, including grasses such as *Phragmites australis* (Clav.) Trin. and *Calamagrostis epigejos* (L.) Roth., forbs such as *Kalimeris integrifolia* Turcz. and *Artemisia mongolica* Fisch., and legumes such as *Lespedeza davurica* Schindler.

Experimental design and treatments

In view of the difficulty of controlling precipitation in a larger area, in early April 2007 we established nine 3.5 × 3.5 m relatively flat plots with homogeneous soil conditions and plant community composition. The plot area was similar to that described in Frampton *et al.* (2000). Adjacent plots were separated by a distance of 3 m. The nine plots were randomly assigned to three precipitation treatments, with each treatment having three replicates. The three precipitation treatments were as follows: (i) control – plots received only natural rainfall throughout the study period; (ii) decreased precipitation (−P) – plots received natural rainfall except from April to October in each experimental year when transparent polyethylene roofs were deployed manually to shield the plots from rainfall, resulting in a 30% decrease in rainfall; the roofs were deployed only during rainfall periods to avoid their potential effects on the light environment; (iii) increased precipitation (+P) – in addition to natural rainfall, plots received an additional 30% rainfall, originating from the decreased rainfall plots. Rainfall was captured from the decreased rainfall treatment plot using four 0.29 × 3.2 m transparent polythene roofs installed above the vegetation at a height of 1.6 m on the southern side and 1.2 m on the northern side. The roofs were deployed evenly above the canopy. The intercepted rainfall was collected into a container through tubes fixed to the lower end of the roofs. The collected rainwater was manually and evenly irrigated throughout the increased precipitation plots. To prevent water uptake by plants surrounding the plots, along the edge of each plot polyethylene barriers (30 cm tall) were inserted 20 cm into the soil to separate the majority of plant roots. The remaining 10 cm of polyethylene barrier was used to avoid surface water exchange between the experimental plots and the surrounding area. Precipitation treatments were conducted from April 2007 to October 2009.

Vegetation measurement

Vegetation measurements were conducted monthly at June–September in 2007, 2008, and 2009. As this experiment was designed as a long-term manipulative experiment, the vegetation survey was performed non-destructively. For each plot, plant species richness and plant height were recorded in 10 randomly located 0.25 × 0.25 m quadrats. Within each quadrat, all plant species were identified, and the height of each plant individual measured to the nearest centimeter using a ruled rod. Above-ground plant biomass (mid-August) was estimated using an empirical relationship between height and biomass (see Table S1 for details in the calculation of above-ground plant biomass). Plants were divided into three functional groups: grasses, legumes, and forbs. Owing to the lower biomass of legumes, the sum of forb and legume biomass was calculated and analysed separately from grass biomass.

Insect sampling and identification

Insect species richness and abundance were measured monthly between July and September from 2007 to 2009 using the standard sweepnet survey method: the light muslin net 40 cm in diameter was described by Evans *et al.* (1983) and Zhu *et al.* (2012). Insect specimens were collected between 09.00 and 15.00 hours under favourable conditions (sunny and calm). To ensure that each sample was representative, insects were collected from 10 beats of the net in the vegetation within each plot and pooled to give a plot sample. Six samples were collected in each plot for each sampling month, each separated by 5 days. Before each insect sampling, we made sure that insects, including those that can fly long distances, could naturally colonise the plants in the experimental plots (Zhu *et al.*, pers. obs.). To minimise the potential effects of insect immigration and migration on the data, the nine plots were swept simultaneously on every given sampling date. The sampled insects were preserved in ethyl acetate and identified to species if possible, otherwise they were categorised into the lowest possible taxonomic level (family or order). Immature insects were excluded from the analysis.

Statistical analysis

The cumulative species richness of plants and insects and the cumulative abundance of insects (abundance of all insects and each trophic guild) throughout sampling periods in each year (from 2007 to 2009) were analysed. The Shannon–Wiener index was calculated as $H = -\sum_{1}^{S} \left(P_i \times \ln\left(P_i\right)\right)$, where P_i is the proportion of individuals represented by species i, and S is the total number of insect species. Insect effective diversity could control difference in species richness caused by differences in sampled insect individuals (Ricklefs & Miller, 2000); this was calculated as e^{H}, where H is the Shannon–Wiener index, and e is Euler's number. Insect community structure was analysed using the regression relationship between abundance of the secondary consumer (predators and parasitoids) and those of the primary consumer (herbivores).

Normality and assumptions of these measured variables of plants and insects were checked, and no transformation was required. The effects of changes in the amount of rainfall on plant species richness, plant biomass (total biomass, grass biomass, and legume and forb biomass), insect species richness, and insect abundance (total insects, herbivores, predators, parasitoids, and detritivores) were analysed using repeated-measures ANOVA, with precipitation treatment as a between-subject factor (main effect) and time as a within-subject factor (repeated), considering plots as experimental units. Further, one-way ANOVA was carried out to examine the effects of precipitation treatments on measured variables within each experimental year. Significance levels were adjusted for multiple comparisons using Tukey's test, and were set at $P \leq 0.05$. Linear regressions were used to determine the relationship between primary consumer (herbivores) abundance and secondary consumer (predators and parasitoids) abundance. All statistical tests were performed using SAS 9.13 statistical package (SAS Institute Inc., Cary, North Carolina).

The effects of altered precipitation on the trophic composition of insects were analysed by multivariate ordination redundancy analysis (RDA) using the program CANOCO 4.0 (ter Braak & Šmilhauer, 1998). The RDA was applied by considering treatment plots as samples, abundance of each insect trophic guild as species variables, and plant biomass (total biomass, grass biomass, and forb and legume biomass) as environmental variables. Data of insect abundance and plant biomass were log-transformed prior to analysis.

Results

Temperature and precipitation

Temperature and precipitation were highest in July over the experimental periods (Fig. S1). The mean annual temperature in 2007 (9.04 °C) was higher than that of 2008 (6.97 °C) and 2009 (7.05 °C). Precipitation during the growing season in 2007

Table 1. Results of repeated-measures ANOVA for the effects of year (Y) and precipitation (P) and their interactions on plant species richness, total plant biomass, grass biomass, and forb and legume biomass over the three experimental years (2007–2009).

Plant variables		Y 2, 18	P 2, 18	Y × P 4, 18
Plant species richness	F	1.39 NS	0.262 NS	0.488 NS
Total plant biomass	F	71.844***	18.972**	3.134*
Grass biomass	F	91.353***	20.831**	5.015*
Forb and legume biomass	F	97.679***	4.821*	23.414***

Significance level: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS: not significant ($P > 0.05$).

(207.9 mm) and 2009 (286.2 mm) was lower than that of 2008 (382.9 mm).

Plant species richness and biomass

Plant species richness showed no inter-annual change, and it was affected neither by altered precipitation nor by interactions of experimental year and precipitation treatment (Table 1 and Fig. 1a). There were strong inter-annual variations in the above-ground biomass (AGB) of forbs and legumes, grasses, and the whole plant community (all $P < 0.0001$, Table 1). Across the 3 years, altered precipitation significantly affected the AGB of the whole community, grasses, and forbs and legumes (all $P < 0.05$, Table 1). In addition, plant community biomass increased significantly in the increased precipitation plots in 2007, 2008, and 2009, and decreased in the decreased precipitation plots (Fig. 1b). A similar pattern was found for grass biomass, but this did not change in the decreased precipitation plots in 2007 (Fig. 1c). The increased and decreased precipitation treatments had no significant effects on legume and forb biomass in 2007 and 2008, but reduced them in 2009 ($P = 0.006$, Fig. 1d).

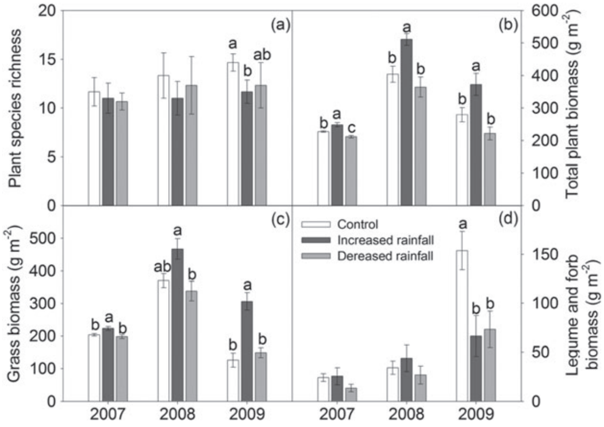

Fig. 1. The effects of altered precipitation on plant species richness (a), total plant biomass (b), grass biomass (c), and forb and legume biomass (d). Data are reported as means ± SE. Different letters indicate that values differ significantly between altered precipitation treatments within each experimental year ($P \leq 0.05$).

Table 2. Results of repeated-measures ANOVA for the effects of year (Y) and precipitation (P) and their interactions on insect abundance, including total insects, herbivores, predators, parasitoids, and detritivores, insect species richness, insect effective diversity, and insect Shannon–Wiener over the three experimental years (2007–2009).

Insect variables		Y 2, 18	P 2, 18	Y × P 4, 18
Insect species richness	F	4.712*	16.217**	4.541*
Insect effective diversity	F	10.91**	6.733*	2.293 NS
Insect Shannon-Wiener index	F	13.753**	9.86*	4.177*
Insect abundance	F	79.72***	23.205**	6.007**
Herbivore abundance	F	74.019***	17.581**	5.878**
Predator abundance	F	2.178 NS	1.86 NS	0.428 NS
Parasitoid abundance	F	1.03 NS	2.969 NS	0.213 NS
Detritivore abundance	F	182.2***	7.889***	5.6*

Significance level: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS: not significant ($P > 0.05$).

Species richness, effective diversity, the Shannon–Wiener index, and abundance of the insect community

Insects collected belong to nine orders (Orthoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, Homoptera, Lepidoptera, Mantodea, and Neuroptera). Approximately 89% of specimens were identified to species, with the remainder to genus (6%), family (4%), or order (1%). Insects were further classified into one of four trophic guilds: herbivores, predators, parasitoids, or detritivores. A small number of species from the total pool of insects (< 0.7%) could not be identified for guild placement and were thus omitted from analysis.

There were significant inter-annual changes in species richness, effective diversity, the Shannon–Wiener index, and abundance of the insect community (all $P < 0.05$, Table 2). Precipitation treatment was found to have significant effects on the species richness, effective diversity, the Shannon–Wiener index, and abundance of the insect community (Table 2 and Fig. 2). Precipitation treatment interacted with time to affect insect species richness, the Shannon–Winner index, and abundance (Table 2). Compared with the control, in 2007, there were no effects of the precipitation treatments on insect species richness, but decreased precipitation caused a decline in insect species richness in 2008, and both increased and decreased precipitation treatments led to a reduction in insect species richness in 2009 (Fig. 2a). Compared with the controls, both the increased and decreased precipitation treatments induced a significant reduction in total insect abundance (Fig. 2b). The insect Shannon–Wiener index in the increased precipitation plots was higher than that of the decreased precipitation plots in 2007, but lower than that of the controls in 2009 (Fig. 2d).

Abundance of herbivores, predators, detritivores, and parasitoids

There were no inter-annual changes in the abundance of predators and parasitoids, but significant inter-annual variation in the abundance of herbivores and detritivores were found (Table 2). Altered precipitation had significant effects on the abundance of

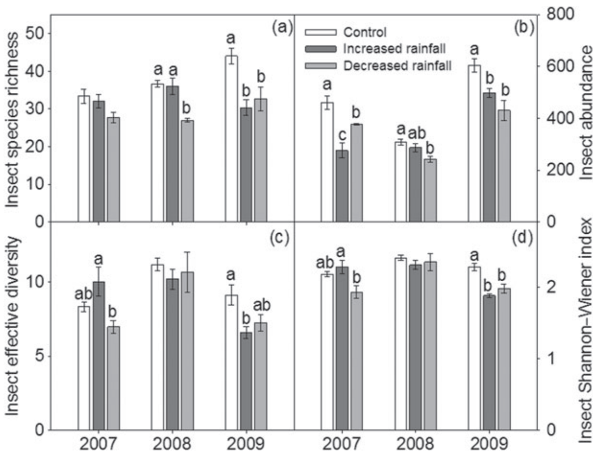

Fig. 2. The effects of alterations in the amount of precipitation on insect species richness (a), abundance (b), effective diversity (c), and the Shannon–Wiener index (d). Data are reported as means ± SE. Different letters indicate that values differ significantly between altered precipitation treatments within each experimental year ($P \leq 0.05$).

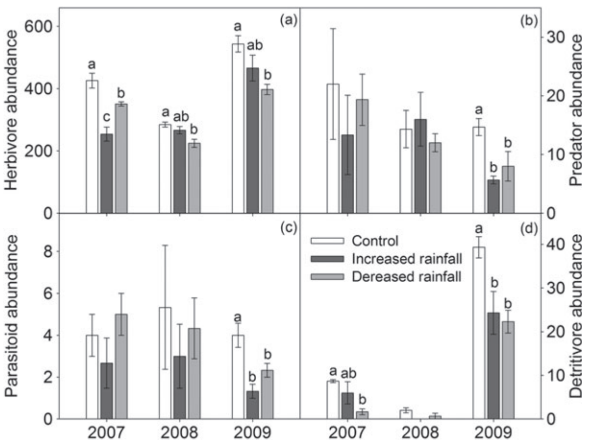

Fig. 3. The responses of abundance of herbivores (a), predators (b), parasitoids (c), and detritivores (d) to altered precipitation. Data are reported as means ± SE. Different letters indicate that values differ significantly between altered precipitation treatments within each experimental year ($P \leq 0.05$).

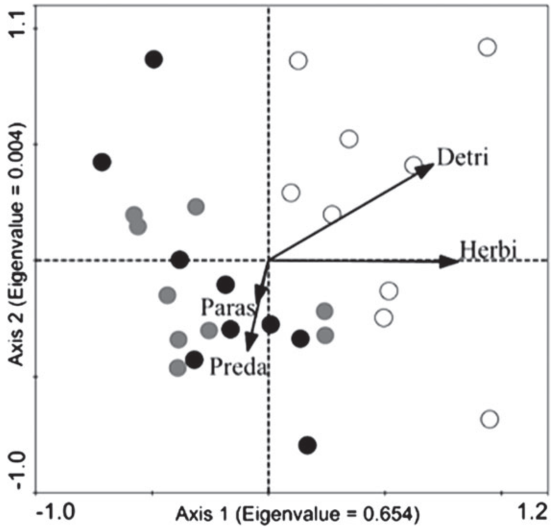

Fig. 4. Species composition of insects in response to altered precipitation using redundancy analysis (RDA). Open circle symbols represent the control treatments. Black circle symbols represent the increased precipitation treatments. Grey circle symbols represent the decreased precipitation treatments. Abbreviated insect trophic guilds: Herbi, herbivores; Preda, predators; Paras, parasitoids; Detri, detritivores.

herbivores and detritivores (both $P < 0.0001$, Table 2), but not for the abundance of predators and parasitoids. Both increased and decreased precipitation treatments significantly reduced herbivore abundance by 21.33% and 22.45%, respectively, and detritivore abundance by 39.35% and 50.69%, respectively (Fig. 3a,c). The effects of altered precipitation on the abundance of insect trophic guilds were examined with RDA (Fig. 4). The results also showed that increased precipitation had a negative impacts on the abundance of herbivores and detritivores, but non-significant effects on the abundance of predators and parasitoids. Likewise, decreased precipitation caused reduction in the abundance of herbivores and detritivores, yet did not change the abundance of predators and parasitoids. In addition, interactive effects of precipitation treatment and time on different guilds were found only for herbivores and detritivores (Table 2).

To identify the trophic structure of the insect community in response to altered precipitation, the relationships between primary consumer (insect herbivores) and secondary consumer (insect predators and parasitoids) abundances were examined. Results showed that the abundance of predators and parasitoids significantly increased with increasing herbivore abundance in control treatments, but it gradually decreased under the increased precipitation treatments. However, under the decreased precipitation treatments, predator and parasitoid abundance did not correlate with herbivore abundance (Fig. 5).

Discussion

There is a growing need to investigate the effects of climate variables on the structure and diversity of the insect community (Walther, 2010), as insects could play important roles in ecosystem functioning (Belovsky & Slade, 2000; Matt & Charlton, 2006). Our results showed that alterations in the amount of rainfall significantly affected the diversity, abundance, and trophic structure of the insect community in a meadow steppe. This knowledge furthers our understanding of the insect community dynamics and their consequent impacts on ecosystem functioning in response to climate change.

Interannual variability in insect diversity and abundance

Strong inter-annual variation in the diversity and abundance of the insect community was observed over the experimental period (Table 2). Although the 3-year experimental period in this study is relatively short, these aspects still make this work

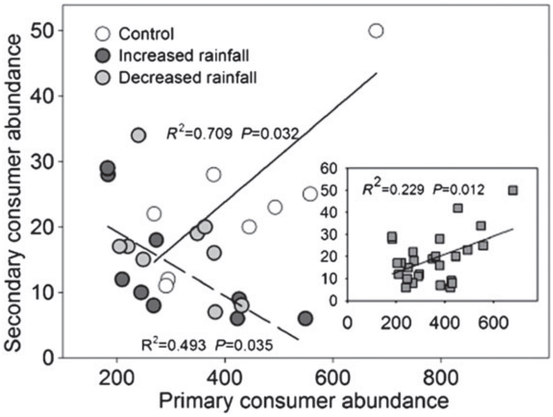

Fig. 5. The relationship between primary consumer (herbivores) abundance and secondary consumer (predators and parasitoids) abundance. In the main figure, the solid line represents their relationship in the control plots, and dashed line represents their relationship in increased precipitation treatment plots. Inset figure shows the relationship between primary consumer abundance (herbivores) and secondary consumer abundance (predators and parasitoids) in all altered precipitation treatments. Each data point represents the value in one plot for each altered precipitation treatment across the experimental 3 years (from 2007 to 2009).

particularly valuable for global change research in general. The study area is located in a semi-arid region where water is a key limiting factor, hence higher amounts of precipitation in the growing season could stimulate plant growth, and in turn lead to an increase in plant biomass (Yang *et al.*, 2011). Our results showed that the amount of precipitation in 2008 was higher than that of 2007 and 2009 (Fig. S1), consequently contributing to strong year-to-year variation in plant biomass, with the greatest plant biomass in 2008 (Fig. 1b). Correspondingly, reduced insect species richness and abundance were detected in 2008 (Fig. 2). It is suggested that the observed change in species richness and abundance of the insect community could not be attributed to altered plant biomass. Interestingly, our results found that insect species richness and abundance increased significantly in 2009. The greater rainfall in 2008 is likely to have induced a more productive plant community, which in turn provided more food resources for insects in July and August – a critical period of oviposition. Thus, insects may have laid more eggs, giving rise to increased insect abundance in the next year. Furthermore, the higher amount of rainfall in the spring of 2009 compared with 2008 (Fig. S1) may have been advantageous for the hatching and development of insect eggs, which may also have led to a greater insect abundance. Overall, the results suggest that inter-annual precipitation may not only drive plant community biomass (Yang *et al.*, 2011), but also affect the insect community structure.

Effects of altered precipitation on the diversity and abundance of the insect community

Decreased precipitation caused reductions in primary production (Fig. 1b) and water availability, which led to lower diversity and abundance of insects, including herbivores, predators, parasitoids, and detritivores (Figs 2 and 3). In this study, we did not attempt to separate out direct and indirect effects of altered precipitation on the insect community, so we did not assess the direct effects of water on insect survival. Our results showed that these effects are more likely to have been plant mediated via changes in induced plant primary production instead of from water availability itself. Correspondingly, increases in insect richness and abundance were expected in the increased precipitation treatments; however, we observed a significant reduction in insect species richness and abundance in the increased precipitation plots (Figs 2a,b and 4b). The ‘resource productivity’ hypothesis predicts that a more productive plant community sustains a greater abundance of consumers owing to sufficient food supplies, thus supporting higher consumer diversity (Perner *et al.*, 2005). In our study, the increased precipitation treatment resulted in a significant increase in plant biomass (Fig. 1b), but this enhancement in plant biomass did not lead to an consistent increase in the species richness and abundance of insects (Fig. 2a,b). The significant increase in grass biomass and decrease in the biomass of forbs and legumes in the increased precipitation plots suggested potential shifts in plant community composition, becoming grass dominated (Fig. 1c,d). A grass-dominated community could support fewer herbivore species as a result of the food preferences of some herbivores (Haddad *et al.*, 2001). Increases in the dominance of grasses could also offer less structural complexity than a mixed grass-forb community for insects, which may cause a reduction in insect species richness due to a lowered chance of escape from natural enemies (Brose, 2003). On another note, increased precipitation could dilute nutrient pools and lead to declining physiological fitness of plants (Masters *et al.*, 1998), decreasing insect species richness due to plants being less nutritious as insect food. Moreover, increased precipitation clearly has been shown to have an impact on the microclimate at the soil surface (Frampton *et al.*, 2000; Wang *et al.*, 2007, pers. obs.), which may explain, to some extent, the observed reduction of insects whose development is critically dependent upon optimal conditions of soil moisture, e.g. *Phytomyza conyzae* (Staley *et al.*, 2006).

Other than the above-mentioned potential causes, the observed reductions in insect diversity and abundance in the increased precipitation plots may partially be attributed to potential artefacts caused by the close distances among plots and the limitations of the sampling technique (sweep netting). We feel, however, that the results give a reasonable approximation of field conditions for a couple of reasons. First, the effectiveness of the sampling method crucially depends on the plant vegetation structure, and the sweep net method is more efficient in collecting insects that inhabit vegetation (Zhu *et al.*, 2012; Harvey *et al.*, 2013). Although sweep netting does not sample all insects in the community, insect community measurements obtained from sweep netting have been shown to be highly correlated with insects sampled by netting and other methods, particularly suction sampling and pitfall trapping (Siemann, 1998; H. Zhu *et al.*, unpublished). Second, previous studies suggest that the insect community varies little with enclosure sizes ranging from 4 to 70 m^2, and distance between plots ranging from 1 to 2 m (Frampton *et al.*, 2000; Haddad *et al.*, 2000; Suttle *et al.*, 2007). Overall, we think the effects of the sampling method and distance between plots are negligible.

Effects of altered precipitation on insect trophic structure

The trophic structure provides an important framework to examine the effects of climate change on the insect community (Villalpando *et al.*, 2009). Our results showed that altered precipitation strongly affected the insect trophic structure, consistent with other studies which found that reduced summer rainfall strongly affected plant-mediated interactions between aphids and parasitoids, in turn altering the above-ground multitrophic structure (Johnson *et al.*, 2011; Aslam *et al.*, 2013). Manipulated precipitation caused a greater reduction in herbivore (as discussed above) and detritivore abundance, but did not have significant effects on predator and parasitoid abundance (Figs 3 and 4). Detritivores are susceptible to food resource abundance changes, such as the frass of insects, so reduced herbivore abundance could lead to reductions in the quantity of insect frass, which may decrease detritivore abundance. In view of our insect sampling method (sweep netting), some ground-dwelling predatory insects that constitute some fraction of the insect community are unlikely to be caught (they are captured optimally by pitfall trapping), perphaps leading to a lower abundance of predators in this study. This may be a main reason why the abundance of predators under altered precipitation treatments remained unchanged. Parasitoid abundance generally correlates the abundance of their hosts, such as larvae of Lepidoptera (Karimzadeh & Wright, 2008; Niogret *et al.*, 2009). However, Lepidoptera larvae comprised a small proportion of the insect community in our sampled plots (see Table S2), resulting in a lower and unchanged abundance of parasitoids. Therefore, herbivores, predators, detritivores, and parasitoids respond differently to altered precipitation across the three experimental years (Fig. 3). These results suggest that altered precipitation patterns may significantly affect the insect trophic structure, and generate an insect community dominated by secondary consumers.

Generally, the abundance of higher trophic levels is positively associated with lower trophic levels as a result of bottom-up effects (Hunter & Price, 1992). In our study, this pattern was also found, that is, the abundance of predators and parasitoids increased with increasing herbivore abundance (Fig. 5). However, a negative relationship was found under increased precipitation (Fig. 5). This may be attributed to the responses of herbivores, predators, and parasitoids to increased precipitation.

Conclusions and implications

To date, a strong focus has been placed on changes in community dynamics as a result of climate change (Adler & Levine, 2007; Villalpando *et al.*, 2009; Yang *et al.*, 2011). Our study provides an empirical assessment of the strong response of the insect community structure to altered precipitation in a meadow steppe. The results of the 3-year study indicated that altered precipitation reduced insect diversity and abundance, especially herbivores, which would be unfavourable to the maintenance of biodiversity in the experimental region; this may potentially influence ecosystem functioning, such as plant productivity (Borer *et al.*, 2012). Additionally, increased precipitation generated an insect community increasingly dominated by secondary consumers, and hence likely to affect food-web stability in grassland ecosystems. Therefore, some attention should be paid to the protection of insect biodiversity under scenarios of altered precipitation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Figure S1. Monthly air temperature (lines) and rainfall (columns) from 2007 to 2009.

Table S1. The regression equations of height and biomass of each plant species in August in each year.

Table S2. The number of insect species and individuals within taxonomic orders pooled from all plots in this study.

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