



Original Articles

The responses of different insect guilds to grassland degradation in northeastern China

Hang Ruan^a, Xuefeng Wu^a, Shengnan Wang^a, Jingjing Yang^b, Hui Zhu^{a,*}, Qinfeng Guo^c, Ling Wang^a, Deli Wang^{a,b}

^a Institute of Grassland Science, Key Laboratory of Vegetation Ecology of the Ministry of Education, Jilin Songnen Grassland Ecosystem National Observation and Research Station, Northeast Normal University, Changchun 130024, China

^b School of Environment, Northeast Normal University, Changchun 130024, China

^c USDA – Southern Research Station, 3041 Cornwallis Road, Research Triangle Park, NC, USA



ARTICLE INFO

Keywords:

Grassland degradation
Insect guild
Response
Richness
Abundance
Ecological indicator

ABSTRACT

Grassland insect diversity in many parts of the world is severely threatened by recent deterioration caused by global change and human activities. Insect species richness and abundance are likely sensitive to grassland degradation because of changes in vegetation structure and microclimates, and yet, our understanding of how diversity of insect community, particularly insect guilds responds to grassland degradation is still limited. Here, we conducted a field experiment to examine the responses of richness and abundance of total insects and different insect guilds along degraded levels (i.e., non-degraded, moderately, and severely degraded site) in meadow steppe at northeastern China. We found that higher species richness of total insects was detected in the moderately degraded sites, and there was no difference in abundance between the three sites. Furthermore, the responses of richness and abundance of each insect guild were significantly different. Hemiptera richness was significantly higher at moderately degraded sites, and Orthoptera richness was higher in severely degraded sites. Abundance of Hemiptera and Orthoptera increased with the increasing levels of degraded grasslands, but the abundance of Hymenoptera and Coleoptera decreased. Moreover, effect size of grassland degradation on Orthoptera abundance was larger from non-degraded to moderately degraded grassland; and larger effect size on Coleoptera abundance from moderately to severely degraded grassland. The different responses of insect guilds to grassland degradation are mainly attributed to changes in food and microclimate availability. In the light of convenience and operability, the finding from the study suggested that the abundance of an insect guild, rather than total insects and insect diversity seem to be a useful ecological indicator when assessing the levels of grassland degradation.

1. Introduction

Grasslands are one of the most common types of vegetation around the globe, accounting for nearly 20% of the global land surface (Scurlock and Hall, 1998). However, almost half (49.25%) of world's grasslands experienced degradation, approximately 5% of which suffered extreme degradation in recent several decades due to climate change and anthropogenic activities (e.g. overgrazing) (Gang et al., 2014). Grassland degradation is characterized by reduction in dominance of dominant plant species, plant diversity, biomass, and soil nutrients, etc (Wang et al., 2009; Dong et al., 2012; Li et al., 2016). Clearly, such degradation leads to remarkable ecological consequences for

community stability and ecosystem functioning (Babel et al., 2014; Wang et al., 2019a; Wang et al., 2019b). Most studies have focused on how plant community composition and soil properties respond to grassland degradation (Wang et al., 2009; Guo et al., 2019), while the responses of insect communities are poorly understood. As well known, insects as an important component of grassland ecosystem, play a key role in enhancing nutrient cycling and community stability (Belovsky and Slade, 2000; Eisenhauer et al., 2011). Elucidating the responses of insect community is therefore essential for evaluating grassland degradation and developing conservation strategies.

Most insects have been demonstrated to show strong sensitivities to changing environmental conditions where vegetation provides food

* Corresponding author.

E-mail address: zhuh824@nenu.edu.cn (H. Zhu).

<https://doi.org/10.1016/j.ecolind.2021.108369>

Received 19 January 2021; Received in revised form 17 September 2021; Accepted 8 November 2021

Available online 12 November 2021

1470-160X/© 2021 The Authors.

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resources and habitats for their development and oviposition (Dempster, 1963; Tschamtkke and Brandl, 2004; Zhu et al., 2015a). Mixed results have been found about the responses of insects to altered plant diversity (species richness and functional richness), including positive, neutral, or negative responses. Such responses may depend on a variety of factors, such as insect guilds, plant diversity, microclimate, and so on (Haddad et al., 2001; Zhu et al., 2012; Lin et al., 2015). For example, the richness of herbivorous and predatory insects increases with increasing plant species richness, and there are opposing responses of abundances, with a decline in herbivore abundance and an increase in predator abundance (Haddad et al., 2009; Joern and Laws, 2013). And furthermore, changes in plant species richness have no effects on richness of parasitoids and detritivores (Haddad et al., 2001). A few studies have argued that complex plant structural heterogeneity support greater species richness of insects, compared with simple one (Zhu et al., 2012; Jerrentrup et al., 2014). But, some grasshopper species, like *Psooessa texana* and *Hadrotettix trifasciatus* prefer to select structurally simple plant communities (Joern, 1982). As ectothermic organisms, each insect species has specific requirements for temperature and humidity. For instance, leafminers and parasitoids prefer to living into the habitat with lower moisture (Bernaschini et al., 2020). Thus, changes in temperature and humidity of microclimate could affect insect diversity and abundance. Moreover, the predators' presence could reduce insect abundance through predation (consumptive effects) (Oksanen et al., 1981; Abrams, 2007; Bucher et al., 2015). Thus, the availability of both food resource and habitat is key determinant for alterations in insect diversity and abundance.

The restored and degraded processes of grassland after disturbances are often accompanied by changes in biotic and abiotic properties, including plant diversity, vegetation structure, and habitat microclimate, etc. (Dong et al., 2020), which subsequently affects insect community composition (Luong et al., 2019). A part of previous studies have mostly indicated sensitive responses of insect community during grassland restoration (Barber et al., 2017; Woodcock et al., 2010). For example, bees rapidly colonize into restored prairie habitat, and their abundance and richness increased with restoration ages (Griffin et al., 2017; Lettow et al., 2018). Barber et al. (2017) found higher species richness and abundance of ground beetles in early restoration stages. These conclusions show that the responses of insect diversity and abundance to grassland restoration are guild-specific. Hitherto, it hypothesized that insect guilds may show highly unpredictable responses during grassland degradation. However, whether and how insect community responds to grassland degradation is largely unexplored. Particularly, few studies focus the responses of insect guilds to grassland degradation.

The Songnen grassland, a meadow steppe, located at the eastern region of the Eurasian steppe, which is an important natural rangeland for livestock husbandry and provides many ecosystem functions and services, such as biodiversity maintenance, carbon sequestration and water conservation (Yin et al., 2018; Wang et al., 2019a; Wang et al., 2019b). It is now commonly agreed that this grassland is an ecologically fragile system facing an irreversible trend of degradation due to both saline parent material and disturbances, including the intensification of livestock overgrazing (Li and Yang, 2011; Li et al., 2014). In this region, our previous studies have found that the insect community as a whole, grasshoppers, and ants responded significantly to large herbivore grazing, elevated air temperature, and altered precipitation at non-degraded site in experimental area (Zhu et al., 2012; Zhu et al., 2015b; Zhong et al., 2017; Zhu et al., 2017). Here, we performed a field experiment to examine (1) how diversity and abundance of insect guilds responds to each degradation level, (2) what environmental factors explain variation in richness and abundance of each insect guild?

2. Materials and methods

2.1. Study site and experimental design

The study was conducted at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, China (44°40'–44°44'N, 123°44'–123°47'E; 150 m ASL). The area has a semiarid continental monsoon climate, with cold and dry winter, warm and rainy summer. Mean annual temperature and precipitation are 6.1 °C and 393.0 mm respectively during 2004 to 2013, and more than half of the precipitation occurs during April–August. Annual evaporation varies from 1200 mm to 1600 mm. The main soil type is castanozem with high salinity and alkalization (pH 8.5–10.0) and low nitrogen, phosphorus, magnesium, and calcium (Liu et al., 2015; Song et al., 2017). The vegetation is dominated by perennial grass *Leymus chinensis* (Wang et al., 2019a; Wang et al., 2019b). Other common species include the grasses *Phragmites australis* and *Calamagrostis epigejos*, the forbs *Artemisia scoparia* and *Artemisia anethifolia*, and the legumes *Lespedeza davurica* (Liu et al., 2015). There is a species-rich insect community including Orthoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, Lepidoptera, Mantodea, Neuroptera, and others (Zhu et al., 2015a; Zhong et al., 2017).

In May 2017, we selected three experimental sites to represent three degradation levels: non-degraded grassland (ND), moderately degraded grassland (MD), and severely degraded grassland (SD) based on relative cover of *L. chinensis*, annuals biomass, soil pH, and electrical conductivity (EC) (Wu et al., 2021). Each two sites were separated by about 1500 m. Non-degraded site is dominated by *L. chinensis* with higher relative cover (about 50%). Plant community in moderately degraded sites mainly consisted of *L. chinensis* (40% relative cover), *Setaria viridis*, *A. anethifolia*, and *Kochia sieversiana*. The vegetation in severely degraded sites is characterized by *Chloris virgata* and *L. chinensis* with lower relative cover (about 20%). The detailed information on properties of plant and soil of the three degraded levels was shown in Table S1. There were six 25 m × 25 m plots at each site (i.e. each degradation level), and the distance between neighboring plots was at least 20 m.

2.2. Vegetation measurements

In mid-August 2017, plant species richness and height were measured along four 25-m parallel transects at 5-m intervals within each plot. To avoid edge effects, these transects were 5-m away from the plot boundary. Four 0.5 m × 0.5 m quadrats were evenly placed along each transects. All plant species within a quadrat were identified; the height of five typically selected individuals of each plant species was measured to the nearest centimeter using a ruled rod. Plant height heterogeneity was estimated as the coefficient of variation (CV) of plant height in each quadrat (Zhu et al., 2012). Aboveground biomass in each quadrat was sampled by clipping standing plant materials of each plant species to 1 cm above the ground using shears, and then plant materials were oven-dried at 65 °C for 48 h to obtain dry weights. The biomass of annuals and perennials, and grass biomass were calculated separately, and the total aboveground biomass was calculated as the sum of annual and perennial biomass. The cumulative plant species richness and plant biomass per square meter transferred from accumulative plant biomass of all quadrats in each plot were calculated for further analysis. Plant height per plot was calculated the average of all measured individuals in each quadrat.

2.3. Insect sampling and identification

We used two sampling methods: sweep nets and pitfall traps (Evans et al., 1983; Barber et al., 2017), to estimate insect species richness and abundance. We followed the standard sweep net survey method (40-cm in diameter) to sample insects that dwell in plants under favorable conditions (sunny days with minimal cloud cover and calm or no wind)

from 09:00 to 15:00 h (Evans et al., 1983; Haddad et al., 2001). Insects were also sampled along four, 2-m wide and 25-m long parallel transects within each plot, and these transects were at least 3-m away from the plot boundary to minimize edge effects. Ten nets were evenly swept vigorously while walking steadily along each transects, and 40 sweeps in each plot were conducted together. Sampled insects of each sampling were preserved in bottles containing ethyl acetate to kill them. All plots were sampled in random order in each sampling date. We sampled ground insects using pitfall traps method (Barber et al., 2017). In each plot, we established a pitfall trap array consisting of nine pitfall traps (360 ml plastic jars), evenly distributed in three parallel transects that separated by 6 m. A fluid comprising 120 ml water, 50 ml 75% alcohol and 10 ml glycerin was used in the traps as a fixative and preservative. All traps were opened on the same day and remained for three days. The contents of the pitfall traps were preserved in centrifuge tubes containing 75% alcohol. Insects were collected monthly from July to September 2017, with sweep netting performed firstly, in order to avoid disturbance of the pitfall traps.

All insect adult individuals were identified to species (Yuan et al., 2006), and specimens that could not be identified to species were separated into recognizable taxonomic units (morphospecies). We collected 33,688 individuals totally, belonging to 9 orders: Orthoptera, Hemiptera, Coleoptera, Diptera, Hymenoptera, Lepidoptera, Neuroptera, Thysanoptera and Odonata. The cumulative insect species richness and accumulative insect abundance of the two sampling methods throughout sampling periods in each plot were calculated. Lepidoptera (0.17%), Neuroptera (0.18%), Thysanoptera (1.73%) and Odonata (0.59%) with lower ratios in abundance were omitted from further analysis.

2.4. Microclimate measurements

Microclimate was measured in conjunction with insects sampling monthly. Light intensity, air temperature and relative humidity were measured with evenly 10 points in each plot using air temperature and humidity meter (GM-1361) and portable light intensity tester (DT-1308) at two plant height levels: 5 cm and 30 cm above the ground. The average of each microclimate variable of all sampling points throughout the sampling periods in each plot was calculated for further analysis.

2.5. Statistical analysis

All response variables were tested for normality and homogeneity of variance, and we used different models based on the distribution pattern of each measured variable. Firstly, linear models (LM) with degradation levels as fixed factor were used to test the effects of grassland degradation on the richness of insects, Coleoptera, Diptera, and Hymenoptera, the abundance of insects, Hemiptera, Hymenoptera, Coleoptera, Diptera, and Orthoptera, aboveground biomass of whole plant community, annuals, grasses, plant height, variation in height of plants, and relative humidity (5 cm and 30 cm), light intensity (5 cm) that were assumed Gaussian distribution. We used generalized linear models (GLM) to assess the effects of grassland degradation on richness of Hemiptera and Orthoptera, and plant richness assuming Poisson distribution. These variables were compared using Tukey tests with the packages *multcomp*, and results were considered significant at $P \leq 0.05$. Aboveground biomass of perennials, light intensity (30 cm), and air temperature (5 cm and 30 cm) were analyzed with Kruskal-Wallis test, as the assumptions for Gaussian distribution and Poisson distribution were not met. Differences in these variables between degradation levels were compared with the function of *kruskal* from the package *agricolae*, and Bonferroni corrections were used to correct for multiple hypothesis testing. LM, GLM and Kruskal-Wallis test were achieved using the function of *lm*, *glm* and *kruskal.test* respectively from the package *stats*.

We performed a redundancy analysis (RDA) using the function *rda* in the *vegan* package aiming to elucidate the relationships between insect

community composition and environmental variables. We considered the treatment plots as observations, the vegetation parameters and microclimate variables as environmental variables, and the abundance of insect guilds as species variables. The multicollinearity between environmental variables was checked with variance inflation factors (VIF), and the variable with VIF greater than 10 was discarded. Then, to select the significant environmental variables in predicting the variations of insect community composition, the forward selection method was performed using the function *ordstep*. In addition, Adonis (999 permutations) was used to quantitatively test the compositional similarity of insect community between degradation levels. Post hoc pairwise adonis test were done using the function *pairwise.adonis* from package *pairwiseAdonis* (Martinez Arbizu, 2017) with Bonferroni correction. Variation partitioning was used to test the pure effects of annual biomass and light intensity (30 cm aboveground level) with the function of *varpart*. We used partial least squares regression (PLSR) to identify the relationships between environmental variables with insect richness and abundance (Carrascal et al., 2009). It is possible to determine whether which predictor strongly interact with response variables (Yan et al., 2013). We used the function *plsreg1* in the package *plsdepot* with 2 components chosen to implement PLSR. All analyses were performed with software R version 3.6.1.

The effect sizes of grassland degradation on individual variables (i.e. richness and abundance of insect guilds) were quantified (Liu et al., 2018). The following equation was used:

$$ES = (D - R) / R \times 100\%$$

Where *ES* is the effect size, in%, *D* is the value of the corresponding variable in the relevant degradation level (moderately or severely degraded level), and *R* is the value of each variable in the reference degradation level (non-degraded or moderately degraded level). When the effect size is positive, or zero, or negative, this indicates an increase, no change or a decrease, respectively, of the parameter compared to the reference degradation level. The variables which significantly differed between degradation levels were further analyzed for PLSR and effect sizes.

3. Results

3.1. Variables of plants and microclimates

Plant aboveground biomass, annual biomass, and grass biomass increased with grassland degradation, but perennial biomass decreased (Fig. S1A, B, C, D). Plant height and variation in plant height were not affected by grassland degradation (Fig. S1E, F). Plant richness was significantly higher in moderately degraded plots than that in severely degraded plots (Fig. S1G). Light intensity, air temperature, and relative humidity at 5 cm aboveground level did not differ across the three levels of grassland degradation (Fig. S2A, B, C). At 30 cm aboveground level, light intensity was significantly lower, but air temperature was significantly higher in severely degraded plots, and relative humidity did not change (Fig. S2D, E, F).

3.2. Insect richness

Insect richness was significantly higher in moderately degraded plots compared to non-degraded and severely degraded plots (Fig. 1A). The richness of Hemiptera was significantly higher in moderately degraded plots, compared to that in severely degraded plots (Fig. 1B). The richness of Hymenoptera, Coleoptera, and Diptera did not change across the three degradation levels (Fig. 1C, D, E). Orthoptera richness was significantly greater in severely degraded plots than that of non-degraded plots (Fig. 1F).

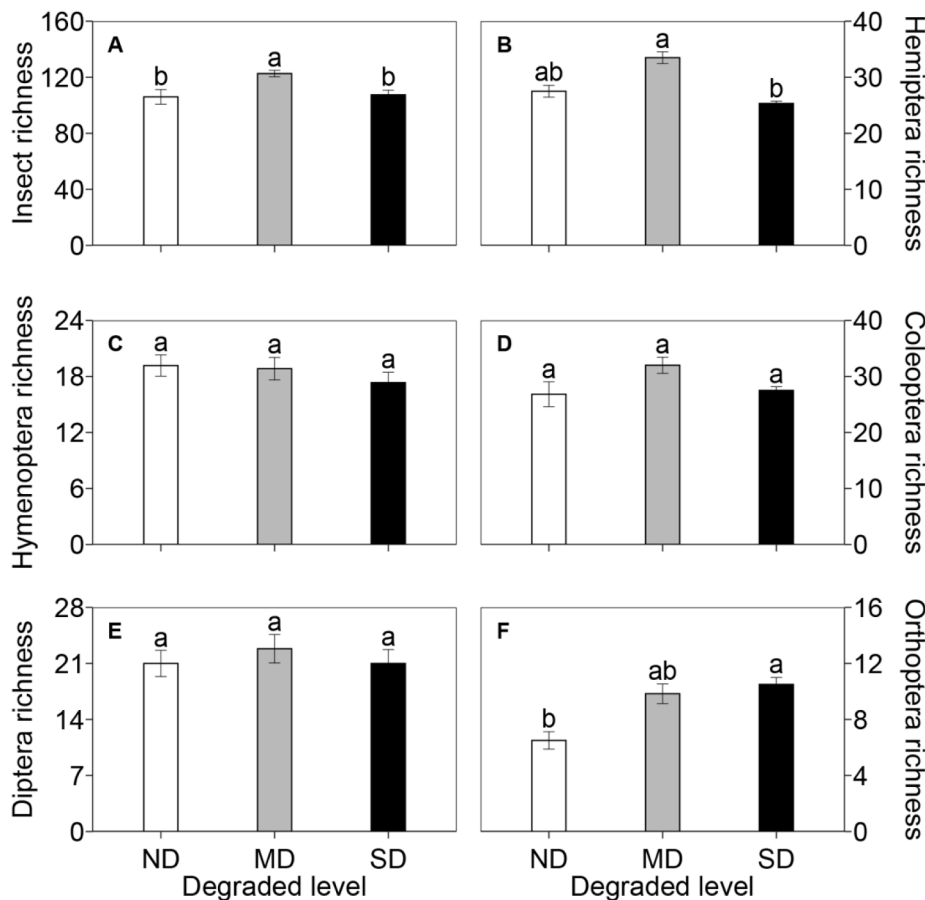


Fig. 1. The richness of all insects (A), Hemiptera (B), Hymenoptera (C), Coleoptera (D), Diptera (E), and Orthoptera (F) in non-degraded (ND), moderately degraded (MD), and severely degraded (SD) sites. Values are means \pm SE ($n = 6$). Significant differences between degradation levels are indicated by different lower case letters ($P \leq 0.05$).

3.3. Insect abundance

Insect abundance did not differ between the three levels of grassland degradation (Fig. 2A). However, grassland degradation significantly increased the abundance of Hemiptera and Orthoptera (Fig. 2B, F), with greater Hemiptera abundance in severely degraded plots and higher Orthoptera abundance in moderately and severely degraded plots. Hymenoptera abundance was significantly lower in moderately and severely degraded plots, and Coleoptera abundance was significantly lower in severely degraded plots (Fig. 2C, D). The abundance of Diptera did not differ along the degradation levels (Fig. 2E).

3.4. The relationship of insect community composition with environmental variables

For the RDA analysis, the environmental attributes were constrained to the first and second sorting axes, explaining 45.12% of the variations in insect community composition, and RDA 1 explained 32.95% of the total variation (Fig. 3). Annual biomass, and light intensity at 30 cm aboveground level were significant factors influencing insect community composition (Fig. 3). Adonis analysis indicated that insect community composition significantly differed among the plots ($F = 13.826$, $P = 0.001$). Significant differences in insect community composition were found between non-degraded and moderately degraded plots ($R^2 = 0.40$, $P = 0.027$), non-degraded and severely degraded plots ($R^2 = 0.65$, $P = 0.015$), moderately degraded and severely degraded plots ($R^2 = 0.58$, $P = 0.003$). The variation partitioning analysis showed that annual biomass explained 28.2% of the total variation in the insect community composition, whereas light intensity (30 cm aboveground

level) explained 11.4% of the variation (Fig. S3). The interaction among annual biomass and light intensity (30 cm aboveground level) explained 5.5% of the variation.

3.5. Contributions of plants and microclimates on insect richness and abundance

The changes in plant richness, aboveground biomass, and light intensity (30 cm aboveground level) appeared to dominate the first component of insect richness in the PLSR model (Table 1). The first component of the Hemiptera richness model was dominated by positive relation of plant richness and light intensity (30 cm aboveground level) and by negative relation of grasses biomass (Table 1). The changes in grasses biomass, aboveground biomass, and air temperature (30 cm aboveground level) dominated on the positive relationship of the first component of the Orthoptera richness PLSR model (Table 1).

The changes in grasses biomass and aboveground biomass dominated the first component of the Hemiptera abundance PLSR model, whereas light intensity (30 cm aboveground level) changes dominated on the negative side of the first component (Table 2). Air temperature (30 cm aboveground level) showed the highest negative effect on Hymenoptera abundance, followed by aboveground biomass and grasses biomass (Table 2). Light intensity (30 cm aboveground level) and plant richness showed strong positive influence on Coleoptera abundance PLSR model, whereas grass biomass and aboveground biomass showed strong negative effect (Table 2). The first component of Orthoptera abundance PLSR model was dominated by grasses biomass, aboveground biomass, and air temperature (30 cm aboveground level) (Table 2).

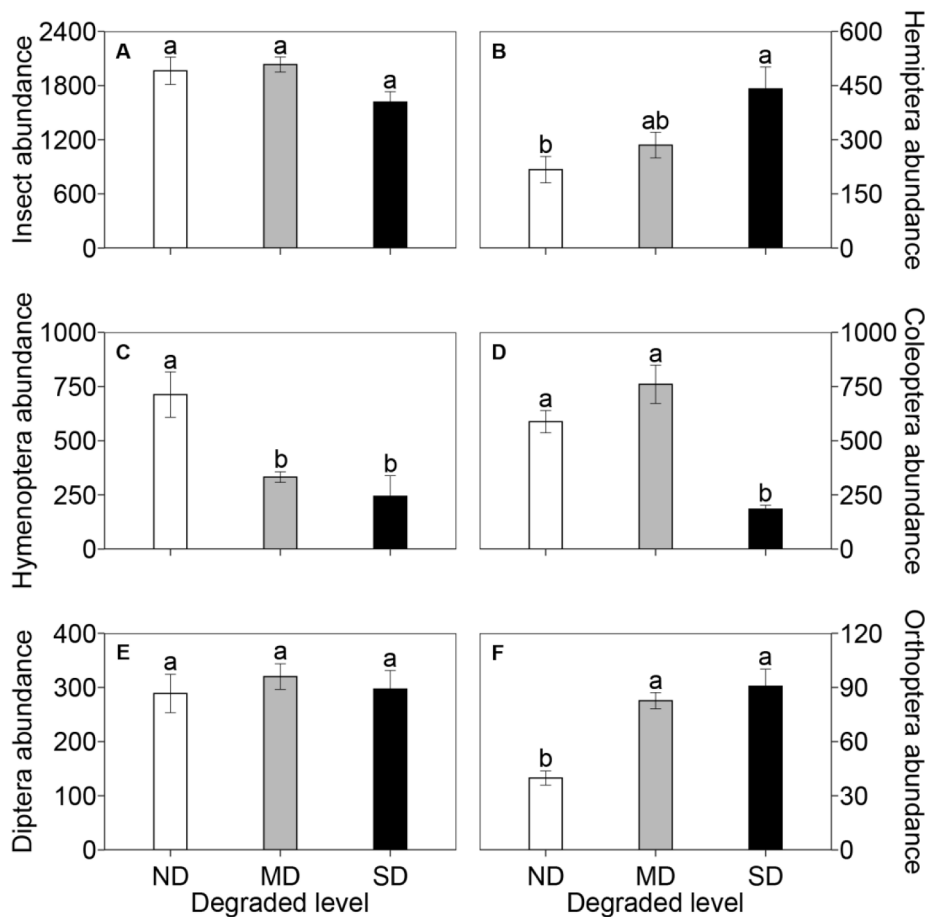


Fig. 2. The abundance of all insects (A), Hemiptera (B), Hymenoptera (C), Coleoptera (D), Diptera (E), and Orthoptera (F) in non-degraded (ND), moderately degraded (MD), and severely degraded (SD) sites. Values are means \pm SE (n = 6). Significant differences between degradation levels are indicated by different lower case letters ($P \leq 0.05$).

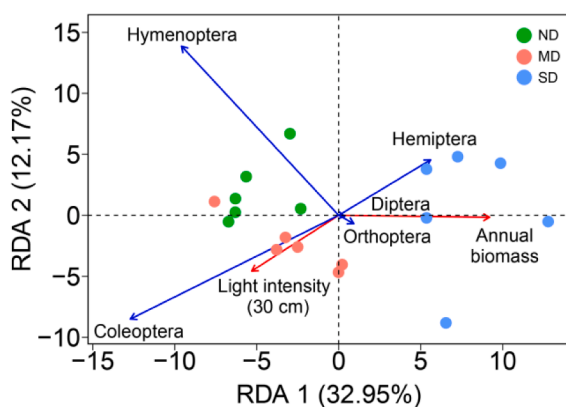


Fig. 3. Insect taxonomic composition (orders) in relation to grassland degradation and environmental variables based on redundancy analysis (RDA). Only significant environmental variables are shown. Green symbols represent for non-degraded (ND), red symbols represent for moderately degraded (MD), and blue symbols represent for severely degraded (SD) sites.

3.6. Effect size of grassland degradation on insect richness and abundance

Relative to non-degradation, moderate degradation had positive effects on richness of total insects, Hemiptera, and Orthoptera, with greater effect size for Orthoptera richness (Fig. 4A). Richness of total insects and Hemiptera showed negative effects, and Orthoptera richness showed positive effects in severely degraded site compared to

moderately degraded site (Fig. 4A). For abundance, there were positive effects for Hemiptera, Coleoptera, and Orthoptera, except for Hymenoptera in moderately degraded site (Fig. 4B). Abundance of Hemiptera and Orthoptera showed positive effects, and Coleoptera and Hymenoptera abundance showed negative effects in severely degraded site (Fig. 4B).

4. Discussion

Biotic organisms show a series of different sensitivities to grassland restoration and degradation (Dong et al., 2020). Our study showed that higher total insect richness is detected in moderately degraded grassland, and no difference in insect abundance is found between the experimental degraded plots. And furthermore, insect assemblages responded inconsistently to grassland degradation. Our results provide new and detailed evidence regarding the remarkable sensitivity of insect community to grassland degradation.

4.1. Changes of insect richness

In our study, richness at both total insects and order levels was sensitive to grassland degradation. Total insect richness and Hemiptera richness showed a unimodal pattern along degradation levels (Fig. 1A, B), which is consistent with the results in alpine meadow of the Qinghai-Tibetan Plateau (Wu et al., 2015). Many herbivores exhibit feeding specialization to some degree (Forister et al., 2015). For Hemiptera, especially Auchenorrhyncha, have different life strategies ranging from polyphagous pioneer species to strictly monophagous specialists (Nickel

Table 1
Partial least squares regression (PLSR) weights for the model of insect richness.

Predictors	Insect		Hemiptera		Orthoptera	
	W*[1]	W*[2]	W*[1]	W*[2]	W*[1]	W*[2]
Aboveground biomass	0.473 ^a	0.522	0.064	0.723	0.563	-0.322
Grasses biomass	-0.024	0.493	-0.430	0.269	0.646	0.317
Plant richness	0.749	0.036	0.709	0.566	0.089	0.445
Light intensity(30 cm aboveground level)	0.464	-0.116	0.544	-0.292	-0.095	0.662
Air temperature(30 cm aboveground level)	0.022	-0.712	0.115	0.193	0.499	0.460
R ²	0.383	0.017	0.502	0.022	0.498	0.052
P	0.006	0.6	0.001	0.56	0.001	0.36

^a The bold-faced values are larger than 0.3 and indicate that the PLSR components are mainly loaded on the corresponding variables.

Table 2
Partial least squares regression (PLSR) weights for the model of insect abundance.

Predictors	Hemiptera		Hymenoptera		Coleoptera		Orthoptera	
	W*[1]	W*[2]	W*[1]	W*[2]	W*[1]	W*[2]	W*[1]	W*[2]
Aboveground biomass	0.506 ^a	-0.202	-0.578	0.063	-0.338	0.283	0.577	-0.217
Grasses biomass	0.628	-0.018	-0.496	0.120	-0.513	0.556	0.647	0.285
Richness	-0.106	0.828	0.166	0.280	0.496	0.655	-0.001	0.292
Light intensity(30 cm aboveground level)	-0.542	-0.502	-0.071	-0.886	0.569	0.186	-0.118	0.767
Air temperature(30 cm aboveground level)	0.212	0.183	-0.622	-0.453	-0.231	-0.409	0.484	0.492
R ²	0.622	0.030	0.685	0.090	0.645	0.028	0.481	0.039
P	<0.001	0.49	<0.001	0.23	<0.001	0.51	0.001	0.43

^a The bold-faced values are larger than 0.3 and indicate that the PLSR components are mainly loaded on the corresponding variables.

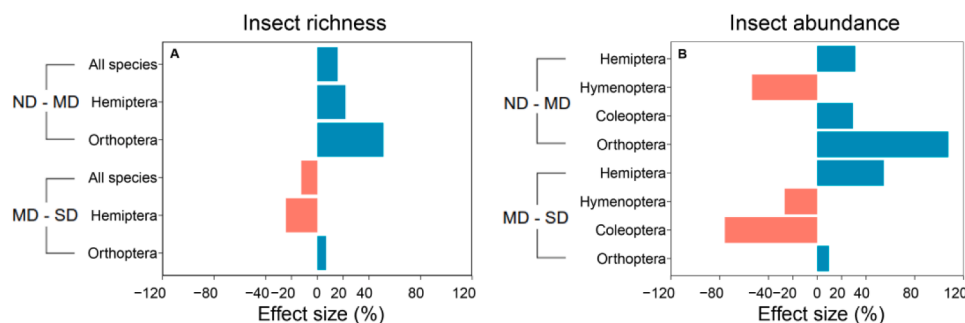


Fig. 4. The effect sizes on insect species richness (A) and insect abundance (B) for moderately degraded site (MD) compared to non-degraded site (ND) and severely degraded site (SD) compared to moderately degraded sites (MD). Blue bars represent for positive effects; and red bars represent for negative effects.

and Hildebrandt, 2003), and therefore higher plant diversity can support higher Hemiptera diversity because of distinct food niche (Biedermann et al., 2005; Rowe and Holland, 2013). Consistent with previous studies, our results indicated that plant species richness has been considered as an important factor in influencing total insects and Hemiptera richness (Table 1). In this study, a dominant grass *L. chinensis* suppresses the growth of forbs and other grass species. The reduction in the dominance of *L. chinensis* in moderately degraded site could consequently increase plant species richness (Fig. S1G). Therefore, higher plant species richness provides a greater diversity of Hemiptera due to abundant food resources.

Unlike total insects and Hemiptera, Orthoptera richness increased along the degradation levels (Fig. 1F). Higher productivity provides sufficient food for consumers, thereby increasing the number of consumer species (Wright, 1983; Srivastava and Lawton, 1998). Results from our study indicated that higher aboveground biomass of grasses support greater Orthoptera richness (Fig. S1D, Table 1). Meanwhile, plant spatial heterogeneity is also an important factor in determining Orthoptera richness species in grasslands (Kruess and Tschamtkke, 2002; Joern, 2005). For example, grasshoppers require habitats that provide a vegetation mosaic of bare ground for oviposition and vegetation for food (Dempster, 1963). In severely degraded site, *L. chinensis* patches were inlaid into *C. virgata* community, which provides more diverse habitats, thus further enhancing Orthoptera richness. Based on these results, it is

shown that both greater Hemiptera and Orthoptera richness contributed to higher insect richness in moderately degraded site, and the two insect guilds should not be neglected when evaluating the responses of insect community to grassland degradation.

4.2. Changes of insect abundance

Compared to insect richness, total insect abundance was less sensitive to grassland degradation, which is inconsistent with other cases that habitat degradation had a negative impact on the insect herbivores abundance (Rossetti et al., 2017). This is likely due to the fact that the increased Hemiptera and Orthoptera abundance offset the decreased Hymenoptera and Coleoptera abundance in our study (Fig. 2). Insect guilds exhibited different responses to each degradation levels (Figs. 2, 4B), which is similar to the case that the abundance of each insect order respond differently to grazing by large herbivores (Zhu et al., 2015a; Luong et al., 2019). Most Hemiptera and Orthoptera are herbivores, and their abundance often increased with higher resource quantity (Root, 1973; Rand and Louda, 2006). In this study, grassland degradation significantly improved aboveground biomass, especially grass biomass (Fig. S1A, D). Greater grass biomass dominated by *C. virgata* may support more hemipteran and orthopteran in severely degraded grasslands (Table 2, Fig. S1D).

Hymenoptera and Coleoptera abundance strongly responded to

moderately and severely degraded grassland, respectively (Fig. 2C, D). Many studies have confirmed that the abundance of Hymenoptera and Coleoptera increases with grassland restoration (Woodcock et al., 2010; Lettow et al., 2018). Similarly, our results showed that Hymenoptera and Coleoptera abundance decreased with degradation (Fig. 2C, D). PLSR analysis indicated that altered microclimates (i.e. air temperature and light intensity at 30 cm aboveground level) might be considered as the main explanatory variable (Table 2). For hymenopteran bees and wasps, extreme higher air temperature could increase larval mortality (Pitts-Singer and James, 2008). A slight increase in air temperature (30 cm aboveground level) likely led to a decline in their abundance in moderately and severely degraded grassland. The decreased abundance of Coleoptera could be also mainly due to lower light intensity (30 cm aboveground level) in severely degraded grassland (Table 2, Fig. S2D). Lower light intensity is detrimental to the egg production of Coleoptera (Wang et al., 2014), therefore possibly suppressing Coleoptera abundance.

4.3. Implication of the responses of insect guilds to grassland degradation

Although there are some studies focusing on changes in richness and abundance of insects in responses to grassland restoration and degradation (Barber et al., 2017; Lettow et al., 2018), few study highlights direction and intensity of responses (but see Evans et al., 2019). Results from effect size of grassland degradation on insect assemblage suggest that different responses of insect guilds should be considered when evaluating and monitoring grassland degradation.

In fact, some insect guilds, such as dragonfly (Rocha-Ortega et al., 2019) and beetles (Schirmel et al., 2015), are always being used as ecological indicators to examine degradation and restoration of habitat. In grassland ecosystems, Orthoptera are often used as an indicator (Löffler and Fartmann, 2017), because they are dominant guild and main primary consumers, which are sensitive to changed habitats (Alignan et al., 2018). In our study, Orthoptera is an alternative biological indicator only when grasslands degraded moderately (Fig. 4B). However, when grassland degraded from moderately to severely, Coleoptera was a good ecological indicator due to its greater effect size (Fig. 4B). In fact, Coleoptera are often used to monitor ecosystem restoration (Babin-Fenske and Anand, 2010; Paoletti et al., 2009). In contrast to previous studies that use a single insect guild to assess the whole process of grassland restoration or rehabilitation (Alignan et al., 2018; Evans et al., 2019), our results suggest that it is necessary to select different insect guilds as bioindicator when assessing levels of grassland degradation.

Besides insect guilds, selecting appropriate index is also crucial for effectively evaluating habitat changes. Most studies to date have separately or simultaneously used species richness and abundance index of insects (Enkhtur et al., 2017; Löffler and Fartmann, 2017; Evans et al., 2018). However, there is always a mismatch among them. For example, abundance mostly significantly responds to grassland restoration, but richness does not change (Tonietto et al., 2017). And furthermore, when considering richness as index of an indicator, identifying the insect species is necessary, but this is also difficult because of limited taxonomic knowledge (Evans et al., 2019). Thus, some only use abundance as index, particularly for managers and researchers due to convenient sampling and easily counting (Löffler and Fartmann, 2017; Evans et al., 2019). Our results also suggest that abundance is a better index of qualified indicator for serving the assessment of grassland degradation due to its high sensitivity (Fig. 4B).

Our results clearly showed that species richness and abundance of each insect guild had different responses to each level of grassland degradation. In our studied system, Orthoptera abundance could be used as an indicator of moderately degraded grassland, and Coleoptera abundance could be used as an indicator of severely degraded grassland. Previous studies mostly considered richness or abundance of single insect guild to evaluate restoration or degradation processes of grasslands (Schirmel et al., 2015; Evans et al., 2019). Our results suggest that

focusing on abundance of different guilds should be potentially considered in each stage in experimental area, and it may be a straightforward and cost-effective method. Thus, the study introduces a new viewpoint on the use of ecological indicator for non-specialists in future grassland management and monitoring. However, the complexity of climate as well as grassland types, and their interactions, will influence the responses of insect guilds to grassland degradation. Therefore, additional experiments are needed in the future to quantify the responses of insect guilds to degradation in different grassland types.

Author Contributions

H.R., H.Z., D.W., and L.W. conceived and designed the experiment. H.R., X.W., S.W. and J.Y. conducted the experiment. H.R. and H.Z. analyzed data. H.R., H.Z., Q.G. and D.W. wrote the manuscript. All authors read and approved the manuscript.

CRediT authorship contribution statement

Hang Ruan: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft. **Xuefeng Wu:** Investigation, Writing – review & editing. **Shengnan Wang:** Investigation, Writing – review & editing. **Jingjing Yang:** Investigation, Writing – review & editing. **Hui Zhu:** Conceptualization, Methodology, Funding acquisition, Project administration, Supervision, Visualization, Writing – review & editing. **Qinfeng Guo:** Writing – review & editing. **Ling Wang:** Resources, Writing – review & editing. **Deli Wang:** Conceptualization, Methodology, Funding acquisition, Project administration, Supervision, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the following individuals for help with the field and lab work: our colleagues Yinong Li, Xuan Zhao, Tongtong Xu, Yueqing Song, Man Xu and Zhiqiang Li. This project was supported by the National Key Research and Development Program of China (No. 2016YFC0500602), and National Natural Science Foundation of China (No. 31770520, 3201101150) and the Program for Introducing Talents to Universities (B16011).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.108369>.

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