Original Articles

Linkages of plant-soil interface habitat and grasshopper occurrence of typical grassland ecosystem

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ABSTRACT

How to understand the interactive influence of environmental changes on the total grasshopper density (TGD) becomes an urgent issue in grassland ecosystems. Large-scale studies are ideal for assessing the relative contributions of multiple factors on grasshopper community dynamics. Using data from 634 sites, linkages of community habitats (plant functional groups (PFGs), vegetative litter (VT) and soil types (ST)) and grasshopper occurrence were studied in a farming-pastoral zone across Inner Mongolia. Each of the three primary grassland ecosystem drivers influenced total grasshopper density. The absence of VT ($VT_{absence}$) can decrease the total grasshopper density by degrading the habitat conditions. Similarly, grasshopper communities prefer to feed on legumes and forbs rather than grasses due to the plant-trait variance in PFGs. Moreover, total grasshopper density was driven by complex interactions, caused by PFGs, soil types and vegetation litter. Our results improve the understanding of where grasshoppers might occur and provide helpful strategies to prevent the outbreak of grasshoppers.

1. Introduction

Grasshoppers are the dominant invertebrates in grassland ecosystems and are important in maintaining normal ecosystem function (Belovsky and Slade, 2000). However, grasshopper outbreaks are frequently reported worldwide and can have tremendous influences on the ecosystem services provided by grasslands (Lomer et al., 2001). Moreover, grasshoppers have been considered as one of the most devastating pests in grassland ecosystems, with grasshopper outbreaks seriously affecting livestock grazing and the lives of local people. Due to the considerable economic impacts caused by grasshopper outbreaks, grasshopper control has long been a central issue in the study of plant-herbivore interactions (Joern and Behmer, 1998). Herbivores, which affect plants by altering competitive interactions between species, have been widely studied in recent years (Schuldt et al., 2012; Borer et al., 2014). Grasslands simultaneously influence the habitat selection of grasshoppers, which depend on a complex combination of different—and often interrelated—environmental factors. For instance, plants possess a wealth of structural and chemical mechanisms to

defend themselves against a wide range of grasshopper attacks (Hanley et al., 2007), and plant-produced metabolites have defensive functions and are rich sources of novel bio-active compounds (Mithofer and Boland, 2012). Nevertheless, insect herbivores still depend on plants for their survivals either by feeding on dominant plants or consuming rarer species. Previous studies have described the relationship between the composition of plant communities and their herbivorous counterparts (Kursar et al., 2009). At the plant level, grasshopper-digestibility (the digestibility of plants by grasshoppers) is related to many plant functional traits. However, whether those relationships can be scaled up to the community level in large-scale grasslands, and how such relationships are modulated by environmental conditions, remain unknown.

Functional traits provide better generality in understanding and predicting the formation and structure of plant communities (McGill et al., 2006); hence, functional traits enable the refinement of predicting community composition along environment gradients (Douma et al., 2012). Community-level patterns in functional traits relate to community assembly and ecosystem functioning (Dubuis et al., 2013). Recently, plant functional groups (PFGs) have been used and largely
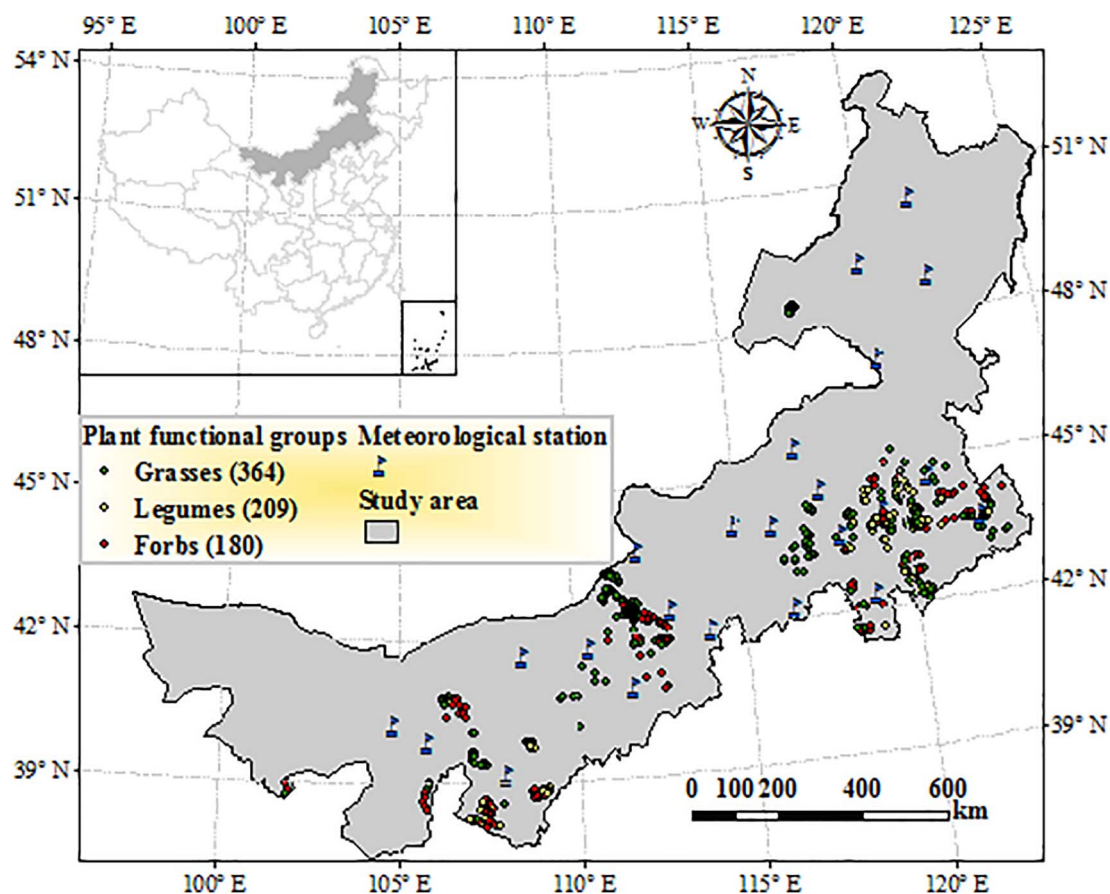
Fig. 1. Location of the study area and field plots in Inner Mongolia, China.

improved, providing a useful means of revealing the general rules that include the relationships between vegetation and environmental conditions (Diaz et al., 2016). PFG-based analyses have identified large-scale patterns in relation to climate and anthropogenic drivers (Engemann et al., 2016), and they have revealed broad consistencies in the effects of competition on vegetation communities (Kunstler et al., 2016). However, categorizing species into PFGs might also conceal essential inter- and intra-specific variability, resulting in no identifiable patterns of PFG distribution along environmental gradients (Dormann and Woodin, 2002; Albert et al., 2010). Despite successful global analyses, the extent to how PFGs predict the responses to a changing environment is still poorly understood. Moreover, the effects of PFGs on grasshopper density are rarely researched in large-scale grassland zones.

Habitat selection by grasshoppers often depends on a complex combination of different and interrelated environmental factors. The main determinants are vegetation structure and microclimate (Strauss and Biedermann, 2006). On the one hand, plant preferences of grasshoppers are well known (Bernays et al., 1994; Raubenheimer and Simpson, 2003). In our study, many of the principle plant species comprise "typical steppe" vegetation and belong to the poaceae family (Gramineae). Though different species of grasshoppers have different daily food consumption rates and diets composed of various plant species, legumes and forbs are preferred by dominant species of grasshoppers. The density, abundance and distribution of grasshoppers are closely associated with vegetation characteristics, including plant species richness or diversity, plant community composition and structure, grass greenness, and plant nutrient contents (Bazelet and Samways, 2011; Abbas et al., 2013). On the other hand, microclimate accompanied with weather fluctuations have obvious effects on overwintering and incubation of grasshopper eggs, as well as on the

geographical ranges and degree of hazard posed by grasshopper infestations (Bassler et al., 2013). Give that grasshoppers are survived by grasslands which are sensitive to climate change, it is necessary to understand how microclimate and PFGs affect grasshopper gestation.

In addition, soil properties (e.g., soil type, texture, temperature, moisture, pH, salinity, inorganic matter content, and rockiness) affect the availability of suitable ovipositor sites, incubation and mortality of eggs, hatching and development of nymphs, number and reproduction of adults, as well as plant diversity, biomass, and cover (Ni and Li, 2000; Crous et al., 2014). Furthermore, grasshopper are closely associated with topographic elements, including landforms, elevation, aspect, slope position, and cragginess (Gong et al., 1999). Human activities (i.e., heavy livestock grazing, forestation, intensive reclamation, fertilization, and fire disturbance) may also cause grasshopper outbreak as a result of changing habitat conditions (Cease et al., 2012). Though these studies have improved our understanding of plant-grasshopper relationship, little is known about how soil types respond to grasshopper survival. Furthermore, the effects of herbivores on N cycling in grassland ecosystems are relatively well studied. However, our understanding of the influence of grasshoppers on the availability and cycling of P, which is also a widespread limiting element in terrestrial ecosystems (Elser et al., 2007), is extremely limited.

Grasshoppers are among the most destructive pests in the largest farming-pastoral zone in China (He et al., 2009), which represents a typical Eurasian semiarid steppe ecosystem. Grasshopper plagues seriously affect livestock grazing and the lives of local people. They also play essential roles in grassland desertification and degradation, as well as the services and functions provided by grassland ecosystems (Branson and Haferkamp, 2014). Therefore, it is both necessary and important to precisely predict grasshopper occurrences and to develop effective preventive and control measures. A large-scale field study was

performed with its sites composed of varying PFGs and microclimate (soil types and litter). We simultaneously evaluated which PFGs were preferred by grasshoppers, and which habitat conditions were more suitable for grasshopper survival. Moreover, as studies on the combined effects of micro-environmental factors on grasshopper density were not known to us, we designed a sampling program study the interaction of soil types and litter of three different PFGs (grasses, forbs and legumes) on grasshopper density, and determine the contributions of PFGs and environmental variables to the variation in grasshopper density.

2. Materials and methods

2.1. Study site

The study was conducted across a typical ecologically vulnerable region in the northern farming-pastoral zone of Inner Mongolia (37°24′–53°23′N, 97°12′–126°04′E), China, with elevations ranging between 152 and 2303 m above sea level (Fig. 1). The study site is characterized as typical temperate continental monsoon climate, with annual average temperature ranging from 0 °C to 8 °C and precipitation ranging from 50 mm to 450 mm. The topography in this region consists of desert, gently rolling plains, tablelands, and hills, while the dominant land-cover type is grassland, which includes meadow steppe, typical steppe and desert steppe on a gradient from east to west. The soil types are multiple, comprising brown pedocals, Aeolian soils, castanozems, meadow soils, grey desert soils and brown earths. Furthermore, the study area belongs to an ecotone of agriculture and animal husbandry and is prone to grasshopper plague. In this study, three plant functional types, including grasses, forbs, and legumes, were selected as the principal objects of our research.

To sample grasshopper data along the farming-pastoral zone, a total of 634 sites with dimensions of 30 × 30 m were selected using a random sampling design, and the quantity of grasshoppers was inventoried between July 2nd and July 24th, 2006. All grasshopper individuals that were heard or seen in plots were noted. The natural count method represents an efficient way to achieve quantitative data on grasshopper density, as the natural count method is less influenced by vegetation type than sweep netting (Hochkirch and Adorf, 2007). However, the method strongly depends on the insects' activity, which is affected by weather conditions. All counts were, therefore, performed during sunny and windless weather conditions and between 10 a.m. and 5 p.m. We inventoried a total of 20 grasshopper species, including seven subfamilies. To understand the effect of ecological drivers on grasshopper community, the overall total density of each site was then estimated for a 1 × 1 m area.

Meanwhile, vegetation types were sampled by three 1 × 1 m² quadrates in each site. All plots were selected among open, non-woody areas in order to limit the potential spatial autocorrelation. All plant species present in the plots were inventoried, and their relative abundance estimated visually using the simplified cover scheme: dominant, frequent, occasional, and rare. According to the dominant vegetation, sampling points were clearly identified and classified into three PFGs (grasses, legumes and forbs), which was used in all further analyses. Similarly, presence of vegetation litter (VT$_{presence}$) and soil types in PFGs were recorded in each plot for further analysis.

2.2. Environmental data

To evaluate how environmental factors influence PFGs, mainly by grasshopper feeding, climate data (average daily rainfall, average annual evaporation, the annual accumulated temperature above 10 °C) were available from the meteorological station in Inner Mongolia and provided by the China Meteorological Data Service Center (Table 1, Fig. 1). These meteorological stations are scattered throughout all of Inner Mongolia, and they cover a range of different geographic features; additionally, they have provided a dataset of daily climate data since

Table 1

The characteristics of meteorological data in Inner Mongolia.

Station	Elevation (m)	MAT (°C)	MAP (mm)	MAE (mm)	MAW (m/s)	SD (hr)	MAT10 (°C)
Tulihe	732.60	−4.37	189.26	2451.61	2.18	7.12	1578.50
Halar	610.20	−0.37	260.49	1904.86	2.27	6.51	2466.70
Bugt	739.70	−0.46	350.58	2173.77	3.06	7.66	1965.40
Arxan	1027.40	−1.96	565.45	2209.32	11.11	7.94	1760.60
Dong Ujimqin Banner	838.70	2.64	528.96	1905.28	2.58	8.10	2760.90
Bayan Road	1323.90	8.39	161.59	1360.17	3.77	8.84	3694.30
Erenhot	964.70	5.58	385.56	1906.41	3.40	8.48	3226.90
Abag Banner	1126.10	2.80	412.91	1905.54	3.22	7.86	2674.10
Zhurihe	1150.80	6.41	430.50	1906.48	4.81	8.33	3233.60
Urad Middle Banner	1288.00	6.68	269.20	1636.80	2.76	17.28	3222.40
Daerhan Unite Banner	1376.60	5.52	287.45	1905.67	2.79	8.14	2985.70
Huade	1482.70	4.08	385.81	1905.11	3.11	7.27	2586.70
Huhehot	1063.00	17.63	296.44	1905.16	10.85	7.31	6870.70
Jartai	1031.80	10.36	233.18	1359.67	3.03	8.96	4191.00
Otog Banner	1380.30	8.53	188.84	1905.41	2.38	8.14	3474.30
Xi Ujimqin Banner	1000.60	2.20	421.72	1905.60	4.27	7.98	2427.80
Jarud Banner	265.00	7.41	224.73	1905.37	2.20	7.47	3470.70
Bairin Left Banner	484.40	6.79	287.26	1905.45	2.32	8.56	3259.30
Xilin Hot	989.50	3.50	251.40	1905.37	3.57	7.99	2852.40
Linxi	799.00	5.49	188.90	1626.92	2.53	7.95	2925.00
Tongliao	178.50	7.42	368.60	1662.86	2.97	8.02	3461.90
Duolun	1245.40	3.52	574.49	1904.76	2.91	7.76	2433.40
Chifeng	568.00	8.12	162.08	1626.85	2.14	8.04	3486.30

MAT, mean annual temperature; MAP, mean annual precipitation; MAE, mean annual evaporation; MAT10, the mean annual accumulated temperature above 10 °C; MAV, mean annual wind; SD, sunshine duration.

2006. The region's main climate and ecological variables such as mean annual temperature (MAT), mean annual accumulated temperature above 10 °C (MAT10), mean annual evaporation (MAE), and mean annual precipitation (MAP) were then calculated. In addition, the topographical data were acquired from the National Earth System Science Data Staring Infrastructure, using GIS to extract the geomorphic information and altitude.

2.3. Data analysis

The vegetation presence-absence data from 2006 were analysed by a constrained linear ordination technique, i.e., redundancy analysis (RDA), using the community ecology package vegan for Cor R (Oksanen et al., 2007). Species that occurred infrequently (< ten times) were removed from the dataset and considered rare species, as they may have had an unduly large influence on the analysis. Prior to analysis, vegetation data were "*pa*"—presence- or absence-transformed—and environmental variables were standardized to obtain approximately normal distributions and homogenous variances. The statistical validity of the ordination was tested using a Monte Carlo permutation test (null model: 9999 unrestricted permutations). This test was carried out for each environmental variable and all canonical axes (i.e., the complete model). Moreover, we tested for correlations between environmental factors (i.e., soil types and vegetative litter) using the RDA and the function '*envfit*' in the vegan package. This procedure also generates a measure and significance values that indicate the probability that random permutations of the environmental variables would yield a higher degree of fit than the true environmental variables (Oksanen et al., 2007).

Both ST and VT can influence PFGs, and the effects of the PFGs on the changes in grasshopper density were analysed by non-repeated-measures analysis of variance (ANOVA) followed by Tukey's HSD post hoc test using R. Because the experimental design was fractioned, there
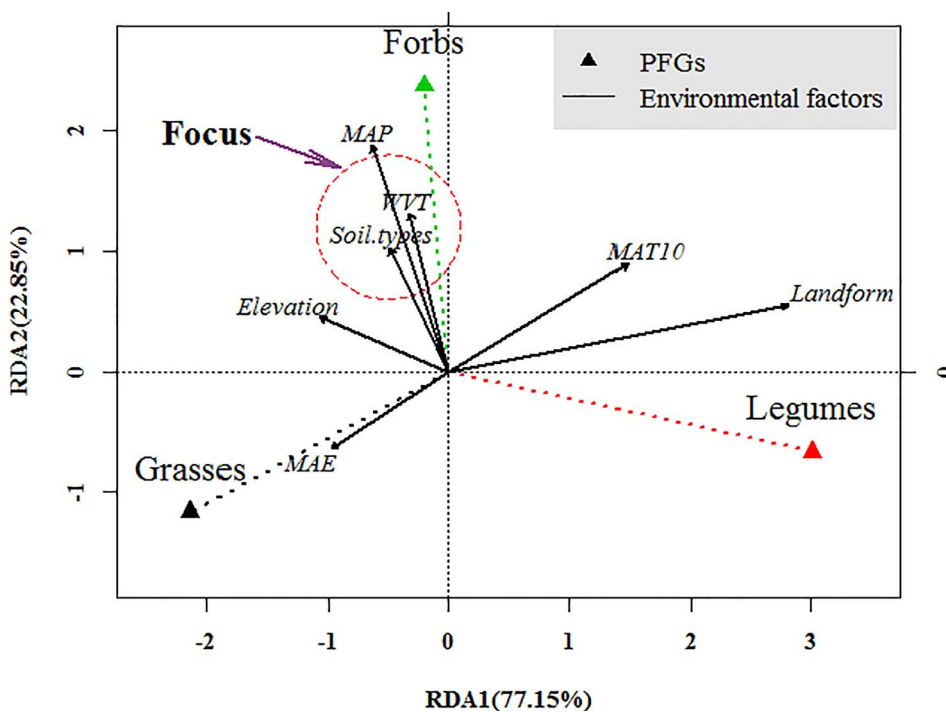
Fig. 2. Redundancy analysis (*RDA*) of the correlations between environment variables and plant functional groups. Blue full arrow and blue fonts are environmental variables and different coloured dotted lines and red fonts are plant functional groups. Environmental variables are abbreviated as follows: WVT, whether contain vegetative litter; MAP, mean annual precipitation; MAT10, the mean annual accumulated temperature above 10 °C; MAE, mean annual evaporation.

were two levels of analysis. The generic function box plots were computed in advance to eliminate outliers in terms of grasshopper density. We used one-way analysis of variance (ANOVA) to test for differences in grasshopper density among plant functional types and between different soil types. When a post hoc test was necessary, we used the function '*glht*' from the *multcomp* package (Hothorn et al., 2008). Two-way analysis of variance was conducted to test the interaction effect on grasshopper density.

3. Results

3.1. Plant functional types and environmental variables

Based on the presence or absence of plant communities, RDA was used to determine the distribution of the PFGs with the environmental variables. According to the analytical results, the first and the second components explained 99.99% of the total variances (first axis: 77.15, second axis: 22.85; Fig. 2). The analysis was significant when tested using a Monte Carlo permutation test ($P < .01$). Based on the examination of the function '*envifit*', all the environmental variables were significantly correlated using the RDA (Table 2). The spatial distribution of PFGs was mainly caused by the interaction of environmental variables, including landform characteristics (Elevation and Landform;

Table 2
Squared correlation coefficients (R^2) and significance (Pr values based on 999 permutations) of environmental variables and plant functional groups, as revealed by redundancy analysis (RDA).

Parameter	RDA1	RDA2	R2	Pr(> r)
MAP	−0.647749	0.761854	0.0306	0.001[***]
MAE	−0.967407	−0.253226	0.0154	0.003[**]
MAT10	0.971678	0.236307	0.0345	0.001[***]
Elevation	−0.985844	0.167663	0.0164	0.004[**]
Landform	0.996886	0.078851	0.1056	0.001[***]
WVT	−0.521422	0.853299	0.0137	0.006[**]
Soil types	−0.766695	0.642012	0.0107	0.018[*]

WVT, whether contain vegetative litter; MAP, mean annual precipitation; MAT10, the mean annual accumulated temperature above 10 °C; MAE, mean annual evaporation. "*", $P < .05$, "**", $P < .01$, "***", $P < .001$.

Fig. 2) and climate factors (MAP, MAE and MAT10; Fig. 2).

Our research was concentrated on the effect of the tree factors on the grasshopper density, including PFGs, soil types, and vegetation litter. Forbs, on the positive side of axis 2, mainly comprising *Artemisia*, were significantly and positively correlated soil types. Legumes, on the positive side of axis 1, principally comprising two genera (i.e., *Caragana* and *Lespedeza*), were more negatively correlated with WVT and soil types. Grasses, on the negative side of axis 2, mainly comprising two genera (i.e., *Stipa* and *Leymus*), were not significantly negatively correlated with vegetative litter or soil types.

3.2. Vegetation litter increases grasshopper density between PFGs

A total of 2,149 counts of 20 grasshopper species were sampled, which represented six subfamilies (Pamphagidae, Pyrgomoppppphidae, Catantopidae, Oedipodidae, Gomphocerinae, and Acridinae) and 16 genera (Appendix A). The PFGs had significant effects on the TGD

Table 3
(a) Result of one-way ANOVAs with post hoc Tukey's HSD among three plant functional groups. (b) Result of one-way ANOVAs among different soil types.

(a) PFGs

	Df	Sum Sq	Mean Sq	F value	Pr(> F)
PFGs	2	1851	925.7	10.11	4.73e−05[***]
Residuals	653	59,771	91.5		
Total	655	61,622			
Forbs × Grasses					0.0021482[**]
Legumes × Grasses					0.0002463[***]
Legumes × Forbs					0.8620885

(b) Soil types

	Df	Sum Sq	Mean Sq	F value	Pr(> F)
ST	5	17,041	3408	17.23	5.06e−16[***]
Residuals	648	128,216	198		
Total	653	145,257			

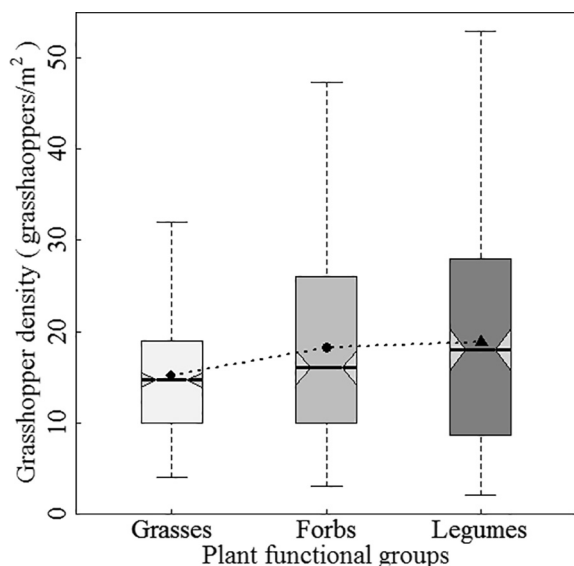PFGs, plant functional groups; ST, soil types. *$P < .05$, **$P < .01$, ***$P < .001$.

Fig. 3. Box plot analysis of grasshopper density in the three plant functional groups. The black rhombic plots are representative of the average grasshopper density for plant functional groups.

Table 4
(a) Result of two-way ANOVAs with post hoc Tukey's HSD with the average grasshopper density as the response variable and 'whether contain vegetative litter' and 'plant functional groups' as the explanatory variables. (b) Result of two-way ANOVAs with the average grasshopper density as the response variable and 'soil types' and 'plant functional groups' as the explanatory variables.

(a) PFGs × VT

	Df	Sum Sq	Mean Sq	F value	Pr(> F)
PFGs	2	1198	599.0	7.040	0.000944 [***]
VT	1	2662	2662.1	31.289	$3.28e-08$ [***]
PFGs × VT	2	811	405.3	4.764	0.008835 [**]
Residuals	650	55,302	85.1		
Total	655	59,973			
Forbs:VTp–Forbs:VTs	0.0000003 [***]				
Grasses:VTp–Grasses:VTs	0.4697				
Legumes:VTp-Legumes:VTs	0.1918				
Forbs:VTp—Legumes:VTa	0.0016 [**]				
Legumes:VTp—Forbs:VTa	0.0018 [**]				

(b) PFGs × ST

	Df	Sum Sq	Mean Sq	F value	Pr(> F)
PFGs	2	4639	2320	32.15	$4.98e-14$ [***]
ST	5	18,773	3755	52.05	$< 2e-16$ [***]
PFGs × ST	10	75,965	7596	105.31	$< 2e-16$ [***]
Residuals	636	45,880	72		
Total	653	145,257			

PFGs, plant functional groups; ST, soil types; VT, vegetation litter; VTp, without vegetative litter; VTs, with vegetative litter.
[*] $P < .05$, [**] $P < .01$, [***] $P < .001$

(Table 3a). In fact, the TGD was significantly lower in the grasses than the forbs and legumes, but did not differ between the forbs and legumes (Table 3a; Fig. 3). Among the three plant community, $VT_{presence}$ significantly increased the TGD and the TGD in the forbs (TGD_{forbs}), with average increase of 35% and 64%, respectively, but did not significantly affect the TGD in the grasses and legumes ($TGD_{grasses}$ and $TGD_{legumes}$) (Table 4; Fig. 4a). Despite the non-significant difference, the $TGD_{grasses}$ and $TGD_{legumes}$ increase much more than 15%, illustrating $VT_{presence}$ potentially attracted more grasshoppers in turn increased the TGD. Moreover, there was significant interaction between PFGs and VT on

TGD, where TGD_{forbs} and $TGD_{legumes}$ at $VT_{presence}$ sites was significantly higher than $TGD_{legumes}$ and TGD_{forbs} in $VT_{absence}$ (P < .01; Table 4).

3.3. Changes in grasshopper density among soil types and PFGs-ST interactions on grasshopper density

The soil types had significantly effects on the TGD in the grassland (Table 3b). Based on the significant test of difference (Fig. 5b), the TGD at different soil types can be categorized into three groups (high-density: brown earths and grey desert soils, medium-density: meadow soils and castanozems, low-density: brown pedocals and Aeolian soils) (Fig. 5a). In fact, the TGD at low-density soil types were averagely 1.2 and 0.5 times lower than the high-density soil types and the medium-density soil groups, respectively. This is partly due to the special heterogeneity of soil types, causing difference of TGD along the ST-gradient.

The TGD in the grassland showed significant interactions between plant community and soil types in the grassland (Table 4b). The peaking TGD were emerged at Meadow soils and Grey desery soils in legumes, while the lowest were at Brown predocals (Fig. 6). On the other hand, the $TGD_{grasses}$ was approximately 0.5 times higher at Brown earths than other four soil types, while the TGD_{forbs} show a consistent increased trend along the ST-gradient, except at Grey desery soils (Fig. 6). Considering the peaking TGD_{lgumes}, this phenomenon indicated that the low-density soil types are not prone to survival for grassland grasshoppers whether the plant community was grasses or forbs.

4. Discussion

The results of our large-scale survey experiment provided evidence for markedly distinct grasshopper densities in response to interactions of different treatments. This finding supported our hypotheses that stated variations in grasshopper density were driven by joint effects of PFGs, vegetation litter and soil types. These joint effects of multiple drivers contrasted with the simple traditional ideas that vegetation characteristics and soil types individually explain grasshopper habitat preference and selection. Rather, our results indicate that grasshopper density responded to PFGs and was influenced by multiple environmental factors (Douma et al., 2012; Diaz et al., 2016). Specifically, our study found that PFGs impacted grasshopper density as a general habitat condition, and PFGs interact with vegetation litter and soil type to alter the dynamics of grasshopper communities. Meanwhile, there are joint effects that influence grasshopper density under the large-scale and multiple sampling site conditions. Moreover, the effects of vegetation litter and soil types varied markedly among PFGs. The RDA showed that the effects of PFGs varied along environmental gradients. This finding was in accordance with the common rules that are believed to shape plant community conditions (Douma et al., 2010). Moreover, the results revealed that vegetation litter-soil type interaction significantly affected plant community composition. These conclusions suggest that the interactions of multiple factors should be considered when exploring the dynamics of grasshopper communities receiving different treatments. However, with grasshopper assemblages, different grasshopper species may respond differently to these changes in PFGs (Branson and Sword, 2010).

4.1. Grasshopper palatability and grasshopper community structure among plant functional groups

PFGs are often used to explain biome-scale plant-environment relationships (Douma et al., 2012), which in turn, can affect the performance of herbivorous grasshoppers, specifically by altering grasshopper density (Saccone et al., 2017). According to the variation in the total grasshopper density along the PFGs, grasshopper populations were associated most closely with plant functional properties. This might be due to differences in accessing food resources (Descombes et al., 2017)
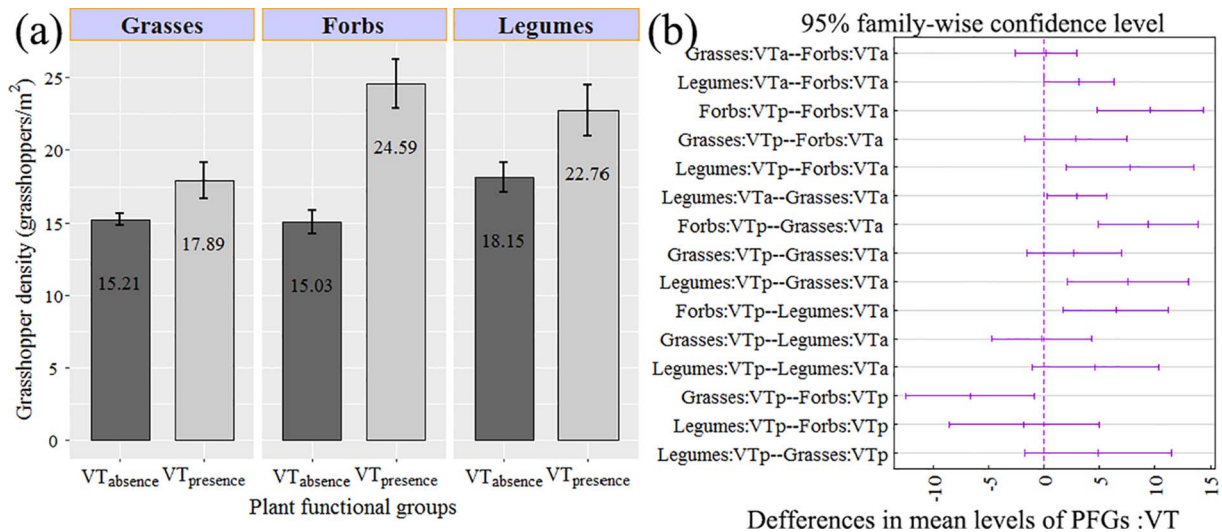
Fig. 4. (a) The total grasshopper density in the three plant functional groups (PFGs) that showed significant or near significant differences when vegetative litter (VT) is present (VT$_{presence}$) or absent (VT$_{absence}$). (b) The pair-wise comparison of total grasshopper density between PFGs and vegetative litter presence (VTp) or absence (VTa) via Tukey's HSD test. Error bars indicate standard errors.
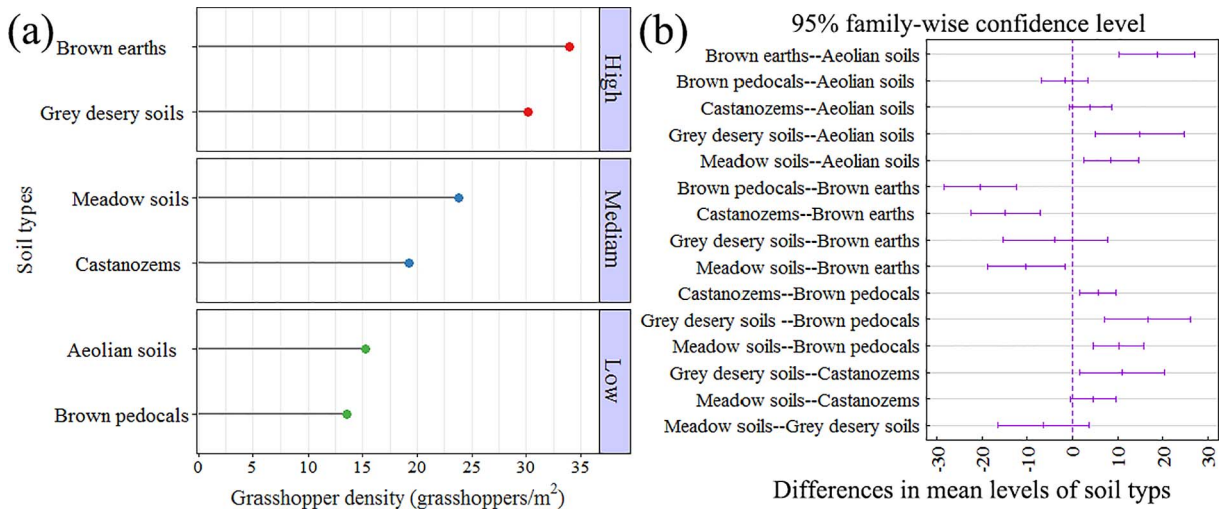

Fig. 5. (a) The total grasshopper density that showed significant differences on different soil types. (b) The pair-wise comparison of total grasshopper density among different soil types. Error bars indicate standard errors.

or could be caused by different PFGs, which have remarkable and distinct community compositions, with unique functional traits that influence the food (i.e., plant) preferences of herbivorous grasshoppers (Raubenheimer and Simpson, 2003). In fact, precipitation and drought-driven effects on food quality and quantity are important for grasshopper population dynamics (Joern et al., 2012).

Generally, legumes and forbs seem to be beneficial for grasshoppers, as grasshopper density was higher in plots dominated by these PFGs versus the sites dominated by grasses, a relationship that was independent of vegetation litter. This illustrates that the grasshopper community tends towards forb-feeding and legume-feeding rather than grass-feeding (Fig. 3). Peak grasshopper density was probably consistent with higher food limitations; as a consequence, the addition of herbivorous grasshoppers increased the food limitation and negatively affected the grasshopper populations. The other main reason for higher grasshopper density at sites with legumes and forbs compared to sites with grasses is probably the variability of host-plant traits (e.g., the levels of nitrogen, carbon, trace elements, defensive compounds) that can positively or negatively affect the performance of herbivorous grasshoppers (Sundqvist et al., 2013). Leaf biomechanical properties (leaf width, leaf strength and leaf toughness) influenced the functional

composition of grasshopper density. Plant chemical defences might be a significant dietary limitation to grasshopper growth and reproduction, because higher grasshopper densities diminish the quality and quantity of available biomass of the preferred food plants. Grasses also have lower leaf N than other PFGs (Falkengren-Grerup, 1998; Pan et al., 2015). Specifically, the tissue-specific feeding behaviour of grasshoppers is likely responsible for the observed changes in host-plant stoichiometry; that is, grasshoppers tend to feed on relatively nutrient-rich parts of the leaf blade and leave relatively low-nutrient biomass behind (Zhang et al., 2011). In addition, plants with nutritionally optimal vegetative tissue are rare, but herbivores can still meet their protein and carbohydrate requirements using a suite of pre-ingestive and post-ingestive mechanisms (Behmer, 2009). Characteristics relating to the geographical distribution of plants might also strongly affect grasshopper community dynamics. Widespread plants provide more opportunities for host-specialization and should sustain more widely distributed populations of herbivores; this reduces the probability of extinction and promotes the accumulation of herbivorous species over time (Lewinsohn et al., 2005).
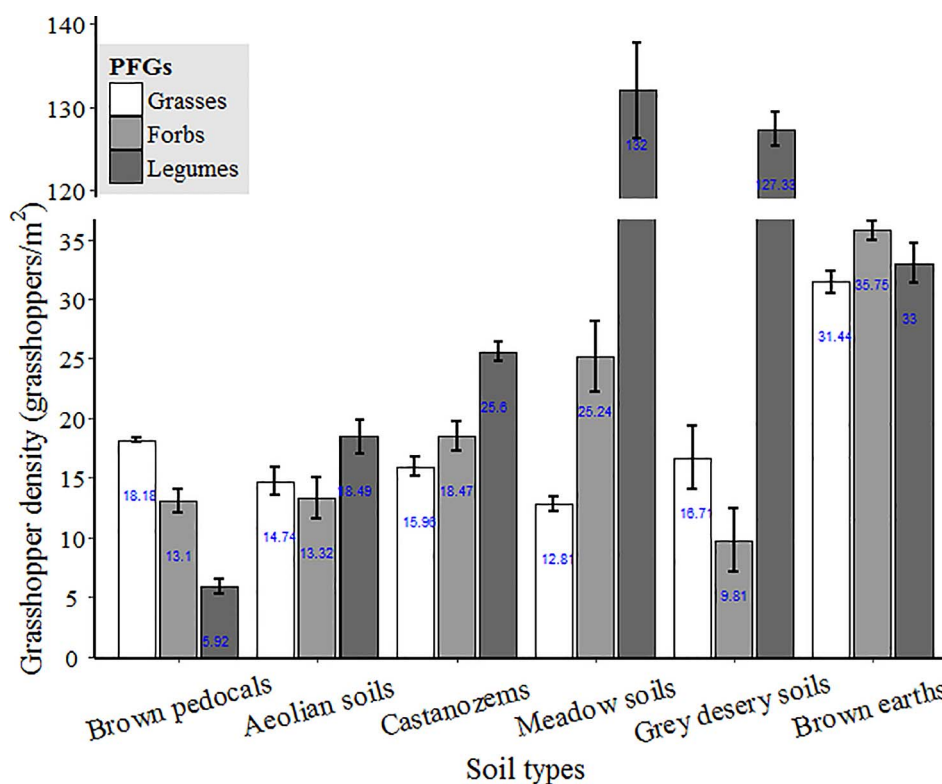
Fig. 6. The interaction effects of three plant functional groups and soil type on grasshopper density. Error bars indicate standard error.

4.2. Soil and litter habitats of grasshopper occurrence

Grasshopper density in grasslands is strongly influenced by both soil types and vegetation litter. Although the effect of different PFGs on grasshopper density did not suggest that PFGs influenced the habitat selection of the grasshopper community, the presence of vegetation litter increased the total grasshopper density up to 35% (Fig. 4a). This result indicates that the grasshopper community prefers to exist in environmental conditions that include litter, since the grasshopper population is prone to select habitats that provide multiple food resources, appropriate mating-sites and adequate oviposition-sites (Simon et al., 2015). This finding suggests that plant litter is conductive to the survival of the grasshopper community as a result of the suitable edaphic conditions and climate (Eckstein and Donath, 2005). For example, plant litter can reduce evaporation and water stress, release nutrients and increase shaded conditions (Brearley et al., 2003). The development of environmental conditions would enhance the rates of grasshopper community survival and hatched offspring, which ultimately results in higher grasshopper density. In contrast, removing litter may accelerate grasshopper phenology and the variation of the upper soil layers (Zhang et al., 2011), which would be harmful to grasshopper survival. Consequently, removing plant litter from the grassland ecosystem may reduce grasshopper density and, as a result, prevent grasshopper outbreaks in grasslands. When considering sites in the PTFs comprehensively, the effect of plant litter on grasshopper density was only significant in forbs. This implies that the observed effects of vegetative litter increasing grasshopper densities among PFGs were significantly different and mainly caused by vegetation types and by spatial-temporal heterogeneity (Jay-Robert et al., 2008). These results emphasize the importance of the combined effects of plant litter and PFGs, as grassland grasshoppers often respond to interactions between different factors, rather than to either factor individually (Joern and Laws, 2013).

Of the three primary grassland ecosystem drivers, the effects of soil type on grasshopper community dynamics are the most stable. Unlike PFGs and plant litter treatments that are vulnerable to environment

factors, soil type is not susceptible to changes in external environmental conditions. Our results found that soil type had a significant effect on grasshopper density. The main reason for the variance in grasshopper density was probably because of the difference in soil properties (Herrmann et al., 2010; Shintani et al., 2011), which primarily depend on the soil types. For example, soil physical characteristics are associated with oviposition; therefore, local soil conditions might be an important selection pressure and behavioural cue for determining oviposition depth (Stahlschmidt and Adamo, 2015). Moreover, the low-density soil group was at least 0.5 times lower than the other groups. This finding may be due to the unique heterogeneity of different soil types. For example, soil moisture is a critical parameter, with significant effects not only on plant growth and crop yield but also on grasshopper activities. In the study area, brown earths and desert soils were associated with higher grasshopper densities because their sandy loam texture and relatively warm environments were particularly suitable for grasshopper ovipositors and hatching of grasshopper eggs. Significantly interactive effects of location (soil types) and PFGs on grasshopper density were found in the large spatial-scale grassland ecosystems (Table 4b). In addition, we simultaneously considered vegetation litter to estimate the interaction of the three aspects. Consequently, the interactive effects of the three factors (PFGs, soil types, vegetation litter) on the total grasshopper density are of great interest and importance in the prevention of grasshopper outbreaks in large-scale grassland ecosystems (Hanley et al., 2007; Crous et al., 2014); in fact, grasshopper outbreaks are the critical driver of vegetation growth during the growing season in grassland. When vegetation litter was present, the peak grasshopper density for each PFG was grasses at brown-earths sites, forbs at brown-earths sites and legumes at sites with meadow soils and grey desert soils. When there was an absence of vegetative litter, the minimum grasshopper density for each PFG were grasses at meadow-soil sites, forbs at grey-desert soil sites and grasses at brown-pedocals sites. We found that large spatial-scale habitat alterations affected the grasshopper community, indicating that the total grasshopper density was highly responsive to extrinsic factors. This

result suggests that grasshopper species density in habitats with three plant functional types is strongly influenced by both soil type and vegetation litter.

5. Conclusions

In conclusion, our study is the first national estimation of the effects of plant-soil interface properties on grasshopper occurrence in grassland ecosystems. Our study found that the absence of vegetative litter could decrease the total grasshopper density by deteriorating the habitat conditions. Similarly, grasshopper communities appeared to prefer legumes and forbs rather than grasses because of the plant-trait variance in different PFGs. In addition, soil type had a significant effect on grasshopper density due to the differences in soil properties. This study demonstrates that total grasshopper density is driven by complex interactions, including PFGs, soil type and vegetation litter. Our findings suggest that decreasing vegetation litter will reduce grasshopper community outbreaks at those sites. This may provide us with a helpful strategy to prevent future grasshopper plagues.

Appendix A

Grasshopper species list

Subfamily	Genus	Species name
Pamphagidae	*Haplotropis* Saussure	*Haplotropis brunneriana* Saussure.
Pyrgomorphidae	*Atractomorpha* Saussure	*Atractomorpha sinensis* Bolvar
Catantopidae	*Oxya* Audinet-Serville	*Oxya chinensis* Thunb.
	Calliptamus Audinet-Serville	*Calliptamus abbreviatus* Ikonn.
	EirenephilusIkonn	*Eirenephilus longipennis*(Shir.)
Oedipodidae	*Oedaleus* Fieber	*Oedaleus decorus asiaticus* B.-Bienko
	Bryodema Fieber	*Bryodema luctuosum*(Stoll.)
		Bryodemagebleri(Fisher-Waldheim)
	Angaracris B.-Bienko	*Angaracrisrhodopa*(F.-W.)
	Epacromius Uvrov	Epacromius coerulipes(Iva.)
	Bryodemella Yin	*Bryodemella tuberculatum dilutum*(Stoll.)
		Bryodema holdereri holdereri(Krauss.)
Arcyptridae	*Paracyptera* Tarbinsky	*Pararcyptera microptera meridionalis*(Ikonn.)
	Omocestus I.Bolivar	*Omocestus haemorrhoidalis*(Charp.)
	Chorthippus Fieber	*Chorthippus brunneus*(Thunb.)
		Chorthippus fallax(Zub.)
Gompphoceridae	*Dasyhippus* Uvarov	*Dasyhippus barbipes*(F.-W.)
	Myrmeleotettix I.Bolivar	*Myrmeleotettix Palpalis*(Zub.)
		Myrmeleotettix brachypterus Liu
Acridae	*Acrida* Linnaeus	*Acrida cinerea* Thunb.

Appendix B

The total grasshopper density among different PFGs list

Rank	PFGs	Number	TGD	sd	se	ci
1	Grasses	315	15.21702	6.85834	0.3864237	0.760307
2	Forbs	172	18.29058	10.95104	0.8350089	1.648252
3	Legumes	169	18.82840	12.07465	0.9288189	1.833661

Notes: PFGs, plant functional groups; TGD, total grasshopper density.

Appendix C

The total grasshopper density in different PFGs among vegetation litter list

Rank	WCL	PFGs	Number	TGD	sd	se	ci
2	W	Grasses	273	15.20513	6.953325	0.4208344	0.8285067
5	Y	Grasses	44	17.89455	8.275189	1.2475317	2.5158875
1	W	Forbs	131	15.03290	9.226322	0.8061075	1.5947872
4	Y	Forbs	39	24.59000	10.387312	1.6633011	3.3671771
3	W	Legumes	144	18.14576	12.469304	1.0391086	2.0539979
6	Y	Legumes	25	22.76040	8.675024	1.7350048	3.5808738

Notes: WCL, whether contain vegetation litter; PFGs, plant functional groups; TGD, total grasshopper density.

Appendix D

The total grasshopper density in different soil types list

Rank	Soil types	Number	TGD	sd	se	ci
3	Brown pedocals	155	13.55477	6.431900	0.5166226	1.020582
1	Aeolian soils	100	15.27340	8.514652	0.8514652	1.689492
4	Castanozems	270	19.18519	9.729743	0.5921333	1.165805
6	Meadow soils	79	23.78519	26.405656	2.9708684	5.914545
5	Gray desery soils	20	30.19950	42.568461	9.5185973	19.922653
2	Brown earths	30	34.00000	3.648335	0.6660917	1.362311

Notes: TGD, total grasshopper density.

Appendix E

The total grasshopper density in different PFGs among different soil types

Rank	Soil types	PFGs	Number	TGD	sd	se	ci
2	Aeolian soils	Grasses	39	14.744103	7.367666	1.1797708	2.3883211
5	Brown earths	Grasses	9	31.444444	2.697736	0.8992452	2.0736632
8	Brown pedocals	Grasses	76	18.184211	1.646900	0.1889124	0.3763328
11	Castanozems	Grasses	142	15.964789	9.736237	0.8170468	1.6152456
14	Gray desery soils	Grasses	8	16.707500	7.434754	2.6285824	6.2156097
17	Meadow soils	Grasses	35	12.809714	3.452420	0.5835655	1.1859477
1	Aeolian soils	Forbs	34	3.322941	9.903842	1.6984949	3.4556139
4	Brown earths	Forbs	16	35.750000	3.276177	0.8190442	1.7457513
7	Brown pedocals	Forbs	35	13.104571	5.733765	0.9691833	1.9696174
10	Castanozems	Forbs	51	18.470588	8.766255	1.2275213	2.4655490
13	Gray desery soils	Forbs	9	9.814444	8.036144	2.6787145	6.1771267
16	Meadow soils	Forbs	41	25.236341	18.938790	2.9577420	5.9778196
3	Aeolian soils	Legumes	27	18.494074	7.487215	1.4409152	2.9618436
6	Brown earths	Legumes	5	33.000000	3.674235	1.6431677	4.5621648
9	Brown pedocals	Legumes	44	5.916591	4.437492	0.6689771	1.3491209
12	Castanozems	Legumes	77	25.597403	6.875407	0.7835254	1.5605260
15	Gray desery soils	Legumes	3	127.333333	3.511885	2.0275875	8.7240049
18	Meadow soils	Legumes	3	132.000000	0.000000	5.7735027	24.8413771

Notes: PFGs, plant functional groups; TGD, total grasshopper density

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