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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

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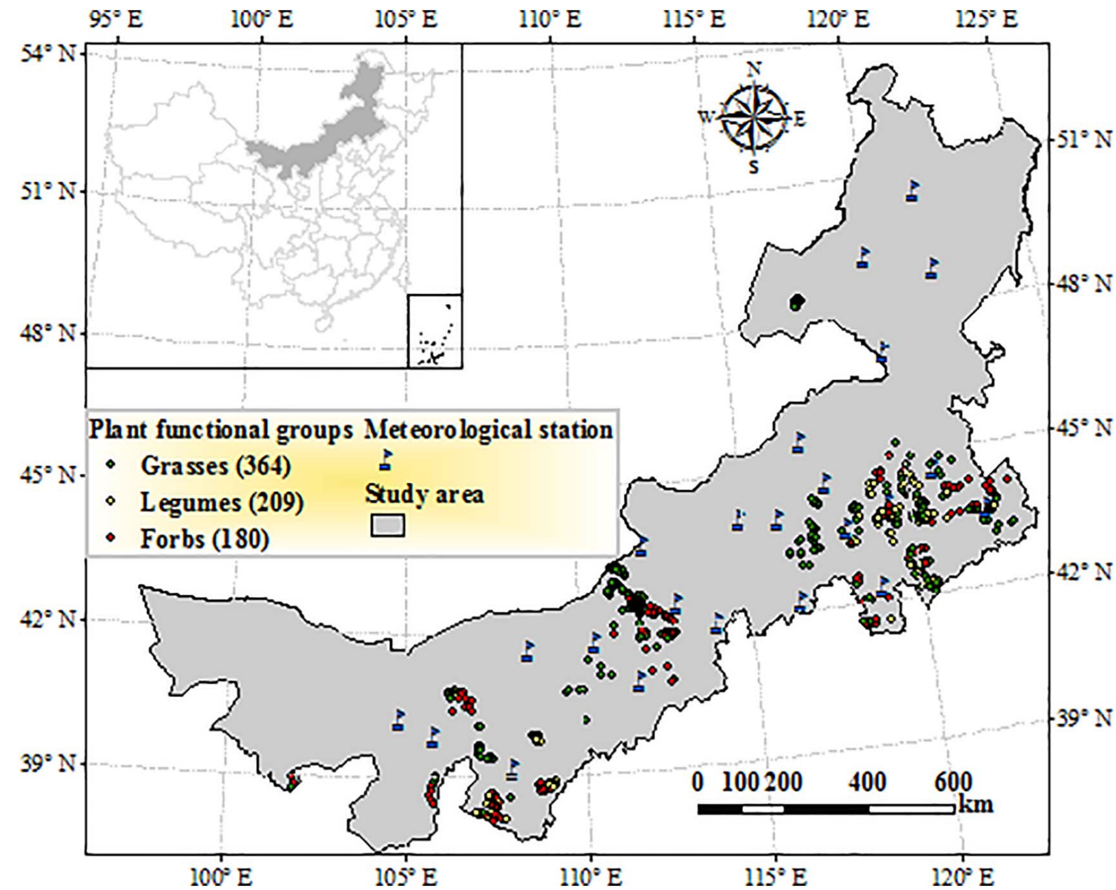

Fig. 1. Location of the study area and field plots in Inner Mongolia, China.

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 (Graminease). 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