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Sheep grazing and local community diversity interact to control litter decomposition of dominant species in grassland ecosystem

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ABSTRACT

Large herbivore grazing, a major land use in grasslands, can constitute a feedback loop with local plant diversity to affect litter decomposition. Here we examined the interactive effects of sheep grazing and local plant community diversity on decomposition of litter of the dominant plant species (*Leymus chinensis*) in the meadow steppe of China. We found a faster litter decomposition rate in the local species-rich communities compared to the local species-poor communities in the absence of sheep grazing. However, in the presence of sheep grazing, the decomposition rate was significantly reduced in the local species-rich communities while increased in the local species-poor communities. Therefore, sheep grazing and local community diversity constituted a negative feedback loop to modify litter decomposition in this grassland ecosystem. The findings of this study indicate one outcome of herbivore grazing could be to homogenize grassland nutrient cycling in space by balancing litter decomposition rate among local communities, which therefore could increase the homogenization of metacommunity structure. Furthermore, reduced local community diversity may slow ecosystem process rates. Our study indicates that sheep grazing, or equivalent, offsets this negative effect of local plant diversity loss on litter decomposition.

1. Introduction

Litter decomposition is the most important source of nutrient input for plants (Swift et al., 1979), and, especially litter decomposition of dominant plant species drives the C and N cycling of the whole ecosystem. Large herbivore grazing, a primary means to manage and utilize the grassland resources, exerts a strong influence on litter decomposition (Wardle et al., 2002; Fornara and Du Toit, 2008). The grassland plant community commonly exhibits complex spatial structure, including many small local communities with different plant composition and diversity, which has been referred to as a metacommunity (Leibold et al., 2004). Although herbivore grazing effects on litter decomposition have been studied extensively in the grassland ecosystem (Risch et al., 2007; Haynes et al., 2014; Banegas et al., 2015), the spatial effects of herbivore grazing on litter decomposition in different local communities, in context of a metacommunity, has rarely been explored.

There is an increasing recognition that local plant diversity exerts a potential impact on litter decomposition. It has been shown that a high diversity plant community could retain higher soil moisture and increase microbial activity, biomass and diversity (Eisenhauer et al., 2013; Lange et al., 2014, 2015), which might therefore enhance litter decomposition (Hättenschwiler et al., 2005; Lorenzen, 2008). In addition, many studies have found that litter mixture often produced positive non-additive effects, thereby improving litter decomposition (reviewed in Gartner and Cardon, 2004). Thus, there could be a large variation in litter decomposition in space within a metacommunity, especially between local communities with different plant diversity.

According to local community composition and diversity characteristics, herbivore grazing could have different consequences for the soil micro-environment and quality of litter inputs and affect litter decomposition. For example, herbivore defoliation can

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stimulate root exudation of grazing-tolerant grass species thereby increasing rhizosphere carbon inputs into the microbial community (Hamilton and Frank, 2001; Murray et al., 2004; Hamilton et al., 2008) and promote litter decomposition (Kuzyakov et al., 2007), but this stimulation was seldom documented for legumes and forbs. Grazing can also increase nitrogen concentrations of grass thereby the quality of litter inputs to soil (Coughenour, 1991). Therefore, different plant functional group species may have different responses to herbivore defoliation. Furthermore, diversity characteristics of plant community significantly affect herbivore foraging behavior (Wang et al., 2010a), which could feed back to plant species compositions and biomass (Liu et al., 2016, 2017), thereby the quantity and quality of litter inputs that become available to decomposers (Pastor et al., 1993; Bardgett et al., 1998). Herbivore grazing can therefore show either negative or positive effects on litter decomposition depending on the context of local community composition and diversity. Herbivore foraging and local community diversity may also constitute a feedback loop which affects litter decomposition in grazed grassland ecosystem. Most studies have reported the effect of local community diversity or herbivore grazing on litter decomposition respectively, while the combined effect of herbivore grazing and local community diversity on litter decomposition has seldom been studied in grazed grassland system.

In our meadow steppe, the perennial grass *L. chinensis* is the dominant species, and decomposition of this litter thus determines nutrient cycling rate of the whole grassland system. The grassland is comprised of multiple local communities with different plant species and diversity. *L. chinensis* communities and *L. chinensis*-forb communities are the two primary local community types distributed randomly in this grassland. In L. *chinensis* communities, over 90% of plant abundance is *L. chinensis*, and plant diversity is very low. In L. *chinensis*-forb communities, a reduced dominance of *L. chinensis* is accompanied by the presence of forbs, and plant diversity is high. Henceforth for simplicity we refer to the two types of community as local species-poor community and local species-rich community. In this region, sheep are the principal grazers that prefer patches with higher species richness especially that of forbs (Wang et al., 2010b, c). Grazing management of sheep strongly influences the local community composition, diversity and soil microenvironment, thereby litter decomposition.

This study aimed to examine how sheep grazing and local community diversity interact to modify litter decomposition of dominant species. We hypothesized that local community diversity promotes litter decomposition rate and sheep foraging selectivity. Yet, very high sheep foraging selectivity could in turn slow down litter decomposition rate. Thus herbivore grazing and local community diversity might constitute a negative feedback loop to modify litter decomposition in grassland ecosystems.

2. Materials and methods

2.1. Study site

The experiment was conducted at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, P. R. China (44°40′-44°44′N, 123°44′-123°47′E) at the meadow steppe. The local climate is continental with a mean annual temperature ranging from 4.6 to 6.4 °C. Mean annual precipitation from 280 to 400 mm with 70% concentrated in June–August (Changling County Climate Station, Jilin Province). Annual potential evapotranspiration is approximately three times as much as annual precipitation. Soils at the site were mixed saline and alkaline, had high pH (7–10.5) and were low in nitrogen. The main vegetation type is meadow steppe dominated by grass *Leymus chinensis* (Trin.) Tzvelev (Wang and Ba, 2008), which is a rhizomatous plant. Subdominant species at the site include the grass *Phragmites australis* Trin.; the legumes *Lathyrus quinquenervius* (Miq.) Litv. and *Lespedeza davurica* Schindler; and the forbs *Kalimeris integrifllia* Turcz., *Sonchus arvensis* Linn., *Inula japonica* Thunb. and *Potentilla flagellaris* Willd.

2.2. Experimental design

This study was conducted in a long term grazing platform in Songnen grassland. We chose sheep as the grazing animals. Sheep always have a strong preference for forbs. Our experimental setup consisted of three plots that were used by sheep grazing at a moderate intensity (SG), and three that were fenced to exclude large herbivores (NG) in 2010. The plot size was 100 m × 100 m. The sheep grazing period began in June and persisted until September each year. On June 23, 2012, within each plot we randomly selected three local species-poor communities and three local species-rich communities. The two types of plant communities had different characteristics of vegetation and soil (see Table 1). Within each local community we randomly selected a 4 m × 4 m subplot. In total, 36 mesocosms were established, with 9 replicates for each unique combination of local community type and herbivory treatments (2 community type × 2 sheep grazing treatment × 9 replicates). Replicate litterbags with the dominant species (*L. chinensis*) leaf litter were placed in three locations in each subplot on June 24, 2012. The litterbags, 20 cm × 10 cm with nylon net of 1 mm mesh size, contained a total of 10 g dried *L. chinensis* leaf litter that was collected from this grassland on April 20, 2012. On August 23, 2013, a total of 108 litterbags were harvested (36 × 3 sample replicates). Litter samples were carefully cleaned with tap water, dried at 65 °C for 48 h, and weighed with an accuracy of 0.1 mg. At the same time, the vegetation was surveyed in 0.5 m × 0.5 m quadrats above each litterbag within each subplot. The number of each plant species and plant canopy cover of all plant species were recorded in each quadrat. Furthermore, three replicates of 0- to 10-cm soil samples were collected from each quadrat beneath each litterbag using a 4-cm-diameter soil auger and then pooled into one single sample, homogenized and sieved (2 mm). For each soil sample, fresh soil was used and retained at 4 °C for the analysis of soil microbial biomass C and soil water content. Measurements of soil microbial biomass C (mg C g^{-1} soil dry mass) were performed using chloroform fumigation extraction method (FE) (Vance et al., 1987). The mean values of litter mass loss, vegetation characteristics and soil properties from three sample replicates for each subplot were used in analyses.

Table 1
Characteristics of plant community and soil properties in two types of local communities.

Local community types	Parameters							
	F/G	FDI	Soil pH	EC (μ s/cm)	SWC (%)	TOC (g/kg)	TN (g/kg)	TP (g/kg)
Local species-poor communities	0.05 ± 0.02	0.04 ± 0.01	9.85 ± 0.03	533.30 ± 8.93	12.81 ± 0.41	8.92 ± 0.82	0.82 ± 0.03	1.59 ± 0.13
Local species-rich communities	0.53 ± 0.15	0.53 ± 0.07	8.59 ± 0.06	102.47 ± 2.34	16.85 ± 0.28	6.06 ± 0.62	1.70 ± 0.12	1.95 ± 0.09

F/G: ratio of forb and grass; FDI: plant functional group diversity index; EC: electric conductivity; SWC: soil water content; TOC: total organic carbon; TN: total nitrogen; TP: total phosphorus.