ECOSYSTEMS

Standing Litter Modifies Top-Down Effects of Large Herbivores on a Grassland Plant Community

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ABSTRACT

Large herbivores can exert pronounced top-down effects on plant communities in grassland ecosystems. Previous studies highlighted the importance of the composition and traits of living plants in regulating the impact of herbivores on plant community. However, there has been little consideration of whether and how plant litter, a ubiquitous "after-life" plant component, affects the outcome of herbivore grazing on grasslands. Here, we conducted a large-scale field experiment in temperate grasslands of northeastern China to investigate how standing plant litter influenced top-down effects of large herbivores (sheep; *Ovis aries*) on plant species richness, evenness, community composition, and productivity. We found that, in the presence of standing litter, sheep grazing significantly reduced living biomass of forbs by 56%, but have no effects on biomass of the dominant grass, *Leymus chinensis*. However, in the absence of standing litter, sheep shifted their diet preference from forbs to the grass *L. chinensis*, leading to a 36% decrease in the biomass of *L. chinensis* and a 21% decrease in total biomass. Such changes in foraging pressure on plant species led to competitive release that in turn significantly altered plant community composition and increased species evenness. *Synthesis and applications*. Our results demonstrate that standing litter can alter foraging behaviors of large herbivores and modifying the outcome of their top-down effects on plant community properties in grasslands. These cryptic but perhaps ubiquitous interactions between litter and herbivores may help us better understand the organization and dynamics of plant communities in the grazed grasslands, with important implications for developing effective management and conservation plans.

INTRODUCTION

Top-down effects of large herbivores are key drivers of ecosystem structure (Augustine and McNaughton 1998; Filazzola and others 2020; Young and others 2013) and functioning (Eldridge and others 2016; Forbes and others 2019; Wang and others 2019). Such herbivore-mediated processes are inextricably linked to the issue of what factors control the patterns and strengths of the top-down effects of herbivores. Despite the complexity of plant–herbivore interactions, the composition and traits of plants and herbivores are the key determinants of how herbivores affect plant communities. It is now well established that plant community properties, like productivity (Bakker and others 2006; Olff and Ritchie 1998), diversity (Liu and others 2015), and dominance (Koerner and others 2018), can modify the patterns and strengths of the top-down effects of herbivores. While these studies focused on the role of living plants, there has been considerably less attention focused on whether plant litter, a ubiquitous ''after-life'' plant component, can also affect the outcome of herbivores on grasslands.

Plant litter is defined as the dead plant materials, including stems and leaves, from previous years' growth (Facelli and Pickett 1991). In grasslands, following leaf and stem senescence, a portion of this material falls to the soil surface and becomes ''fallen litter'' in that year. The rest of this material will become ''standing litter'' that remains attached to the plant for years, creating a unique landscape feature of grasslands, especially in the arid and semiarid regions (Knapp and Seastedt 1986). Previous studies of plant litter often consider both fallen and standing litter as a whole and have explore their collective role in affecting soil carbon and nutrient cycling (Sayer 2006; Hobbie 2015; Veen and others 2019), and plant population and community properties (Carson and Peterson 1990; Facelli and Pickett 1991; Liu and others 2018).

In addition to their effects on soil and living plants, fallen and standing litter may have influences on organisms from higher trophic levels, such as herbivores. This is particularly true for the standing litter in the grazing ecosystems, where previous studies have documented that the even the presence of low amounts of senescent standing stems can alter plant selection and use by large domestic herbivores such as cattle (Ganskopp and others 1992, 1993). The mechanisms behind such changes in herbivore foraging behaviors could be, first, a mix of standing litter and green plant materials may dilute nutritional value and lower the palatability of the host food plants; and second, the presence of standing litter may result in a decrease in apparency of preferred green food items, which in turn alter diet selection of large herbivores (Ganskopp and others 1993; Mingo and Oesterheld 2009; Odadi and others 2011).

In plant communities, the presence of unpalatable plant species can protect palatable neighbors from being attacked by herbivore consumers, a phenomenon termed ''plant associational defense'' (Barbosa and others 2009; Underwood and others 2014). While this concept focuses primarily on the living plant parts, it is plausible that the same principle applies to retained plant materials, both living and dead. Standing litter is ubiquitous and often rich in fibers but low in nutrients, making many large herbivores generally avoid feeding on it (Odadi and others 2011; Liu and others 2015). These plant materials may therefore play a similar role as unpalatable living plants (Callaway and others 2005; Cushman and others 2011; Coverdale and others 2018), and trigger shifts in the behaviors and distribution of grazers, with important consequences for their top-down effects on grasslands. However, until more recently, very few studies have explored the influences of standing litter on foraging activities of large grazers and their consequences for plant population and community dynamics (but see Mingo and Oesterheld (2009) for the effects of senescent leaves on plant–grazer interactions), limiting our understanding of their importance in structuring grassland ecosystems.

In a semiarid grassland of northeastern China, we conducted a large-scale, three-year field experiment to explore whether and how standing grass litter influences the feeding biology and top-down effects of large herbivores (sheep; *Ovis aries*) on the properties of plant communities. In our system, the perennial grass *Leymus chinensis* is the dominant plant species, competing for limiting resources with forbs and other grasses (Zhong and others 2017, 2021). *L. chinensis* often accumulates substantial standing litter until the following early growing seasons (Wang and others 2018; Zhong and others 2022, see Figure 1). Sheep are generalist grazers that consume green grasses and forbs while generally avoiding the low-nutrient standing litter. We hypothesize that standing litter produced by *L. chinensis* will weaken the top-down effects of her-
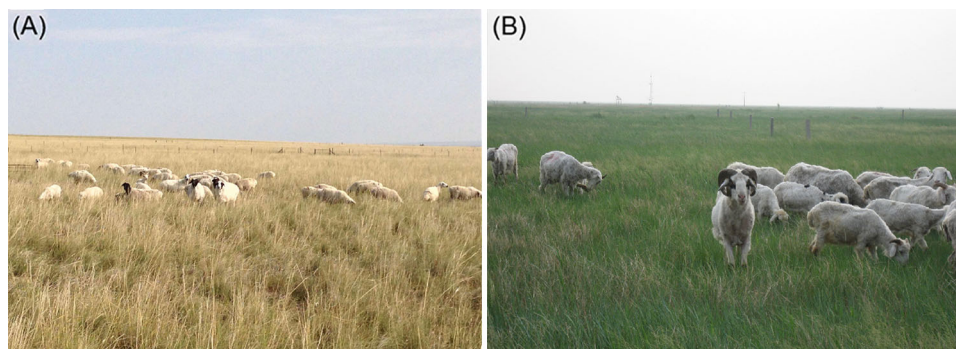
Figure 1. Standing plant litter, primarily from the dominant *L. chinensis* grass, is common and is retained until the early growing seasons (for example, from late May (**A**) to early July (**B**)) of following year, potentially affecting the foraging behaviors of sheep (*Ovis aries*) and thus their top-down effects on plant community in semiarid grasslands of northeastern China. The two photographs were provided by Zhongnan Wang.

bivores on this dominant grass through a behaviorally mediated indirect effect. Specifically, we suggest areas with large amounts of standing litter may be less likely to be fed upon by sheep, leading to reduced species diversity compared to low-litter areas that may be preferred feeding patches. To test these hypotheses, we measured the changes in biomass of different plant groups (for example, *L. chinensis*, other grasses, and forbs), community composition, and species diversity in response to the presence or absence of sheep grazing and standing litter. We combined these vegetation measures with observations of sheep grazing behavior, in particular the changes in diet selections among the three plant groups as a function of the presence or absence of standing litter, to explore the underlying mechanisms responsible for the changes in top-down effects of large herbivores on the plant community.

METHODS

Study System

Our field site is located in the Songnen Grassland in Jilin Province, northeastern China ($44^{o}35.5'$ N, $123^{o}30.5'$ E). The site is characterized by a semiarid continental monsoon climate, where annual mean temperature is 4.6–6.4 °C and annual precipitation is 280–400 mm, with 70% falling in June–August. The perennial grass *Leymus chinensis* is the dominant plant species, accounting for > 60% of total plant biomass (Zhong and others 2014; Li and others 2015). Other plants include the forbs *Kalimeris integrifolia* and *Artemisia scoparia*, and the grass *Phragmites australis* (Liu and others 2015). Plants germinate in late April and reach peak biomass in mid-August. Plants senesce and become

plant litter in late September. Standing litter is the dominant form of dead plant material and is comprised primarily of the dominant grass *L. chinensis*. Dead material can remain attached to this perennial grass during the growing season (May–August) of the following year.

Our study site has a long history of low-intensity livestock grazing and mowing from 1980 to 2004. However, it was fenced in 2005 when it became a research site (Zhong and others 2021). Since then, substantial plant litter has built up in the study site, which allowed us to test its potential influences on foraging behaviors of large herbivores.

Experimental Design

In June 2009, we established six replicate blocks, each containing two 50 m × 50 m plots. Distance between blocks ranged from 80 to 150 m, and the distance among the two plots in a block was on average 20 m. We randomly assigned the two plots to sheep grazing and ungrazed treatment within each block. The grazed plots were grazed by sheep at a light to moderate intensity (< 40% of aboveground plant biomass consumed by grazers) from June to September each year (2010–2012), a recommended grazing intensity by local governments. Within each plot, we randomly placed two 5 × 5 m subplots separated by approximately 7 m. Each subplot was marked by short wooden stakes (for example, lower than canopy height to avoid potential disturbances on sheep grazing behaviors) at the four corners. Two experimental treatments, standing litter removal and standing litter intact, were randomly assigned into the two subplots (Figure S1). For the litter removal treatment, we cut all standing dead material down to a height of 3 cm at ground level using scissors once each year

(from 2010 through 2012) in late May, before the grazing treatment was applied. The remaining dead material resting on soil surface was left intact. In total, we had four experimental treatment combinations with six replicates of each in a fully crossed 2×2 design: ungrazed + litter intact, ungrazed + litter removed, grazed + litter intact, and grazed + litter removed (Figure S1).

Pre- and Post-Treatment Sampling

To investigate the effects of sheep grazing and standing litter manipulations, we sampled the vegetation in our 3-year (2010–2012) field experiment. In mid-August 2009 (pre-treatment initial conditions), one year before the beginning of sheep grazing and plant litter removal treatments were initiated, and then again in mid-August of 2012 (that is, post treatment effects), we quantified properties of the plant community in all plots, including community composition, species richness, species evenness, and productivity of standing live plants, and the quantity of standing dead litter in the subplots. We randomly assigned a 1×1 m sampling quadrat in each subplot. We first measured plant cover, density, and height overall for *L. chinensis*, other grasses, and forbs. Plant cover was visually estimated as the percentage of ground surface covered by each plant group within each quadrat. Plant density was estimated by counting the number of stems of each plant group within each quadrat. Plant height (cm) was measured on five haphazardly chosen stems for each plant group within each quadrat. After which, we harvested all standing plant materials, separating them into live and dead categories. The live plant biomass was further sorted by species, and then dried for 48 h at 70 °C and weighed them. The aboveground biomass of each species was then assigned to one of three groups—*L. chinensis*, other grasses, and forbs. We calculated mean species richness and mean species evenness at the subplot level. Species richness (S) was calculated as the number of species in the quadrat within each subplot. Species evenness was calculated as the standard Shannon index, $J' = (-\sum p_i \ln p_i) / \ln S$, where p_i is the abundance (percentage biomass) of species i in a quadrat (by using the relative biomass/productivity (pi) of each species to total plant community to calculate evenness index, also see Dickman (1968), and Wilson and Hartnett (1997)). We also used principal component analysis (PCA) and analysis of similarities (ANOSIM) to test the dissimilarity of plant community composition among the four treatments. For the standing dead litter, we

separated *L. chinensis* from other plants, and then dried and weighted the two groups as above.

In mid-November (that is, peak of standing dead litter accumulation) of 2012, we also estimated how 3 years of sheep grazing affected the amount of standing plant litter in our experiment. We randomly assigned a 1×1 m quadrat at a random location (but with a different location of the pre-treatment sampling in June 2010) in the standing litter intact treatment subplot within each grazed and ungrazed plot. We then harvested all the standing dead litter within the quadrat, sorted them into *L. chinensis* and other plants, and dried for 48 h at 70 °C and weighed.

Effects of Standing Litter on Sheep Grazing Behaviors

In mid-August of 2012, prior to the biomass harvest, we assessed changes in diet preferences of sheep by measuring their grazing frequency on different plant groups (that is, *L. chinensis*, other grasses, and forbs). We randomly laid out a transect (length × width = 2 × 0.2 m) within each of the two 5 × 5 m subplots in the six 20 × 30 m unfenced (grazed) plots. The transect consisted of 10 contiguous quadrats (0.2 × 0.2 m) to assess the grazing frequency of sheep on the three plant groups. Sheep grazing leaves a distinctive mark, identified by a cutting plane visible in the remaining vegetation. Within each quadrat, we scored each of the three plant groups as being either grazed by sheep (1) or not (0). Values of all 10 quadrats were summed per transect and divided by 10 to obtain a metric of grazing frequency for each plant group, which ranged from 0 to 100% (see Clark and others 2012). We recognize that this assessment of grazing underestimates grazing activities because plant groups that are fully removed by sheep are not scored. However, such feeding behavior is unlikely to be common due to the light to moderate grazing intensity in our study.

Data Analyses

We used the open-source software R version 4.2.2 (R Core Team 2022) for all statistical analyses. We first used the model structure described below to test each response variable for differences among treatments as measured before the experimental manipulations in August 2009. In no case were pre-treatment differences significant ($P > 0.48$; Tables S1 and S2). We therefore focus presentation on analysis of data from the final treatment year (that is, 2012).

We used generalized linear mixed-effect models (GLMMs) in package lme4 (Bates and others 2015) to explore the effects of sheep grazing and standing litter on plant community characteristic response variables (that is, plant biomass, species richness, and species evenness). In our models, the sheep grazing treatment (that is, ungrazed or grazed), standing litter treatment (that is, intact or removed), and their interaction were treated as fixed factors. We also included replicate site as a random factor. We then used two-way ANOVAs to compare the effect of sheep grazing treatment, standing litter treatment, and their interaction on plant community characteristic response variables. In cases where the interaction between sheep grazing and standing litter was significant, we tested for post hoc differences among treatment means using multiple comparisons via the emmeans package (Lenth and others 2023). To assess the impact of standing litter on sheep grazing frequency on different plant groups (that is, *L. chinensis*, forbs, and other grasses), we used GLMM with standing litter treatment treated as a fixed effect and replicate site as a random effect. We then used one-way ANOVAs to compare the effect of standing litter treatment on sheep grazing frequency. We used the same methods to determine the effects of grazing on the quantity of standing litter of *L. chinensis* and other plants in the subplots. Finally, PCA analysis was performed using the pca function from the ''*FactoMineR*'' package, and ANOSIM analysis was performed using the *anosim* function from the ''*vegan*'' package. The dissimilarity analysis was performed using the *pairwise.adonis* function from the ''*pairwiseAdonis*'' package. These analyses were performed on the species richness, biomass, cover, height, and density of the three plant groups in the community from different treatments.

For each model, we specified the error distribution that best fit the response variable data. Specifically, we used a lognormal distribution for variables with positive skewness (that is, biomass), a Poisson distribution for count data (that is, species richness), a beta distribution for proportion data without zeros (that is, grazing frequency on *L. chinensis* and on forbs), a zero-inflated beta distribution for proportion data with zeros (that is,, grazing frequency on other grasses), and a Gaussian distribution for those approximating normality (that is, species evenness).

RESULTS

Effects of Sheep Grazing and Standing Litter on Plant Community Properties

Sheep grazing significantly reduced total plant biomass ($\chi^2_1 = 28.69$, $P < 0.001$), *L. chinensis* biomass ($\chi^2_1 = 26.66$, $P < 0.001$), and forb biomass ($\chi^2_1 = 7.50$, $P = 0.006$), but increased biomass of other grasses ($\chi^2_1 = 21.05$, $P < 0.001$) across the standing litter treatments (Figure 2). In contrast, we failed to find significant effects of standing litter on biomass of any plant groups across the grazing treatments. However, there was a significant interaction between sheep grazing and standing litter on total plant biomass ($\chi^2_1 = 6.04$, $P = 0.014$), *L. chinensis* biomass ($\chi^2_1 = 13.60$, $P < 0.001$), and forb biomass ($\chi^2_1 = 5.82$, $P = 0.016$). In the grazed plots, the removal of standing litter significantly reduced plant total biomass ($t_{20} = 2.29$, $P = 0.033$) and *L. chinensis* biomass ($t_{20} = 3.26$, $P < 0.004$), but increased forb biomass ($t_{20} = -2.484$, $P = 0.022$) (Figure 2A, B, C). In the ungrazed plots, the removal of standing litter failed to exert significant effects on these three variables (Figure 2A, B, C).

The identity of all plant species found in the four treatments is shown in Table S3. At the coarsest level, species richness was not affected by either treatment or their interaction (grazing: $\chi_1^2 = 2.912$, $P = 0.378$; litter: $\chi^2_1 = 1.13$, $P = 0.275$; grazing × litter: $\chi^2_1 = 2.491$, $P = 0.583$; Figure 3A). In contrast, species evenness varied as a function of the combination of treatments imposed. Specifically, removal of standing litter increased species evenness ($t_{20} = -2.27$, $P = 0.038$) when sheep grazing was present, but standing litter removal had no impact on evenness in the absence of grazing ($t_{20} = -1.04$, $P = 0.461$; Figure 3B). The PCA analysis showed that plant community composition was widely divergent between the litter intact and litter removed treatments in the grazed areas, but not in the ungrazed areas (Figure 4). The ANOSIM analysis further confirmed that plant community composition differed among the treatments ($R = 0.510$, $P = 0.001$; Table 1). In the absence of grazing, litter removal did not altered community composition ($R^2 = 0.107$, $P_{adj} = 1.000$, Table 1), but such effect became significant in the presence of grazing ($R^2 = 0.425$, $P_{adj} = 0.040$). In the grazed areas, litter removal altered community
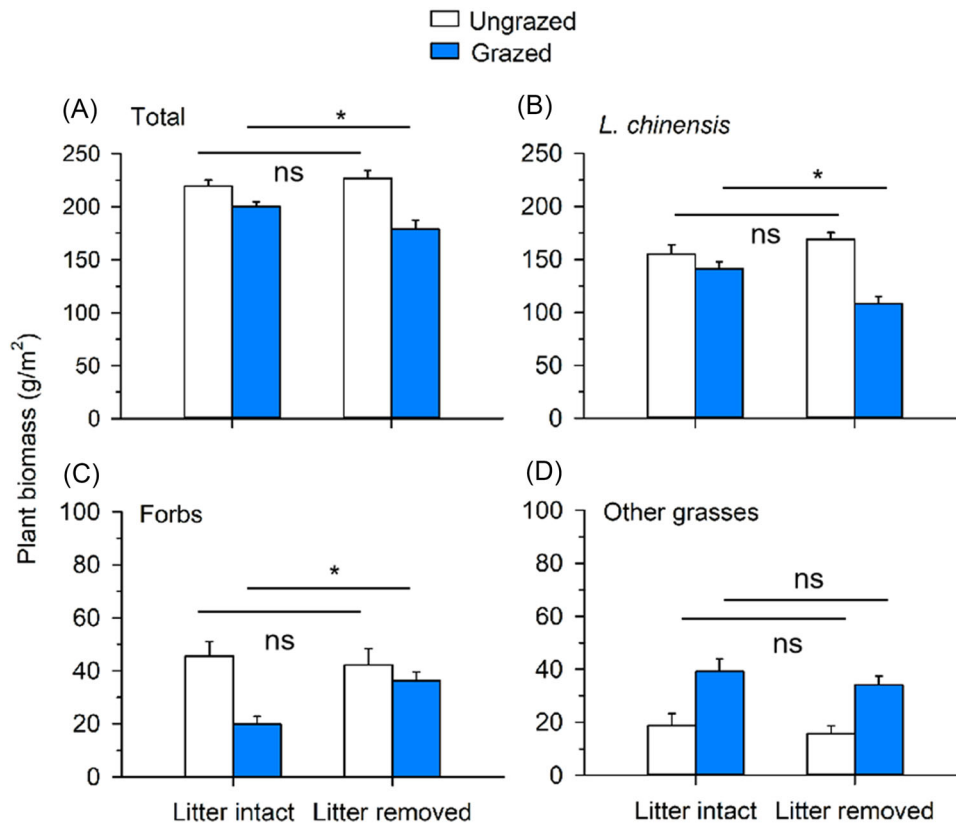
Figure 2. Combined effects of 3-year sheep grazing and standing litter removal treatments on **A** total plant biomass, **B** *L. chinensis* biomass, **C** forb biomass, and **D** biomass of other grasses in the 5 × 5 m subplots in August 2012. For **A–C**, an asterisk (*) between the bars indicates significant ($P < 0.05$) differences based on post-hoc comparisons, whereas ns indicates non-significant differences between treatments. No interactive effects were detected for biomass of other grasses (**D**); see Results for details. Error bars represent ± 1 SE.

composition mainly by decreasing biomass of the dominant *L. chinensis* grass (Figure 2B), but increasing forb biomass (Figure 2C).

In addition, 3 years (2010–2012) of grazing reduced the amount of standing dead litter of *L. chinensis* by 14% ($F_{1,5} = 1.744$, $P = 0.244$) and standing dead litter of other plants by 25% ($F_{1,5} = 0.751$, $P = 0.428$), but neither effect was significant (Figure S1).

Effects of Standing Litter on Sheep Grazing Behavior

In the grazed plots, the removal of standing litter significantly increased sheep grazing frequency on the dominant *L. chinensis* by 183% ($P < 0.001$, Figure 5A), whereas reduced grazing frequency on forbs by 37% ($P < 0.05$, Figure 5B). Standing litter removal had no significant effect on diet prefer-

ences of sheep on other grasses ($P = 0.89$, Figure 5C).

DISCUSSION

As predicted, standing litter modified the top-down effects of large herbivores on grassland plant communities. Such modulation effects of plant litter appeared to be triggered by a behaviorally-mediated indirect interaction: they caused shifts in diet preferences of large herbivores from grasses to forbs. Sheep preferred the dominant *L. chinensis* grass in the absence of standing litter, but changed their diet preferences to forb species in the presence of litter (Figure 5). Such shifts in herbivory loads mitigated the negative grazing effects on *L. chinensis* and increased its dominance (for example, decreases in evenness, Figure 3), which then altered
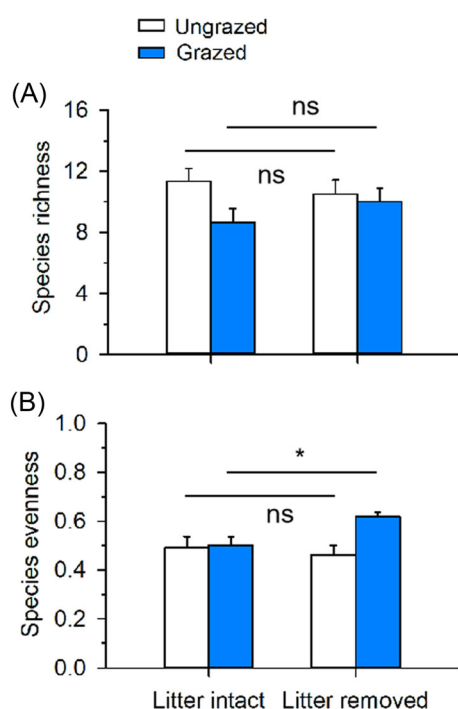
Figure 3. Combined effects of 3-year sheep grazing and standing litter removal treatments on plant **A** species richness, and **B** species evenness in the 5 × 5 m subplots in August 2012. For **B**, an asterisk (*) between the bars indicates significant ($P < 0.05$) differences based on post-hoc comparisons, whereas ns indicates non-significant differences between treatments. No interactive effects were detected for species richness (**A**); see Results for details. Error bars represent ± 1 SE.

the competitive interactions between *L. chinensis* and forbs and led to changes in plant community composition (Figure 4, Table 1) and productivity (Figure 2). In our system, standing litter served a similar role as the unpalatable living plants in the subalpine meadow of the Caucasus Mountains of Georgia, USA, where they provided defense for palatable plant species against herbivory (Callaway and others 2005). Given that both plant litter and large herbivores are pervasive and often co-occur in many grasslands, the protective effects of plant litter on living plants and their modification of the top-down effects of grazers may be a phenomenon that is more common than previously thought.

Standing litter may have inhibited sheep grazing on *L. chinensis* grass via multiple pathways. First, litter retention may decrease visual apparency of preferred diet items (see similar effects of plant associational defense between unpalatable and palatable plants against herbivores in Barbosa and others (2009), Callaway and others (2005), Cushman and others (2011), Zhong and others (2014), Coverdale and others (2018)), thus lowering the

probability of *L. chinensis* grass being attacked by sheep. Second, the dead plant materials in the canopy are often mixed with fresh new leaves. Grazers might find it difficult to separate the fresh green leaves from the low-nutrient plant litter, diluting the forage quality (for example, protein:fiber ratio) and make grass species less preferentially eaten by large grazers (Ganskopp and others 1992, 1993; Mingo and Oesterheld 2009). Third, stems and leaves of grasses may become rigid and sharp as they become senescent, similar to thorns (Forb and others 2014), this dried morphology may damage or irritate the skin, mouths, noses, and eyes of large grazers, and thus deter their foraging activity (Olff and others 1999).

While many studies have demonstrated that unpalatable living plants can facilitate the growth of neighboring plants by reducing herbivory (Barbosa and others, 2009; Callaway and others 2005; Cushman and others 2011; Coverdale and others 2018), fewer studies have explored similar effects of plant litter. One study showed that dead-leaf removal from the palatable grass *Paspalum dilatatum* increased consumption by cattle, with potential consequences for population dynamics of this host food plant in grasslands of the Flooding Pampa in Argentina (Mingo and Oesterheld 2009). In African savannas, introduced livestock like cattle often avoid standing dead grasses; but large wildlife such as zebras, which have a much longer co-evolutionary history with native grasses, consume a large amount of grass litter because of the morpho-physiological adaptations of their digestive system to cropping and processing fibrous grass stems (Duncan and others 1990; Gwynne and Bell 1968). In our study system, native large wild animals have been extirpated and introduced livestock rarely consume plant litter during growing season. Globally, large wildlife are declining rapidly due to human activities, whereas livestock are increasingly introduced into many ecosystems that lacked grazers during recent evolutionary times (Filazzola and others 2020; Ripple and others 2015). If coevolutionary time between large herbivores and grasses is a key determinant of grazers' adaptation and preference to use plant litter in their diet, plant litter may be unfavorable for livestock due to the relatively short coevolutionary history in most grasslands. Therefore, we suspect that plant litter may have the same regulation effects on grazing across many other grassland ecosystems.

The amount of plant litter accumulated in grasslands is affected by both natural and anthropogenic disturbances. Removal of dead plant materials by human activities such as grazing, fires
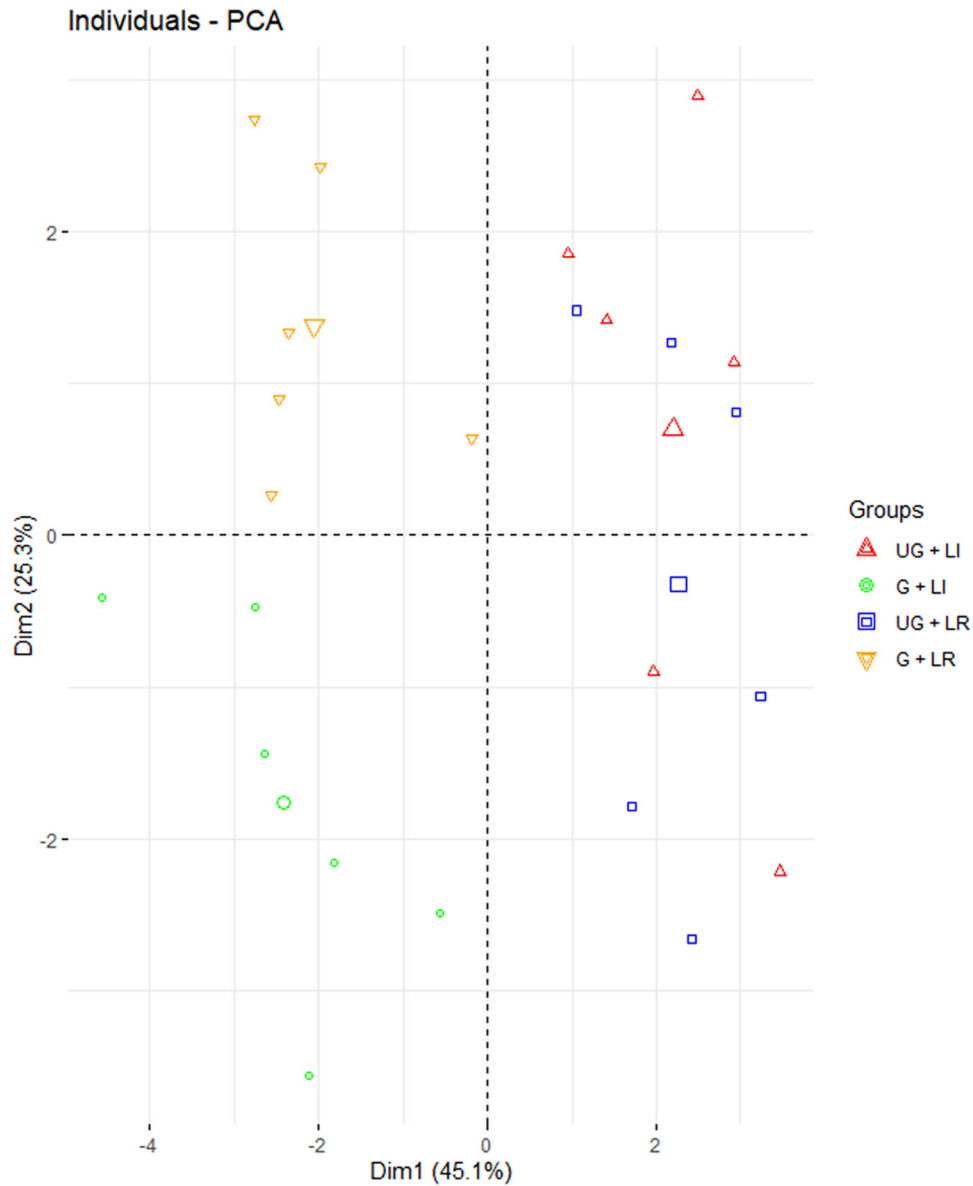
Figure 4. Principal component analysis (PCA) of variation in the plant community composition of the four treatments in the 5 × 5 m subplots in August 2012. $n = 24$. UG = Ungrazed, G = Grazed, LI = Litter intact, LR = Litter removed.

and mowing can quickly and substantially reduce plant litter (Oesterheld and others 1999; Schrama and others, 2013; Penner and Frank 2019; Li and others 2018, 2021). In our system, we found that 3 years of moderate sheep grazing reduced the total amount of standing litter (that is, *L. chinensis* and other plants) by 16% compared with the ungrazed sites (Figure S2). Such a decline in plant litter may in turn weaken their regulation effects on grazing and subsequent plant community. From the perspective of plant productivity conservation, long-term continuous human activities (for example, grazing, mowing, and fire) that can substantially

remove plant litter are therefore not recommended in grasslands. These activities will weaken the grazing refuge effects that plant litter provides to the dominant grass species, leading to a higher risk of overgrazing and habitat degradation. However, retaining a large proportion of standing litter in grasslands may come at the cost of plant diversity (or evenness) by facilitating the persistence of a dominant grass (Figs. 2 and 3). Hence, the best management strategy would be to remove standing litter in some patches while keeping it intact in others across a grazing landscape. Such a solution will allow for high dominance of grass species (also

Table 1. Dissimilarity Test of the Composition of Plant Community Within Different Treatments by ANOSIM Analysis ($R = 0.510$, $P = 0.001$)

Treatments	F. Model	R^2	P	P_{adj}
UG + LI versus G + LI	6.677	0.400	0.005	0.028*
UG + LI versus UG + LR	1.192	0.107	0.328	1.000
UG + LI versus G + LR	10.317	0.508	0.006	0.038*
UG + LR versus G + LI	11.291	0.530	0.003	0.017*
UG + LR versus G + LR	17.715	0.639	0.002	0.014*
G + LI versus G + LR	7.385	0.425	0.007	0.040*

$^*< 0.05$

Statistic R is based on the difference of mean ranks between groups and within groups. The R value is bounded by − 1 and + 1, higher values indicate a greater difference between groups (R > 0), and lower values indicate a greater difference within groups (R < 0). The significance of observed R is assessed by permuting the grouping vector to obtain the empirical distribution of R under the null model. Pairwise comparison of factor matrix showed significant differences. n = 24. UG = Ungrazed, G = Grazed, LI = Litter intact, LR = Litter removed.
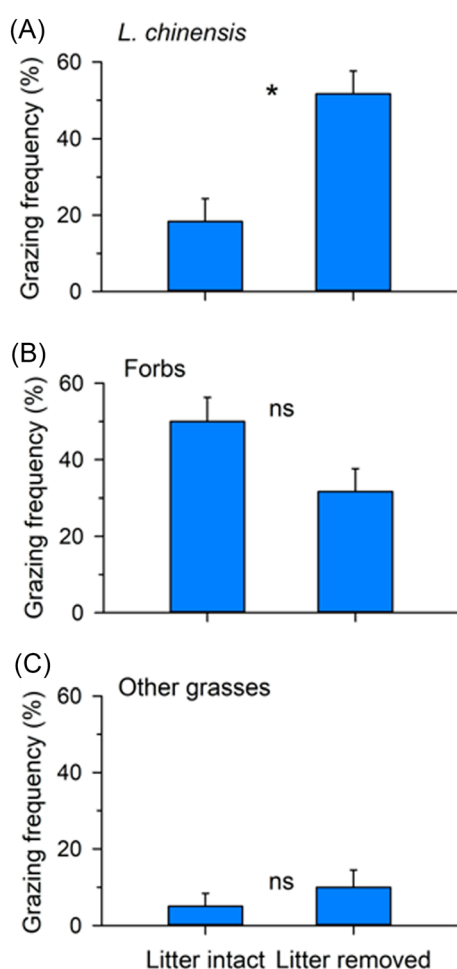

Figure 5. Effects of 3-year standing litter removal treatments on grazing frequency of sheep on **A** *L. chinensis* grasses, **B** forbs, and **C** other grasses in the 5 × 5 m subplots in August 2012. Asterisk (*) between the bars indicates significant differences, whereas ns indicates non-significant differences between treatments. Error bars represent ± 1 SE.

high-quality forage for livestock) in the patches with standing litter, and abundant forb species in the patches with standing litter removal to maintain plant biodiversity.

In conclusion, plant litter, which superficially appears to be an undesirable component of rangeland systems (Ganskopp and others 1992, 1993; Mingo and Oesterheld 2009), may play an important role in maintaining productivity and regulating diversity of grazed plant communities. These indirect effects can be elicited by shifts in feeding behaviors of herbivores, which in turn modify the patterns and outcome of herbivores' top-down effects on plant community. Eliminating these natural grazing refuges by management activities, such as fire and mowing, without reducing grazing intensity may therefore do substantial long-term damage to the ecological integrity of the grazed ecosystems. While this study examines the role of standing litter, whether and how the fallen litter at ground surface can exert similar effects on herbivore consumers remain unclear. We call for further research to explicitly investigate the causes and consequences of these cryptic litter–herbivore interactions through controlled and field experiments to advance our understanding of the roles and significance of plant litter in structuring ecological systems, which will be vital in obtaining information for formulating appropriate management and conservation plans.

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DATA AVAILABILITY

Data (Wang and others 2023) are available in Figshare Dataset at https://doi.org/10.6084/m9.figshare.21971231.v3

Declarations

Conflict of interest   All authors certify that they do not have any conflicts of interest to disclose.

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