Grazing regime alters plant community structure via patch-scale diversity in semiarid grasslands

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Abstract. Selective grazing of livestock creates lightly and heavily grazed vegetation patches, which together contribute to the whole community in grazed grasslands. The intermediate disturbance hypothesis (IDH) predicts moderate grazing intensity can increase species diversity. However, grazing patchiness complicates predicted responses to grazing intensity from ecological theory and may influence how various management regimes affect biodiversity at the whole community scale. We examined effects of management regime and grazing intensity on plant species diversity, community composition, aboveground net primary production (ANPP), and soil compaction. Two management regimes (season-long continuous grazing and grazing and mowing alternated annually) and seven levels of grazing intensity were applied over the past 10 yr. We assessed how \( \alpha \) diversity within patches and \( \beta \) diversity across patches contributed to the diversity of the whole plot and how these relationships responded to both grazing intensity and management regime. We further divided \( \beta \) diversity into nestedness and replacement components across lightly and heavily grazed patches within plots. The mixed grazing–mowing regime differed from the continuous grazing regime in that the former had a higher number of palatable species, higher species evenness, and higher Shannon-Wiener diversity, in both lightly and heavily grazed patches and the whole plots, and especially at moderate and high grazing intensities. The continuous grazing regime and the mixed grazing–mowing regime did not differ in total \( \beta \) diversity. However, the nestedness component of total \( \beta \) diversity was dominant in the continuous grazing regime. In contrast, species richness and ANPP did not differ significantly between the two management regimes, though soil hardness in heavily grazed patches was significantly higher under the continuous grazing regime than the mixed grazing–mowing regime. Loss of rare species under both management regimes, even at low to moderate grazing intensities, suggests that selective grazing and patch formation may not conform with the IDH. Our study indicates that the mixed grazing–mowing regime is more sustainable for long-term grassland management than the continuous grazing regime by controlling the creation of heavily grazed patches. These findings, integrating \( \alpha-\beta-\gamma \) diversity and patch-scale approaches, provide a more thorough evaluation than the intermediate disturbance hypothesis of grazing management in terms of sustainability and biodiversity conservation in semiarid regions.
INTRODUCTION

Grazing represents the main type of land use in grasslands around the world, and grazing intensity is one of the main factors that affects plant species diversity and ecosystem functioning in these systems (Milchunas et al. 1988, White et al. 2000). Many studies have found that moderate grazing intensity promotes species diversity and productivity, whereas overgrazing reduces them at the community scale (McNaughton 1979, Bai et al. 2007, Li et al. 2015, 2017). However, even under a moderate grazing intensity, long-term continuous grazing can also lead to grassland degradation by creating heavily grazed patches that suffer higher grazing pressure and soil compaction than that intended for the area as a whole (Teague and Dowhower 2003, Teague et al. 2011). It is still unclear how differences in grazing intensity and management regime affect the maintenance of biodiversity and productivity of grasslands, especially in a multi-patch context. Thus, research that considers multiple management regimes, grazing intensities, and patch types can give useful insights into the mechanisms of grazing effects on biodiversity maintenance and sustainable grassland management.

Several hypotheses regarding the positive effects of grazing on plant species diversity focus mainly on disturbance intensity. The well-known intermediate disturbance hypothesis (IDH) predicts that species diversity is maximized when ecological disturbance is neither too rare nor too frequent (Connell 1978). In this context, Grime’s CSR (competitor, stress-tolerant, ruderal) strategies also predict that ruderal species will predominate with frequent disturbance and that light-competitive or stress-tolerant species will predominate with low levels of disturbance, depending on environmental conditions such as light, water, and soil nutrients (Grime 2001). At intermediate levels of disturbance, all functional types of plants should persist. Some previous studies found that moderate grazing could promote plant species diversity in high productivity sites by limiting competition from fast-growing, light-competitive species (Collins et al. 1998, Bakker et al. 2006). In contrast, other studies found that grazing had negative effects on species diversity in low productivity sites by excluding grazing-sensitive species (Eldridge et al. 2016, Herrero-Jauregui and Oesterheld 2018, Zhang et al. 2018).

Although much work has emphasized the contribution of differences in site productivity to the responses of plant diversity to grazing (Bakker et al. 2006, Huston 2014, Burkepile et al. 2017), far fewer studies focus on uneven grazing, which is a very common phenomenon in grasslands and which can lead to species loss (Hunt 2001). For example, the abundances and spatial distribution of preferred species affect diet selection by sheep (DuPont et al. 2002) and sheep graze preferentially on the most palatable patches available while avoiding rough, tall swards and tussocky areas (McNaughton 1984). Because regenerating growth of leaves following grazing is often highly palatable, a positive feedback leads to plant communities with heavily grazed and lightly grazed patches (Ren et al. 2015). Furthermore, repeated grazing in heavily grazed patches can increase soil compaction by trampling, which can decrease species diversity due to poor establishment and impeded root growth (Proffitt et al. 1995, Greenwood and McKenzie 2001, Steffens et al. 2008). Thus, patchiness complicates the simplistic predictions of the IDH and it remains unclear how grazing-induced patchiness affects biodiversity maintenance at both patch and whole community scales.
As another important metric for community diversity, β diversity provides a link that connects diversity measures across scales and illuminates mechanisms of community diversity maintenance. Socolar et al. (2016) indicated that β diversity increases when dominant species disappear from two sites or when rare species appear at two sites, and β diversity decreases when rare species disappear from two sites or when the same species become dominant at two sites. Similarly, deterministic competitive exclusion reduces β diversity, whereas stochastic extinctions increase β diversity (Segre et al. 2014). Recently, a growing number of studies have demonstrated the usefulness of partitioning total β diversity into nestedness and replacement components (Gianuca et al. 2017, Mori et al. 2018). The nestedness component reflects a phenomenon in which the less diverse site is a strict subset of the more diverse site, whereas the replacement component reflects changes in species identities between sites (Baselga 2012). Separating the relative contribution of each component to total β diversity can also provide insight into appropriate conservation strategies. For instance, if nestedness accounts for a high proportion of dissimilarity, there is low complementarity among sites and conserving multi-site diversity could be accomplished by preserving sites with high α diversity. Conversely, if the replacement component accounts for a high proportion of dissimilarity among sites, conservation of the species pool requires preservation of multiple sites. Therefore, understanding what ecological processes shape each component of β diversity is crucial for preserving multi-site diversity and can directly help conservation planning and grassland management (Socolar et al. 2016, Gianuca et al. 2017).

The effects of grazing intensity on plant species diversity can also depend on the management regime used. For example, grazing regimes that involve continuous grazing have resulted in extensive habitat degradation and biodiversity loss in arid and semiarid grasslands (Chillo et al. 2017, Li et al. 2017, Herrero-Jáuregui and Oesterheld 2018). Many studies have demonstrated that livestock in the continuous grazing regime often repeatedly use heavily grazed patches created in former years (Weber et al. 1998, Ren et al. 2015). As mentioned before, repeated grazing in heavily grazed patches can increase grazing pressure and soil compaction and decrease species diversity in those patches (Proffitt et al. 1995, Greenwood and McKenzie 2001). Model simulations suggested that patches created by grazing can be preserved for at least a decade (Mouissie et al. 2008). A different management regime, alternating grazing and mowing by year (mixed grazing–mowing), contrasts with continuous grazing by producing a more uniform vegetative cover at the beginning of the grazing season. Therefore, livestock are less affected by the distribution of patches from the previous year (Ring et al. 1985). However, less is known about whether a mixed grazing–mowing regime maintains species diversity better than a continuous grazing regime by alleviating repeated grazing in heavily grazed patches in semiarid grassland.

Besides plant species diversity, grazing also changes aboveground net primary production (ANPP). Milchunas and Lauenroth (1993) synthesized 236 studies and found that most effects of grazing on ANPP were negative, but some were positive when grazing intensity was low. The grazing optimization hypothesis predicts that an intermediate grazing intensity could increase ANPP as a result of plant overcompensation (McNaughton 1979). However, De Mazancourt et al. (1998) demonstrated that such enhancement is controlled by recycling of the limiting soil nutrient. Previous studies found that soil bulk density increased, while soil moisture, organic carbon, soil total nitrogen, and total sulfur concentration decreased with increasing grazing intensity (Steffens et al. 2008, Zhao et al. 2011), which could increase nutrient limitation and reduce ANPP in grasslands (Hooper and Johnson 1999). Ludwig et al. (2005) further found that heavily grazed patches had more runoff and erosion than lightly grazed patches. However, compared to many studies on grazing intensity, less is known about whether the mixed grazing–mowing regime maintains ANPP better than the continuous grazing regime in semiarid grassland by alleviating repeated grazing and soil compaction in heavily grazed patches.

Here, we present results from a 10-yr grazing experiment in a semiarid Inner Mongolian grassland. Specifically, we addressed the following questions: First, how does grazing intensity interact with management regime to affect α, β, and whole plot diversity? Following IDH and the
Fig. 1. Conceptual scheme representing the patch-mediated effects of management regime and grazing intensity on species diversity and aboveground net primary production (ANPP) at the whole community scale. According to the intermediate disturbance hypothesis and grazing optimization hypothesis, we predicted responses of both species diversity and ANPP to grazing intensity would be hump-shaped (a). The effects of management regime on species diversity and ANPP may not differ if neglecting patch effects (a, left). However, heavily grazed patches will receive more grazing and trampling over long-term grazing in a continuous grazing regime than in a mixed grazing–mowing regime; in contrast, lightly grazed patches will receive less grazing and trampling in a continuous grazing regime than in a mixed grazing–mowing regime (a, right). The increased grazing and trampling in heavily grazed patches under continuous grazing could increase loss of rare species more than in the mixed grazing–mowing; at the same time, the decreased grazing and trampling in lightly grazed patches under the continuous grazing could increase competitive exclusion of rare species more than in the mixed grazing–mowing regime (b). Thus, we predicted that long-term continuous grazing could decrease species diversity and ANPP because of positive feedbacks leading to stronger patch formation, compared to a mixed grazing–mowing regime. The thickness of orange arrows indicates the strength of patch selectivity. The density of brown points indicates the degree of soil compaction.
grazing optimization hypothesis, we hypothesized that diversity and ANPP would be highest at intermediate grazing intensities (Fig. 1a). We also hypothesized that at high grazing intensities, the continuous grazing regime would increase rare species loss in lightly and heavily grazed patches more than in the mixed grazing regime, because of positive feedbacks increasing impacts of grazing in heavily grazed patches and decreasing disturbance in lightly grazed patches under the continuous grazing regime (Fig. 1b). If these hypotheses hold, then under the same grazing intensity, the continuous grazing regime should have lower α, β, and whole plot diversity than the mixed grazing–mowing regime. Second, how does grazing intensity affect the components of total β diversity (i.e., nestedness and replacement between patches) in the two management regimes? Consistent with the previous hypothesis, we expected that the continuous grazing regime would have higher nestedness but lower replacement than the mixed grazing regime. Third, does grazing intensity affect ANPP differently in the two management regimes? We hypothesized that the continuous grazing regime would increase soil compaction in heavily grazed patches and that this compaction would lead to lower ANPP than in the mixed grazing–mowing regime (Fig. 1).

Materials and Methods

Study Area

The study area is located in the Xilin River Basin, Inner Mongolia Autonomous Region of China, which is a typical semiarid grassland and is representative of the Eurasian steppe (Bai et al. 2004). Mean annual precipitation is 346 mm, with 60–80% of precipitation falling in the growing season (May–September). Mean annual temperature is 0.3°C, with mean monthly temperatures ranging from ~21.6°C in January to 19.0°C in July. The topography at our experimental site consists of flat block and sloped block, with elevation ranging from 1200 to 1280 m above sea level, and slopes with inclinations of <10° (Hoffmann et al. 2008), Leymus chinensis (grass) and Stipa grandis (grass) are the dominant species in the study area, together accounting for more than 50% of the total aboveground biomass. Other dominant species include Cleistogenes squarrosa (grass), Agropyron cristatum (grass), Achnatherum sibiricum (grass), and Carex korshinskii (sedge). Most rare species are forbs. In our study years, the ANPP of ungrazed plots (102 g/m²) was significantly lower than the 30-yr average value (186 g/m²), likely resulting from low precipitation in those years (246 and 288 mm in 2013 and 2014, respectively). A previous study at our experimental site found that prolonged drought can reduce the abundance of the dominant perennial species, but that grazing “affected species richness more than drought…” (Gao et al. 2009), even when rainfall was low. Thus, we discuss our results in the context of dry years, but further analysis about drought effects is beyond the scope of this paper.

Grazing experiment and grazing-induced patches

The experimental area was used for moderate sheep grazing for centuries by local herdsmen under a nomadic grazing regime (Hoffmann et al. 2008, 2016). Prior to the start of this experiment, grass swards recovered for two years with no grazing. At the end of the growing season in 2004, prior to beginning the experiment, swards in the entire area were cut to 3–5 cm in stubble height for hay (Wan et al. 2011). The experimental plots were established in June 2005 with a split-split plot in a random complete block design. Our data were collected in 2013 and 2014. Wan et al. (2011) provide a detailed description of the experimental design. In brief, the experiment was repeated in two topographic blocks (flat and sloped). In each topography, we had two management regimes (season-long continuous grazing and grazing and mowing alternated annually) as the main plot factor and seven levels of grazing intensity (GI: 0, 1.5, 3.0, 4.5, 6.0, 7.5, and 9.0 sheep/ha), which were randomly arranged within each management regime as the subplot factor. For convenience, we refer to the subplots as “plots” hereafter. The ungrazed plots (0 sheep/ha) had had no sheep grazing for the prior 10 yr. Each plot was 2 ha, except that the plot with 1.5 sheep/ha was enlarged to 4 ha to ensure a minimum of 6 sheep per plot. Our ecosystem-scale study required large land area (160 ha) and high levels of logistics, which limited our ability to replicate treatments to two plots per treatment (Ren et al. 2018). Correspondingly, we used regression- and ANCOVA-based approaches instead of an
ANOVA-based approach to analyze our data, taking advantage of multiple levels of grazing intensity and covering the shortage of replications. Also, the split-plot design considers effects on response variables of environmental factors that cannot be changed (i.e., topography here; Jones and Nachtsheim 2009). Additionally, the arrangement of our experimental site maintains spatial independence of the grazing treatments (Appendix S1: Fig. S1).

In the continuous grazing regime, the same sheep grazed in the plots continuously from June to September each year. In the mixed grazing–mowing regime, grazing and mowing were alternated annually between two plots: animals grazed June–September of one year in one plot, which was then ungrazed but mowed for hay in the middle of August the next year. The second plot was moved for hay in the first year and then grazed the next year. The data reported here were obtained during the grazing year of the mixed regime. In both management regimes, lightly and heavily grazed patches within the plots were visually distinguishable. Heavily grazed patches had nearly all available forage consumed, while lightly grazed patches were ungrazed or minimally defoliated (Ring et al. 1985, Ren et al. 2015). The areas of these patches in each plot were delineated using a GPS unit (Holux M-241; Holux Technology, Hsinchu, Taiwan).

Community structure, aboveground biomass, and productivity

To evaluate how management regime, grazing intensity, and patch type affected plant community composition and species diversity, we measured species abundance in July 2013 and 2014. For each plot, we randomly laid out five 1 × 1 m quadrats within lightly and heavily grazed patches. For ungrazed plots, we also randomly chose five quadrats. In each quadrat, plant species were identified and abundance (the number of individuals) of each species was counted by bunches (bunchgrasses) or stems (rhizomatous grasses). Further, to evaluate soil compaction, we measured soil hardness by using a Yamanaka-type soil hardness tester (Fujiwara Scientific, Japan), and we measured each quadrat five times and took the average of those measurements for each quadrat. Within each plot, we further established five grazing exclosures (3 × 3 m) randomly in early June prior to the start of sheep grazing for measuring ANPP of the whole plot. Within each exclosure, we estimated ANPP by clipping all plant material at ground level using a 1 × 1 m quadrat at the time of peak biomass in early August 2014. Fresh plant material from each quadrat was oven dried at 65°C for 48 h and weighed. Because June–August is the growing season for plants, the averaged total dry mass from five replicates in each plot was used to approximate annual ANPP (Bai et al. 2004).

Data analysis

All statistical analyses were performed using R 3.3.2 (R Core Team 2016). We assessed alpha diversity within lightly and heavily grazed patches within each plot, beta diversity between patch types within a plot, and whole plot diversity. For α diversity, all calculations were based on the average value of five quadrats for each patch type in each plot. For calculating whole plot diversity, we defined the whole community as a plot, including both lightly and heavily grazed patches. We used three indices to describe species diversity at patch and whole plot scales: (1) the number of species, S; (2) the exponential Shannon-Wiener index (e^H), \( H' = -\sum p_i \ln(p_i) \), where \( p_i \) represents the relative abundance of the \( i \)th species; and (3) species evenness: \( J = H'(\ln S)^{-1} \). The metric e^H gives the number of equally abundant species that would yield that value of \( H' \). For total β diversity, we calculated Bray-Curtis dissimilarity coefficients between lightly and heavily grazed patches in each plot based on species’ relative abundances (Anderson et al. 2011, Legendre and De Cáceres 2013). We combined species lists and abundances for all lightly and all heavily grazed patches within a plot to focus on β diversity as driven by patch type, rather than variation within patch types. We used similarity-based β diversity to guarantee its independence from α diversity and used e^H to make alpha, beta, and whole plot diversity accord with Whittaker’s multiplicative law, such that β diversity = whole plot diversity/α diversity (Jost 2007). In this formulation, whole plot diversity is conceptually similar to gamma diversity when assessing alpha and beta diversity across larger spatial gradients; we use the term “whole plot diversity,” however, to avoid confusion with regional species richness.
Further, we partitioned β diversity into its nestedness and replacement components using the betapart statistical package:
\[
\beta_{\text{total}} = \beta_{\text{replacement}} + \beta_{\text{nestedness}} = \frac{b+c}{2a+b+c} \left( \frac{c-b}{2a+b+c} \right) \left( \frac{a}{b+a} \right)
\]
where \(a\) was the number of shared species between patches, \(b\) was the number of species unique to the poorest patch, and \(c\) was the number of species unique to the richest patch (Baselga and Orme 2012, Baselga 2013, Legendre 2014). The nestedness component reflected in the degree to which the less diverse patch was a strict subset of the more diverse site, whereas the replacement component reflected changes in species identities between patches. To evaluate the effects of α diversity on whole plot diversity, we correlated α diversity (\(e^H\)) of lightly and heavily grazed patches, and their average value, with whole plot diversity (\(e^{fl}\)). To evaluate the effects of β diversity on whole plot diversity, we correlated total β diversity and its components with whole plot diversity (\(e^{fl}\)).

To reveal grazing effects on community composition, including dominant and rare species, we analyzed rank abundance curves and species composition. For the rank abundance curves, individual number was log10-transformed. For the five most abundant species, we compared the slope of regression lines of relative abundance vs. rank between the continuous grazing regime and the mixed grazing–mowing regime, using a t-test with the standard errors from the individual regressions. For species composition, we did non-metric multi-dimensional scaling (NMDS; Bray-Curtis distance) using species relative abundance data in each plot. To alleviate effects of dominance of abundant species, we transformed data by using its square root. We chose two dimensions with a stress value of 0.17, which allowed for clear interpretations. We also calculated NMDS by using untransformed data (see Appendix S1). Then, we used PERMANOVA to test for significant differences in species composition among management regimes, grazing intensities, and patch types, with 999 permutations. For each species, we calculated Pearson correlation coefficients (\(r\)) between relative abundance and scores of NMDS axes to identify which species were most responsible for the compositional changes within the treatment communities. For NMDS and PERMANOVA, we used the metaMDS and adonis functions of the vegan package in R (Oksanen et al. 2014).

Because we found no difference between topographic blocks, we have two spatial replications for each treatment and two years of data. Analyses of grazing effects on all response variables included four values for each treatment (i.e., two topographic blocks \times two years). First, we used a general linear model to examine effects of management regime and grazing intensity on each response variable with management regime, grazing intensity, and their interaction as fixed effects. Second, we used linear or non-linear regression models to determine relationships between grazing intensity and responses of species diversity in the continuous grazing and the mixed grazing–mowing regimes. Third, we used a priori contrasts to compare whether the responses differed between the two management regimes within the same grazing intensity.

**RESULTS**

Responses of species richness, species evenness, and Shannon-Wiener diversity to management regime and grazing intensity

The proportion of the area occupied by heavily grazed patches increased as grazing intensity increased, though more so for mixed grazing–mowing than for continuous grazing (Appendix S1: Fig. S2). In neither the grazing-only nor the mixed grazing–mowing treatments did patterns of species richness follow the unimodal patterns predicted by the IDH. Species richness in the continuous grazing regime decreased with increasing grazing intensity in both lightly grazed and heavily grazed patches and at the whole plot scale (Fig. 2). For example, 8% (~2 species) and 40% (~10 species) of species were lost at 1.5 and 9.0 sheep/ha, respectively, for the continuous grazing regime in whole plots. In contrast, species richness of the mixed grazing–mowing regime decreased as grazing intensity increased from 0 to 1.5 sheep/ha, but did not drop after that (Fig. 2c): 31% and 30% of species were lost at 1.5 and 9.0 sheep/ha, respectively, for the mixed grazing–mowing regime in whole plots. In both the continuous grazing and the
mixed grazing–mowing regimes, the lost species were mainly rare species (Appendix S1: Fig. S3; Tables S3, S4). This effect was strongest in the grazed-only plots, particularly with GI greater than or equal to 4.5 sheep/ha.

The interaction between management regime and grazing intensity indicated lower species evenness in the continuous grazing than in the mixed grazing–mowing regime, but only at moderate and high grazing intensity (4.5–9.0 sheep/ha; Fig. 2; Appendix S1: Table S1). The effects at the whole plot scale primarily arose from those in the heavily grazed patches. However, small reductions in evenness in continuously grazed treatments also occurred across the spectrum of grazing intensities in lightly grazed patches (main effect of management regime; Appendix S1: Table S1). The species abundance distribution showed that the mixed grazing–mowing regime resulted in more even distribution of the dominant species in both lightly and heavily grazed patches (shallower slopes; Appendix S1: Fig. S3), which would increase species evenness. In addition, lightly grazed patches had much more even

![Fig. 2. Responses of species richness, species evenness, and Shannon-Wiener diversity to management regime and grazing intensity at patch and whole plot scales. Each point is the mean value across year and topography (n = 4), with error bars denoting SE. Solid lines are linear or negative exponential regression between grazing intensity and response values and are only shown when significant. R^2 and P values indicate statistics for the regressions. Asterisk indicates significant difference (P < 0.05) between grazing and grazing–mowing regimes under the same grazing intensity. Abbreviations are G, the continuous grazing regime; GM, the mixed grazing–mowing regime; and UG, ungrazed plots.](image-url)
distribution of relative abundance across the dominant species than did heavily grazed patches, especially for the mixed grazing–mowing regime (Appendix S1: Fig. S3). This was because the most abundant species C. korshinskyi decreased in relative abundance, whereas other dominant species increased (Appendix S1: Table S3).

Shannon-Wiener diversity of the grazing–mowing regime was higher than the continuous grazing regime at the patch scale and the whole plot scale at moderate and high grazing intensities, showing the same patterns as species evenness, due to the interaction between management regime and grazing intensity (Fig. 2; Appendix S1: Tables S1, S2). As with species richness, the Shannon-Wiener diversity index did not follow predictions of the IDH with increasing grazing intensity. The Shannon-Wiener index under the continuous grazing regime decreased significantly with increasing grazing intensity at the patch and the whole plot scale, whereas it was unchanged from 1.5 to 9.0 sheep/ha in the mixed grazing–mowing regime (Fig. 2; Appendix S1: Table S1).

**Responses of β diversity to management regime and grazing intensity**

Total β diversity decreased with increasing grazing intensity, indicating grazing-induced species loss and smaller differences in species composition between lightly and heavily grazed patches (Fig. 3). While changes were negligible at low grazing intensities, total β diversity decreased 40% and 37% at 9.0 sheep/ha for the continuous grazing and the mixed grazing–mowing regimes, respectively. This increasing compositional similarity of lightly and heavily grazed patches was reflected in the replacement component of β diversity, which decreased significantly with increasing grazing intensity in both management regimes (Fig. 3b). This mainly resulted from the loss of different rare species in lightly and heavily grazed patches (Appendix S1: Tables S3, S4). Compared to the replacement component, grazing intensity increased the nestedness component of β diversity from low to moderate intensity, but decreased it from moderate to high intensity in both management regimes (Fig. 3c). Although only marginally significant (Appendix S1: Table S1), the continuous grazing regime tended to have a slightly higher nestedness component of β diversity than the mixed grazing–mowing regime in these relatively dry experimental years. Increases in the

![Fig. 3. Effects of management regime and grazing intensity on total β diversity, the replacement component, and the nestedness component. Each point is the mean value across year and topography (n = 4), with error bars denoting SE. Solid lines are quadratic or negative exponential regression between grazing intensity and response values. We found no significant differences between management regimes either overall (Appendix S1: Table S1) or at the same level of grazing (Appendix S1: Table S2). All symbols are derived as in Figure 2.](image-url)
nestedness component mean that species in less diverse patches were more closely subsets of those in more diverse patches.

**Relationships between α, β diversity and whole plot diversity**

We found that α diversity ($e^{H_1}$) contributed more to whole plot diversity ($e^{\beta_2}$) than did total β diversity in this system. Alpha diversity in both lightly and heavily grazed patches had a strong positive correlation with whole plot diversity, whereas the relationship of whole plot diversity with total β diversity was positive, but not quite significant (Fig. 4). The weak effects of β diversity likely occurred because the two components of β diversity had opposite relationships with whole plot diversity: While higher species turnover (replacement component of β diversity) increased with whole plot diversity, higher nest- edness between patches correlated with decreased whole plot diversity (Fig. 4e, f).

**Responses of community composition to management regime, grazing intensity, and patch type**

Compared to ungrazed plots, the continuous grazing regime changed the community composition more than did the mixed grazing–mowing regime. This shift primarily occurred along NMDS axis 1 in the continuous grazing regime ($P = 0.0010$; Fig. 5a). According to species-level analysis, six species were positively correlated with NMDS axis 1 and 12 species were negatively correlated with NMDS axis 1 (Fig. 5b). Therein, the continuous grazing regime reduced abundance of many palatable species, for example, *A. cristatum* (dominant), *C. squarrosa* (dominant), *S. grandis* (dominant), *Allium senescens* (rare), *Iris tenuifolia* (rare), *Dontostemon micranthus* (rare), and *Festuca ovina* (rare). On the contrary, heavily grazed patches increased abundance of unpalatable species, for example, *Lepidium apeidalum* (rare) and *Cnidoscolus nutans* (rare). Shifts in community composition with increasing grazing intensity were more subtle. In the continuous grazing regime, all intensities >0 are similar on NMDS axis 1, and the clearest shift downward on NMDS axis 2 is with GI = 9 (Fig. 5c). On the contrary, grazing intensity had smaller effects on community composition in the mixed grazing–mowing regime (Fig. 5d).

When using the untransformed data, the pattern of NMDS was similar to the results by using square-root-transformed data, although rare species had a smaller effect on community composition (Appendix S1: Fig. S4).

**Effects of management regime and grazing intensity on soil hardness and ANPP**

For both management regimes, low grazing intensity maintained ANPP at levels similar to ungrazed plots, whereas moderate to high grazing intensity reduced ANPP by 35–50% (Fig. 6). However, grazing effects on ANPP did not differ between the continuous grazing regime and the mixed grazing–mowing regime in dry experimental years (Fig. 6; Appendix S1: Table S1). For both management regimes, soil hardness increased with increasing grazing intensity in lightly and heavily grazed patches. Specifically, soil hardness of lightly grazed patches was similar between the continuous grazing regime and the mixed grazing–mowing regime (Fig. 6b). However, in heavily grazed patches, the continuous grazing regime had significantly higher soil hardness than did the mixed grazing–mowing regime at moderate and high grazing intensity (Fig. 6c).
DISCUSSION

Effects of management regime, grazing intensity, and patch type on $\alpha$, $\beta$, and whole plot diversity

Through the drought years, our results demonstrated that the mixed grazing–mowing regime was more beneficial for the maintenance of patch and whole plot diversity than the continuous grazing regime in semiarid grassland, particularly under moderate and high grazing intensity. First, species evenness was higher in the mixed grazing–mowing regime than in the...
Fig. 5. Non-metric multi-dimensional scaling (NMDS) ordination of community composition using square-root-transformed relative abundances. Comparisons between two management regimes (a), levels of grazing intensity (c, d), and patch type (e, f) within each management regime. The upper right panel (b) shows the species whose relative abundances correlated significantly with scores on NMDS1 and NMDS2. The numbers in brackets indicate correlation coefficients. See Appendix S1: Table S3 for plant Latin names.
continuous grazing regime. This difference mainly resulted from management impacts on dominant species. We found that the abundance of dominant species was distributed more evenly in the mixed grazing–mowing regime than in the continuous grazing regime. Indeed, many studies demonstrate that mowing can decrease species competition by preventing dominant species from reaching high population densities and foliage cover and result in increased species evenness (Fischer and Wipf 2002, Catorci et al. 2014, Lepš 2014). Second, Shannon-Wiener diversity was higher in the mixed grazing regime than in the continuous grazing regime under moderate and high grazing intensity. This difference was primarily caused by the higher species evenness in the mixed grazing–mowing regime than in the continuous grazing regime, rather than higher richness, because the difference in richness between continuous grazing and mixed grazing–mowing was relatively small. Previous studies have also found that mowing had positive effects on Shannon-Wiener diversity in a temperate grassland (Smith et al. 2018) and that responses of Shannon-Wiener diversity to grazing had the same pattern as species evenness (Török et al. 2016). However, in contrast to Török et al. (2016), we found a strong decline in Shannon-Wiener diversity with increased grazing intensity. The higher annual precipitation (550 mm) in their steppe than ours (346 mm) may have led to higher resistance of their plant community to grazing and hence caused the different responses (Xu et al. 2014). However, the richness differences between management regimes were smaller than we expected. This might have occurred because grazing effects on species richness depended on productivity (Milchunas and Lauenroth 1993, Cingolani et al. 2005a, Huston 2014). The dry and low productivity years of our experiment could limit plant growth and reduce the difference of species richness between the two management regimes. On the other hand, selective grazing by sheep, rather than generalist grazing, could similarly decrease plant species richness in both treatments, independent of productivity, through direct consumption of rare, palatable species (Wan et al. 2015). Directed experiments would be necessary to differentiate between these hypotheses.

Fig. 6. Effects of management regime and grazing intensity on ANPP (a), and soil hardness in (b) lightly and (c) heavily grazed patches. Each point is the mean value across year and topography ($n = 4$), with error bar denoting SE. The gray dashed line in (a) indicates the 30-yr (1980–2010) average ANPP in the ungrazed plots. Solid lines are linear and exponential regressions. Linear models for the response variables used management regime (MR), grazing intensity (GI), and interaction between them as fixed effects. Treatments (ANOVA) and differences between G and GM (a priori comparisons) are significant at $^*P < 0.05$; $^{**}P < 0.01$; and $^{***}P < 0.001$. All symbols are derived as in Figure 2.
In contrast to our expectation, the mixed grazing-mowing regime was not superior for the maintenance of total β diversity compared to the continuous grazing regime in the dry experimental years. For instance, the difference in total β diversity between the two management regimes was not significant under any grazing intensity. One possible reason was, compared to ungrazed plots, both the continuous grazing regime and the mixed grazing-mowing regime had large loss of rare species, as just described. Most rare species were not grazing-tolerant (Li et al. 2015). Hence, the deterministic exclusions of grazing-intolerant rare species likely reduced similarly across both management treatments (Segre et al. 2014, Socolar et al. 2016). Further, neither did the components of total β diversity, replacement and nestedness, differ significantly across management types. However, at intermediate grazing intensities the nestedness component tended to account for a higher proportion of total β diversity in the continuous grazing regime than in the mixed grazing regime. The increased nestedness indicated that heavily grazed patches were more close subsets of the species in lightly grazed patches under continuous than mixed grazing. Hence, conserving multi-site diversity may be accomplished by preserving lightly grazed patches with high α diversity in the continuous grazing regime, though this hypothesis should be tested at broader scales. Declines in nestedness at the high end of the grazing intensity spectrum, as well as continual declines in replacement and total β diversity across levels of grazing intensity, occurred because heavy grazing selects for different species, as indicated by shifts in community composition toward grazing-tolerant species, independent of management regime. Hence, lightly and heavily grazed patches became more similar in species composition as grazing intensity increased. A previous study also revealed that conservation management should aim to minimize nestedness (Wright and Reeves 1992). In addition, we found low grazing intensity could maintain total β diversity, whereas high grazing intensity decreased it, due to reduced replacement between patches. Our results were consistent with a recent synthesis study that found grazing decreased β diversity in unproductive or over-grazed habitats (Bloor and Fottier 2014).

Further, our results revealed that averaged α diversity rather than total β diversity had greater impacts on whole plot diversity in our experiment. Similarly, other studies in wet grasslands also have found that grazing can affect community scale diversity by altering small scale diversity, though the contribution of α diversity and β diversity can vary across communities (Marion et al. 2010). In our study, the positive but weak relationship between total β diversity and whole plot diversity may result from the opposite effects of the two β diversity components on whole plot diversity. For example, although higher replacement increased whole plot diversity, higher nestedness decreased it. In our study, selective grazing resulted in loss of palatable rare species first. The non-random loss of these species led to higher nestedness (Baselga 2012, Legendre 2014), decreasing whole plot diversity.

Contrary to IDH, species diversity did not increase at the moderate grazing intensity in our experiment. Multiple mechanisms could be responsible. One mechanism might be that responses of species diversity to grazing often depend on habitat productivity (Bakker et al. 2006, Huston 2014); the generally observed increases of species richness at medium grazing intensity may only happen in areas with high productivity, such as tallgrass prairie, by limiting light competition (Milchunas et al. 1988). However, our study highlights a second mechanism, selective grazing and patch formation, which could invalidate IDH. IDH predicts that grazing could reduce competition with dominant species in high productivity sites and increase diversity of subdominant and rare species compared to ungrazed treatments (Connell 1978, Olff and Ritchie 1998), but see also Fox (2013). Consistent with IDH, many studies have found that generalist grazers (usually larger and less selectively feeding herbivores, e.g., cattle) increased richness in high productivity sites because they reduced biomass of the most abundant species (Olff and Ritchie 1998, Bakker et al. 2006). In contrast, in our semiarid study site with comparatively lower productivity, selective grazing led to the loss of many rare species, even in lightly grazed patches at lower grazing intensities (see difference between ungrazed and GI 1.5 lightly grazed patches). These results are consistent with other studies finding that selective grazers (usually
smaller herbivores, such as the sheep in our experiment) decreased richness by selectively feeding on palatable forbs (Rook et al. 2004, Wan et al. 2015). Second, other patches were heavily grazed, with similar reductions in species richness across moderate to high grazing levels (Fig. 2b). These results suggest that, with selectively grazing sheep, the increased grazing intensity treatments did not result in an even distribution of intensity of grazing across locations within a plot. Rather, even low sheep densities led to formation of lightly and heavily grazed patches. Increased sheep grazing intensity primarily increased the area of heavily grazed patches, with secondary increases in grazing intensities within those patches.

**Effects of management regime, grazing intensity, and patch type on species composition**

At moderate and high grazing intensity, and during the comparatively dry years of this experiment, the mixed grazing–mowing regime was more beneficial for the maintenance of rare species than the continuous grazing regime. For example, the rank abundance curve showed that not only the number of rare species but also the abundances of subdominant species were consistently higher in the mixed grazing–mowing regime than in the continuous grazing regime at moderate to high grazing intensities. Consistent with our hypothesis, this was because the two management regimes had different effects on the creation and maintenance of heavily grazed patches. We found in this study that heavily grazed patches in the continuous grazing regime had smaller area (Appendix S1: Fig. S2) but higher soil compaction (Fig. 6) than they had in the mixed grazing–mowing regime. These results concur with other studies. Under a continuous grazing regime, livestock often repeatedly use heavily grazed patches created in former years because they prefer eating the new growth (Weber et al. 1998, Ren et al. 2015). Because of this increased use, continuous grazing also increased soil compaction more than rotational grazing (Vecchio et al. 2018). In our study, heavily grazed patches under continuous grazing showed stronger shifts in community composition than under mixed grazing–mowing, which could occur by two different, but non-exclusive, mechanisms. First, grazing-intolerant, rare species had lower abundances in the continuous grazing regime than in the mixed grazing–mowing regime; such rare species that are less tolerant of grazing are eliminated as grazing intensity increases in semiarid grassland with a long history of grazing (Milchunas et al. 1988). Second, repeated trampling led to greater soil compaction in the continuous grazing regime than in the mixed grazing–mowing regime, which could lead to the loss of rare species due to poor establishment and impeded root growth (Proffitt et al. 1995, Greenwood and McKenzie 2001). In our experiment, the mixed grazing–mowing regime lessened the intensity of grazing in heavily grazed patches created in previous years and reduced repeated eating and trampling. Hence, impacts of consumption and soil compaction of heavily grazed patches on rare species were lower in the mixed grazing–mowing regime than in the continuous grazing regime.

For lightly grazed patches, we found that rare species in the continuous grazing regime also decreased more than in the mixed grazing–mowing regime, but only at moderate to high grazing intensity. The opposite was true at low grazing intensity. This might occur because grazing disturbance was lower in lightly grazed patches under the continuous grazing regime than in the mixed grazing–mowing regime, because sheep avoided plants with higher fiber content (Ren et al. 2015). The different responses of two management regimes to grazing further supported the selective mechanism described above, which suggested that even low grazing with selective species can lead to loss of rare, palatable species, in contrast to the predictions of IDH, which are based on even distribution of disturbance by generalist grazers.

Our results also revealed that the mixed grazing–mowing regime was more beneficial for the maintenance of abundant, not just rare, palatable species than the continuous grazing regime. According to the NMDS results, the palatable dominant grasses (e.g., *A. cristatum*, *C. squarrosa*, and *S. grandis*) had higher relative abundance in the mixed grazing–mowing regime than in the continuous grazing regime. A study that used the same experimental design found this pattern arose because these species had significantly lower density of reproductive tillers in the continuous grazing regime than the ungrazed plots,
but had no difference between the mixed grazing–mowing regime and the ungrazed plots (Wan et al. 2011). Our results were consistent with previous studies in steppe grasslands, which also found that the continuous grazing regime reduced the abundance of palatable species, while a management regime with periodic resting of grasslands could promote the abundance of palatable species (Cingolani et al. 2005b, Zhang et al. 2018). However, all these studies used sheep in the experiments. Thus, selective grazing might result in different responses of species abundance to grazing between management regimes than when using generalist grazers, such as cattle, where palatable species abundance could persist under the continuous grazing regime (Sternberg et al. 2015). At the same time, benefits of mixed grazing and mowing in our study occurred primarily at moderate to high grazing intensities. But these benefits were relative—high grazing intensities (7.5–9.0 sheep/ha) still caused large declines in species richness and beta diversity even in the mixed grazing–mowing management.

**Effects of management regime and grazing intensity on ANPP**

In our dry experimental years, grazing intensity had a larger effect on ANPP than did management regime. Low grazing intensity maintained ANPP and high grazing intensity decreased ANPP. Consistently, we also found that ANPP declined when grazing intensity exceeded 3.0 sheep/ha in our 2009 experiment (Li et al. 2017). Such reduction in ANPP might result from stronger nutrient limitation caused by enhanced soil compaction. With increased grazing intensity, soil compaction increased in both lightly and heavily grazed patches, but most strongly in the latter. Many studies have shown that soil water and nitrogen availability decreased significantly with increasing soil compaction in semiarid steppe (Steffens et al. 2008, Zhao et al. 2011), which could decrease productivity. However, different from the prediction of the grazing optimization hypothesis, our results revealed that ANPP did not increase under moderate grazing intensity. On the one hand, previous research indicated that the enhancement of ANPP by grazing depended on resource availability (De Mazancourt et al. 1998). However, our experiment was carried out in years with reduced precipitation, which could decrease ANPP by limiting plant compensatory growth (Maschinski and Whitham 1989). Differences in effects of management regime on ANPP might be masked by the low precipitation year as well. On the other hand, and more importantly, the decline in ANPP might result from a positive feedback between livestock and heavily grazed patches. For instance, previous studies indicated that heavily grazed patches had higher runoff and lower soil water availability than lightly grazed patches in semiarid landscapes (Ludwig et al. 2005, Veldhuis et al. 2014). Thus, the increased limitation of water availability in heavily grazed patches might reduce ANPP at the whole plot scale.

**Conclusions and implications**

Several studies have reported general patterns of grassland biodiversity and productivity response to grazing in comprehensive reviews and meta-analyses (e.g., Milchunas et al. 1988, Bakker et al. 2006). However, consequences of grazing-induced patches in grasslands have not been fully explored (Bloor and Pottier 2014, Ren et al. 2015). Overall, we found that patch formation driven by selective grazing led to different patterns from those predicted by the IDH. Instead of increased grazing intensity leading to higher diversity at intermediate levels of grazing, as might be expected with even grazing pressure throughout a plot by generalist herbivores, we found decreased diversity due to loss of rare palatable species, even at light grazing intensity. These results have important implications for conservation efforts aimed at maintaining populations of rare species: Even light to moderate grazing, no matter what the management regime, leads to rare species loss. This suggests that maintaining some ungrazed areas, or having a mix of areas with generalist and specialist herbivores (Liu et al. 2015), will be necessary to maintain population reservoirs of these species. However, the extent of species loss interacted with management type. The mixed grazing–mowing regime was more beneficial for the maintenance of species diversity and community composition than the continuous grazing regime under moderate to high grazing intensity. Furthermore, although they had the same effects on
ANPP, the continuous grazing regime suffered higher risk of degradation because of its higher soil compaction. Here, we highlight a patch mechanism that needs to be considered in future grazing research. In brief, continuous grazing resulted in repeated grazing disturbance (i.e., eating and trampling) at heavily grazed patches created in previous years, leading to higher grazing disturbance there. However, the mixed grazing–mowing regime reduced repeated grazing, leading to relatively lower grazing disturbance in heavily grazed patches. According to our results, we recommended lowering grazing intensity overall and using the mixed grazing–mowing regime for long-term grassland management in semiarid grasslands.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3547/full