



LETTER

Grazing-induced biodiversity loss impairs grassland ecosystem stability at multiple scales

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Funding information

National Key Research and Development Program of China, Grant/Award Number: 2016YFC0500503; the Natural Science Foundation of China, Grant/Award Number: 31988102 and 31870505; the Open Project Program of 'Ministry of Education Key Laboratory of Ecology and Resources Use of the Mongolian Plateau', Grant/Award Number: KF2020003

Editor: Ian Donohue

Abstract

Livestock grazing is a major driver shaping grassland biodiversity, functioning and stability. Whether grazing impacts on grassland ecosystems are scale-dependent remains unclear. Here, we conducted a sheep-grazing experiment in a temperate grassland to test grazing effects on the temporal stability of productivity across scales. We found that grazing increased species stability but substantially decreased local community stability due to reduced asynchronous dynamics among species within communities. The negative effect of grazing on local community stability propagated to reduce stability at larger spatial scales. By decreasing biodiversity both within and across communities, grazing reduced biological insurance effects and hence the upscaling of stability from species to communities and further to larger spatial scales. Our study provides the first evidence for the scale dependence of grazing effects on grassland stability through biodiversity. We suggest that ecosystem management should strive to maintain biodiversity across scales to achieve sustainability of grassland ecosystem functions and services.

KEYWORDS

asynchrony, grazing intensity, herbivory, metacommunity, scale dependence, sheep

INTRODUCTION

Grasslands occupy more than one-third of Earth's terrestrial land surface and support about 40% of global agricultural domestic products, making them the largest coupled human-natural systems on Earth (Herrero et al., 2013). The sustainable delivery of functions and services by grasslands is critical for human society and

wildlife living upon it. However, human activities are altering Earth's environment with extreme weather events becoming more frequent worldwide, which threatens the ability of grassland ecosystems to reliably provide functions and services to humanity (Fetzel et al., 2017; Liang & Gornish, 2019; Sloat et al., 2018). Understanding the stability of grassland ecosystems in the face of anthropogenic environmental changes is

thus critical for sustainable ecosystem management and decision-making.

Livestock grazing is the most intensive land-use activity in grasslands, which presents a major driver shaping the biodiversity, functioning and stability of grasslands (Filazzola et al., 2020; Koerner et al., 2018; Wang et al., 2019a). A growing number of experiments have examined the effects of grazing on grassland community stability (Beck et al., 2015; Bluthgen et al., 2016; Ganjurjav et al., 2019; Hallett et al., 2017; Post, 2013; Qin et al., 2019). In these studies, stability was measured as the temporal invariability of a particular ecosystem property, for example, the ratio of mean community biomass to its interannual standard deviation. These studies revealed differential effects of grazing on grassland community stability, including positive (Beck et al., 2015; Hallett et al., 2017; Post, 2013), neutral (Bluthgen et al., 2016; Ganjurjav et al., 2019) or negative (Qin et al., 2019) effects. Such mixed results may be understood from the effects of grazing on species diversity. A large body of experimental and theoretical work has demonstrated that biodiversity increases community stability (Loreau, 2010; Tilman et al., 2014) because asynchronous responses among species to environmental fluctuations (species asynchrony) can offset each other and hence reduce ecosystem-level fluctuations (Yachi & Loreau, 1999). Previous studies have shown that grazing could either increase or decrease species diversity depending on the type and intensity of grazing (Collins et al., 1998; Filazzola et al., 2020; Wang et al., 2019a). Such idiosyncratic responses of species diversity to grazing may be responsible for the differential effects of grazing on grassland community stability.

Although experimental studies have significantly improved our understanding of the functional consequences of grazing, they have mostly focused on a particular spatial scale, usually much smaller than the scale of ecosystem management (Gonzalez et al., 2020; Isbell et al., 2017). The practical implications of grazing experiments rely on whether findings from such experiments at small scales can be extrapolated to larger scales. In grazing systems, herbivore activities can significantly modify the landscape and alter habitat heterogeneity at different scales (Adler et al., 2001; de Bello et al., 2007; Olff & Ritchie, 1998). For instance, large herbivores can reduce spatial heterogeneity in soil nutrients and their mineralization by trampling at fine scales (0.1–2 m), increase patchiness and thus spatial heterogeneity in soil nutrients by selective foraging at broader scales (5–30 m) and spatially redistribute and homogenize nutrients through metacommunity processes at landscape scales (100–10,000 m) (Adler et al., 2001; Augustine & Frank, 2001; Pausas & Bond, 2020). Such scale-dependent grazing effects on habitat heterogeneity could translate into differential effects of grazing on species diversity at different scales (Ben-Hur & Kadmon, 2020; Tonn et al., 2019). However, whether grazing affects stability differently at

different scales and whether such effects are mediated by biodiversity changes across scales remain largely unknown.

Recently, new theory has been developed to study ecosystem stability and its relationship with biodiversity across scales (Wang & Loreau, 2014, 2016), which provides an ideal theoretical framework to examine the potential scale dependence of grazing effects on stability. This framework proposes consistent measures of stability (i.e. temporal invariability) across organizational levels and spatial scales (Figure 1). Specifically, in a landscape consisting of many local communities, *species stability* is defined as the average of local population stability weighted by population abundance (e.g. density, biomass, etc.) across species within local communities, *α stability* is defined as a weighted average of ecosystem stability across local communities and *γ stability* is defined as the stability of total ecosystem function at larger spatial scales (i.e. a landscape or aggregation of communities) (Figure 1). The insurance hypothesis predicts that asynchronous dynamics among species (*species asynchrony*) can enhance local community stability (i.e. *α stability*) and asynchronous dynamics across local communities (*spatial asynchrony*) can enhance community stability at larger scales (i.e. *γ stability*) (Loreau et al., 2003; Wang & Loreau, 2014; Yachi & Loreau, 1999). Consequently, stability increases consistently from species to local communities and further to larger spatial scales, due to the insurance effects by species and spatial asynchrony (Wang et al., 2019b).

Metacommunity theory predicts that biodiversity, both local species diversity (*α diversity*) and spatial turnover of species (*β diversity*), can provide insurance effects by increasing species and spatial asynchrony, respectively (Wang & Loreau, 2016). Many experiments have shown the positive effect of *α diversity* on species asynchrony (Hautier et al., 2014; Hector et al., 2010; Tilman et al., 2006), but the relationship between *β diversity* and spatial asynchrony is in its infancy. Whereas an earlier empirical study failed to detect a significant relationship across sites with varying environmental conditions and sampling regimes (Wilcox et al., 2017), two recent studies that used global datasets of experimental and natural grassland communities and better controlled potential confounding factors confirmed the positive effects of *β diversity* on spatial asynchrony (Hautier et al., 2020; Wang et al., 2021). In addition, metacommunity theory also predicts that *α diversity* can either increase or decrease spatial asynchrony, depending on the context of spatial environmental correlation and species responses (Wang & Loreau, 2016), but so far this relationship has rarely been investigated.

In this study, we conducted a grazing experiment to quantify the impact of grazing intensity on stability at different scales and assess whether these effects are mediated by changes in plant diversity. By 'scale', we consider both spatial scales (i.e. local and larger spatial scales)

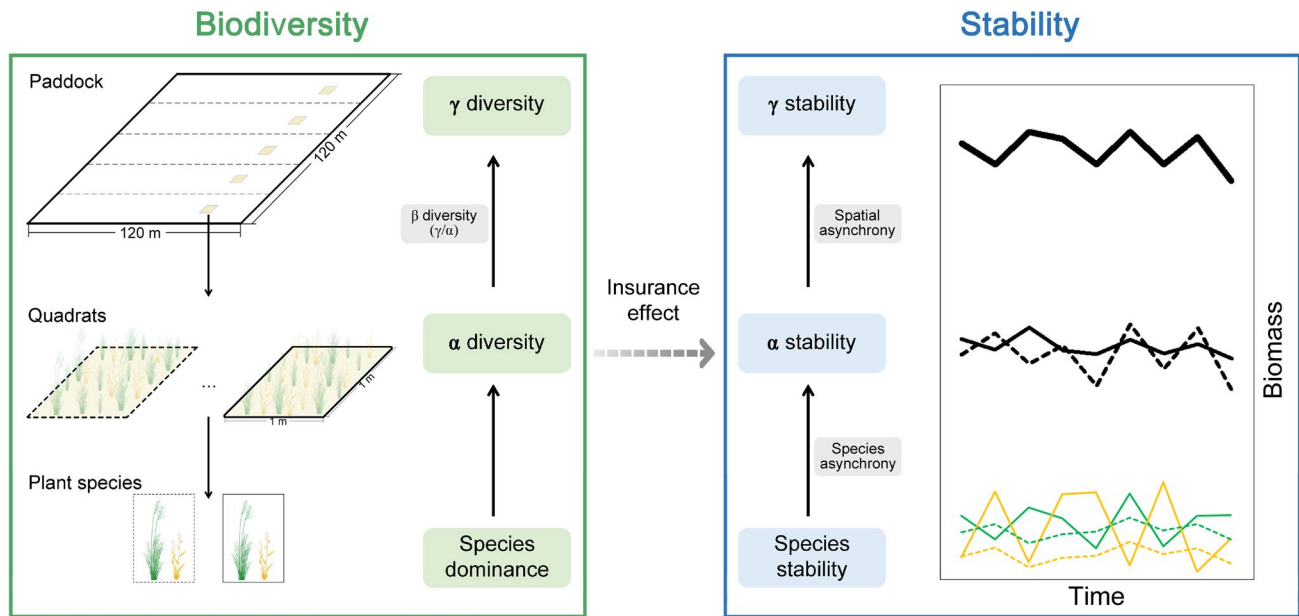


FIGURE 1 A theoretical framework of biodiversity and stability across scales illustrated with our experiment. Within each paddock ($120 \times 120 \text{ m}^2$), five local communities (1-m^2 quadrat) were sampled. We regard each quadrat as the local (α) scale and aggregation of the five quadrats as the larger (γ) spatial scale. Species diversity was quantified at both α and γ scales and β diversity was defined as the ratio of γ diversity to α diversity. Ecosystem stability is defined as the mean of an ecosystem function divided by its standard deviation through time across organizational levels (i.e. from species to community) and spatial scales (i.e. from local to larger spatial scales). Theoretically, stability at larger spatial scale (γ stability) is determined by three components, namely *species asynchrony*, *species asynchrony* and *spatial asynchrony*. At the local scale (i.e. quadrats), asynchronous dynamics among species (i.e. *species asynchrony*) leads to a high α stability (solid black line). At the large spatial scale (i.e. paddock), asynchronous fluctuations between local communities (i.e. *spatial asynchrony*) contribute to increasing γ stability. Biodiversity can provide insurance effects by increasing species asynchrony and spatial asynchrony, which enhance stability from species to local communities and further to larger spatial scales

and organizational levels (i.e. species- and community-levels). In our experiment, the local (α) and larger (γ) spatial scales correspond to our sampling quadrat ($1 \times 1 \text{ m}$) and paddock ($120 \times 120 \text{ m}$), respectively (Figure 1). We hypothesized that grazing influences stability at multiple scales by changing local biodiversity and spatial species turnover (i.e. α and β diversity). These effects will alter species asynchrony and spatial asynchrony that govern the scaling of stability from species to local communities and further to larger spatial scales (Figure S1). To address this hypothesis, we examined the following two questions: (1) How does grazing influence biodiversity and stability at different scales? (2) Are the effects of grazing on stability across scales mediated by grazing-induced biodiversity changes through their insurance effects (i.e. species and spatial asynchrony)?

MATERIAL AND METHODS

Study site

The study site is located at the Xilin Gol Grassland Nature Reserve, Inner Mongolia, China ($44^{\circ}08'N$, $116^{\circ}19'E$, 1,129 m) (Figure S2a). The biome type is the typical steppe grassland, which is dominated by rhizome grass (*Leymus chinensis* (Trin.) Tzvel.) and bunchgrass

(*Stipa grandis* P. Smirn) (Liang et al., 2019). Soil taxonomy was classified as the Calcic-Orthic Aridisol based on the USDA soil classification. The study area is characterized as semiarid climate (BSk) in the Köppen climate classification. During the past six decades, the mean annual air temperature (MAT) was $2.6 \pm 1.1^{\circ}\text{C}$ and mean annual precipitation (MAP) was $266.9 \pm 84.2 \text{ mm}$ (mean \pm SD), with more than 90% of the precipitation falling in the growing season (<http://data.cma.cn/>). Between 2013 and 2018, during which our experiment was run, the MAT was $4.1 \pm 0.7^{\circ}\text{C}$ and the MAP was $282.8 \pm 79.6 \text{ mm}$ (Liang et al., 2021).

Grazing experiment and plant sampling

In 2011, we fenced 12 equal-sized ($120 \times 120 \text{ m}$) paddocks to exclude natural grazing and implemented four grazing intensity treatments from 2013 to 2018, including 0, 2, 4 and 8 sheep·ha⁻¹, referred to as no- (NG), low- (LG), medium- (MG) and high-grazing (HG), respectively (Figure S2b). Each treatment had three replicates. We implemented sheep grazing in four bouts (i.e. four grazing events) during the growing season of each year, from June through September. Each bout was exposed to a particular treatment for 21 days, starting from the beginning of each month. Plant species biomass data were

collected in the last week of each month (i.e. 9–10 days after grazing) since June 2014. To reduce the influence of transient dynamics, we had not collected data in 2013. More detailed experimental descriptions can be found in Liang et al., (2019, 2021).

We regarded each paddock (120 × 120 m) as a community at the larger spatial scale, which consisted of five subplots (120 × 20 m) (Figure S2c). We placed one 1-m² quadrat in each subplot, such that the five quadrats laid out a south–north transect that is ~30 m away from an east-side fence boundary. For each subplot, we used scissors to clip the residual living aboveground tissue of all vascular plants (i.e. green plant biomass) above the soil surface in a quadrat, which was used to represent the community at the local spatial scale. After these tissues of plants have been oven-dried at 65°C in 48 h, we weighed them to estimate biomass for each species (g·m⁻²). We collected these data in June, July, August and September between 2014 and 2018. In total, we measured more than 7000 plant species biomass values in 1200 quadrats from 2014 to 2018, that is 5 years × 4 months (or bouts) × four treatments × three replicates × five quadrats.

Biodiversity, stability and asynchrony across scales

We used abundance-based metrics to calculate species diversity across scales (Figure 1 and S2c). At the local spatial scale (e.g. a local community l), we calculated the Simpson index: $\phi_l = \sum_i^S p_{il}^2$, where p_{il} represents the relative biomass of species i in the local community l and S is the number of species in the local community l . We then defined α diversity as the inverse of the weighted average of Simpson index: $\alpha_{simp} = 1 / \sum_{l=1}^5 \omega_l \phi_l$, where ω_l is the ratio of total biomass of the local community l to that of the aggregate community (i.e. aggregation of the five quadrats) at the larger scale (Wang & Loreau, 2016). The γ diversity was defined as $\gamma_{simp} = 1 / \sum_i p_i^2$, where $p_i = \sum_{l=1}^5 \omega_l p_{il}$ denotes the relative abundance of species i in the aggregate community at the larger scale. β diversity was defined multiplicatively, that is $\beta_{simp} = \gamma_{simp} / \alpha_{simp}$. To test the robustness of our results, we also calculated the Bray–Curtis dissimilarity among the five quadrats in each plot as an alternative measure of β diversity. We also calculated species richness at the local quadrat (α_{rich}) and larger (γ_{rich}) scales and the multiplicative beta diversity as: $\beta_{rich} = \gamma_{rich} / \alpha_{rich}$.

Furthermore, we defined species stability, as well as community stability at α and γ scales (Wang et al., 2019b; Wang & Loreau, 2014). We calculated stability by temporal invariability, that is the ratio of mean to standard deviation, which characterizes the capacity of ecosystems in maintaining their functioning in a fluctuating environment (Liang et al., 2021). Species stability was defined as the weighted average of local species stability across species and local communities; α stability was calculated

as the weighted average of community stability across local communities; γ stability was calculated as the community stability at a larger spatial scale (Figure 1). The mathematical formulas for these definitions are (Wang et al., 2019b):

$$\text{Species stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sum_{i,k} \sqrt{v_{ii,kk}}} \quad (1)$$

$$\alpha \text{ stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sum_k \sqrt{\sum_{i,j} v_{ij,kk}}} \quad (2)$$

$$\gamma \text{ stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sqrt{\sum_{i,j,k,l} v_{ij,kl}}} \quad (3)$$

where $\mu_{i,k}$ denotes the temporal mean of the biomass of species i in local community k and $v_{ij,kl}$ denotes the covariance between species i in local community k and species j in local community l .

The spatial stability framework shows how asynchrony among lower-level components (e.g. species or communities) is key to the scaling of stability (Lamy et al., 2019; Wang et al., 2019b). In the light of this framework, we defined *species asynchrony* as the ratio of α stability to species stability, which captures the incoherence in population dynamics among species within local communities; we also defined *spatial asynchrony* as the ratio of γ stability to α stability, which captures the incoherence in community dynamics among local communities. As such defined, γ stability can be expressed as the product of *species stability*, *species asynchrony* and *spatial asynchrony*. Lastly, we defined *total asynchrony* as the product of *species asynchrony* and *spatial asynchrony*, which quantifies the total insurance effect provided by species and spatial asynchrony from local species to communities at larger spatial scales. More details about the equations of the stability and synchrony indices can be found in Wang et al., (2019b).

Statistical analysis

To assess the effects of grazing on biodiversity and stability of plant communities at multiple scales (our first question), we ran linear mixed-effects models (MEMs) using the R package *lme4* (Bates et al., 2015). In these models, the fixed effect was *grazing intensity* and random effects were *month/year* and *month* for examining biodiversity and stability (including asynchrony), respectively (Table S1). To facilitate comparison of effect sizes of grazing on these biodiversity and stability metrics, we used the natural log-transformed response variables. We used the Fligner–Killeen test to test homogeneity of variances among four grazing intensities; if homoscedasticity was

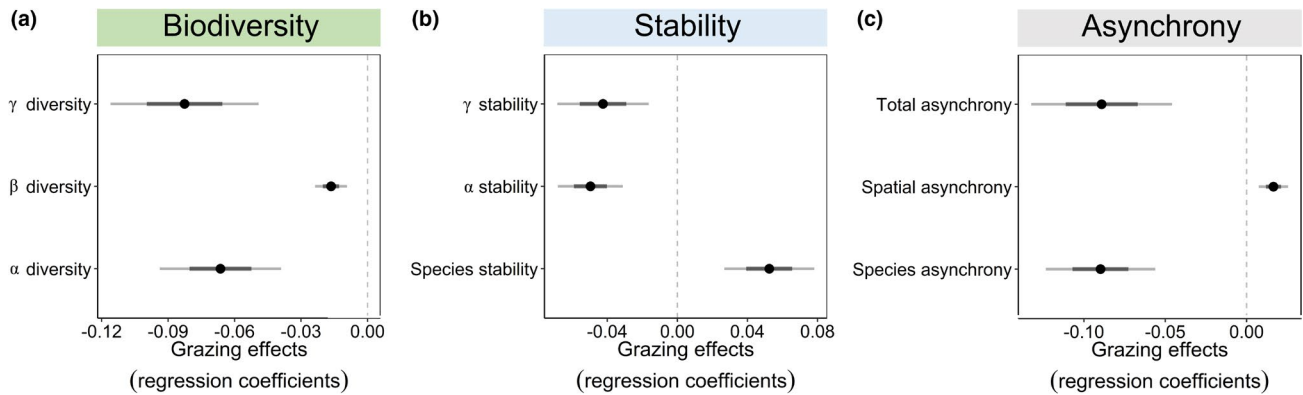


FIGURE 2 Grazing effects on biodiversity, asynchrony and stability at multiple scales. Shown are the regression coefficients from linear mixed-effects models, which quantify the effects of increasing grazing intensity on (a) biodiversity (α diversity in 1-m² quadrats, $F_{1,10} = 22.58$, $p = 0.0008$; γ diversity in 120 × 120 m² paddock, $F_{1,10} = 23.50$, $p = 0.0007$; β diversity (γ/α), $F_{1,10} = 20.12$, $p = 0.0012$), (b) stability metrics (species stability, $F_{1,10} = 16.01$, $p = 0.003$; α stability, $F_{1,10} = 27.50$, $p = 0.0004$; γ stability, $F_{1,10} = 10.17$, $p = 0.010$) and (c) asynchrony metrics (species asynchrony, $F_{1,10} = 27.35$, $p = 0.0004$; spatial asynchrony, $F_{1,10} = 12.81$, $p = 0.005$; total asynchrony = species asynchrony × spatial asynchrony, $F_{1,10} = 16.27$, $p = 0.002$). The darker bar denotes the standard error and the lighter bar represents the 95% confidential interval. Here, species diversity was defined by the reverse of Simpson index that incorporates both the number and abundance of species. The repeated-measurement ANOVA and Tukey's range test for multiple comparisons under four grazing intensities are provided in Tables S4 and S7 and Figures S3, S8 and S9, respectively

not met, we added weights for MEMs using *gls()* function in R (Zuur et al., 2010). Considering the autocorrelations among observations through time, we compared models without autocorrelation structure to MEMs including a first-order autoregressive model (AR (1)). All these MEMs gave similar results and we thus chose the best fit model based on the lowest Akaike information criterion (AIC). We used the package “MuMIn” to calculate the marginal R^2 (R^2_m), which quantified the proportions of model variation explained by the fixed effect (Nakagawa & Schielzeth, 2013). As a test of robustness, we ran similar MEMs using non-transformed response variables and *grazing intensity* as a categorized variable (GI: NG, LG, MG and HG) to compare effect sizes among different grazing intensities using Tukey's range test. We also performed repeated-measures ANOVA to test whether the main effects of *grazing intensity* on these variables vary with *year* and *month* or any interactions. *Grazing intensity* explained the largest proportion of variance in total of biodiversity (except for plant richness) and stability metrics (Tables S3–S7).

To examine how changes in biodiversity mediate the effects of grazing on stability and asynchrony at different scales (our second question), we first used MEMs to test the relationships between diversity and asynchrony and then developed a structural equation model (SEM) to illustrate the different pathways through which grazing influences γ stability. In the MEMs, the response variables are species or spatial synchrony and the fixed effect was α or β diversity and random effects were *grazing intensity* and *month* (Table S2). Specifically, we tested the relationships of species asynchrony with α diversity, of spatial asynchrony with α or β diversity and of total asynchrony with γ diversity. For the relationship of spatial asynchrony with α or β diversity, we ran partial linear

MEMs by first running a MEM between spatial asynchrony and α diversity (β diversity) and then extracting the residuals of spatial asynchrony and testing their relationship with β diversity (α diversity) using MEMs (with *grazing intensity* and *month* as random factors). We then constructed a SEM to quantify the different pathways between grazing intensity and γ stability. In the light of recent theory, we constructed a hypothesized SEM that characterized the effect of grazing on species stability, species asynchrony and spatial asynchrony via altering species dominance, α and β diversity, which propagated to community stability at local and larger scales (Figure S1; Wang et al., 2019b). The hypothesized SEM was fitted with linear MEMs (with *month* as the random effect) using the R package *piecewiseSEM* (Lefcheck, 2016). We used Shipley's test of *d*-separation to ensure that we did not miss any potential pathways (e.g. direct effects of grazing on γ stability) and chose the final model that had the lowest AIC. Based on the fitted SEM, we calculated the net effects of grazing on stability at different scales by summing up the direct and indirect effects along all pathways (Grace, 2006). All analyses were programmed in R v 3.6.0 (R Development Core Team, 2019).

RESULTS

Grazing effect on biodiversity and stability across spatial scales

Increasing grazing intensity decreased plant species diversity at both local (α diversity; $F_{1,10} = 22.58$, $p = 0.0008$) and larger (γ diversity; $F_{1,10} = 23.50$, $p = 0.0007$) spatial scales (Figure 2 and S3a). Grazing also reduced β diversity (Figure 2a, $F_{1,10} = 20.12$, $p = 0.0012$), regardless of the

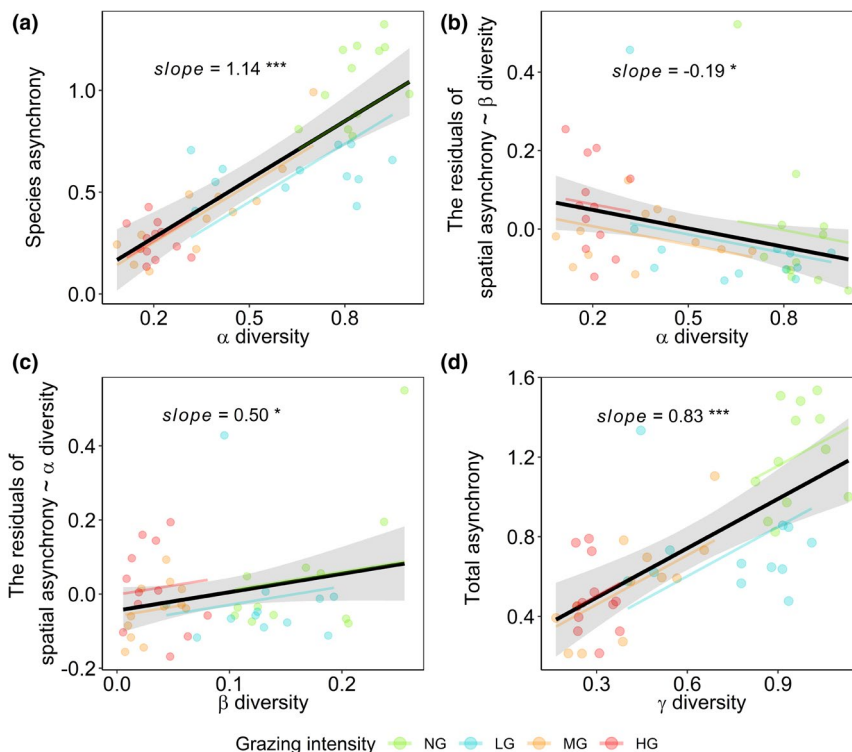


FIGURE 3 Relationships between asynchrony and biodiversity: (a) species asynchrony and α diversity ($R^2_m = 0.68$, $F_{1,35} = 44.83$, $p < 0.0001$), (b) spatial asynchrony and α diversity after the effect of β diversity on spatial asynchrony was controlled ($R^2_m = 0.11$, $F_{1,35} = 5.51$, $p = 0.025$), (c) spatial asynchrony and β diversity after the effect of α diversity on spatial asynchrony was controlled ($R^2_m = 0.06$, $F_{1,35} = 3.18$, $p = 0.083$) and (d) total asynchrony and γ stability ($R^2_m = 0.48$, $F_{1,35} = 22.90$, $p < 0.0001$). Information about the model fit is provided in Tables S8 and S9. Each point represents values for a paddock at a given grazing intensity and particular month. Black line represents the overall relationship from a linear mixed-effects model (with the shaded areas denoting the 95% confidence intervals) and the coloured lines indicate random-effect variations for no-grazing (NG, green), low-grazing (LG, blue), medium-grazing (MG, orange) and high-grazing (HG, red) intensities. The significant level: * $p < 0.1$; ** $p < 0.01$; *** $p < 0.0001$

diversity metrics used (Figure S5, e.g. the Bray–Curtis dissimilarity). Compared to the no-grazing (NG) treatment, α , β and γ diversities were decreased on average by 41%, 12% and 49%, respectively, in the high-grazing (HG) treatment (Figure S3). The reduction of plant species diversity was due to a shift in species composition under grazing, but not to a reduction in the number of species (Figure S4). Specifically, grazing increased the relative abundance of the dominant species, that is *S. grandis* across the study area (Figure S5a, $F_{1,10} = 16.09$, $p = 0.003$), which decreased α diversity and β diversity due to spatial homogenization. We also found that biodiversity metrics exhibited temporal variations that are potentially driven by environmental fluctuations, but overall grazing intensity alone explained the largest proportion of variance in plant diversity (Tables S4 and S5).

At the species level, increasing grazing intensity increased the stability of the dominant species (Table S7, $F_{1,10} = 10.38$, $p < 0.0001$). This is because grazing reduced the temporal standard deviation of the biomass of the dominant species (Figure S6d, $F_{1,10} = 11.38$, $p = 0.007$) but did not affect its temporal mean (Figure S6c, $F_{1,10} = 1.33$, $p = 0.277$). Such increased stability of the dominant species led to increased average species stability (Figure 2c, $F_{1,10} = 16.01$, $p = 0.003$). In contrast, grazing decreased

community stability at both local (α stability: $F_{1,10} = 27.50$, $p = 0.0004$) and larger (γ stability: $F_{1,10} = 10.17$, $p = 0.010$) spatial scales (Figure 2c). Compared to those in the NG treatment, species stability was on average 55% higher, α stability was 29% lower and γ stability was 24% lower in the HG treatment (Figure S8). Such differential effects of grazing on stability were explained by its effect on asynchrony (Figure S10 and Table S8). Grazing significantly decreased species asynchrony (Figure 2b, $F_{1,10} = 27.35$, $p = 0.0004$) but increased spatial asynchrony (Figure 2b, $F_{1,10} = 12.81$, $p = 0.005$). Specifically, species asynchrony was 55% lower and spatial asynchrony was 13% higher in the HG treatment, compared to those in NG. From local species to communities at larger spatial scales (i.e. aggregate communities), species and spatial asynchrony together contributed to enhancing stability by 242% in the NG treatment, but their contribution was reduced to only 69% in the HG treatment (Figure S9).

Biodiversity-mediated effects of grazing on asynchrony and stability across scales

The effects of grazing on stability were mediated through effects on biodiversity, which impacts asynchrony at

different scales. At the local spatial scale, species asynchrony was positively related to α diversity (Figure 3a, $R^2_m = 0.68$, $F_{1,35} = 44.83$, $p < 0.0001$) and at the larger scale, spatial asynchrony was associated with both α and β diversities (Figure 3b and S9). Specifically, spatial asynchrony was negatively related to α diversity after the effect of β diversity was controlled (Figure 3b, $R^2_m = 0.11$, $F_{1,35} = 5.51$, $p = 0.025$) and it was positively related to β diversity after the effect of α diversity was accounted for (Figure 3c, $R^2_m = 0.06$, $F_{1,35} = 3.18$, $p = 0.083$). These relationships were robust to different metrics of β diversity (Figure S12 and Table S9). Combined, total asynchrony was positively related to γ diversity (Figure 3d, $R^2_m = 0.48$, $F_{1,35} = 22.90$, $p < 0.0001$). Therefore, by decreasing species diversity at different scales, grazing impaired species and spatial asynchrony and thus the insurance effects for community stability at larger spatial scales.

We used a SEM to disentangle the various pathways through which grazing influenced γ stability. Specifically, we examined how grazing affected the three components of γ stability (= species stability \times species asynchrony \times spatial asynchrony) by altering species diversity (Figure S1). Our final SEM showed that an increase of grazing intensity increased the relative abundance of the dominant species, which led to a higher stability of the dominant species and the average species stability (Figure 4). However, by increasing the dominant species abundance, grazing decreased both α and β diversities. Decreased α diversity in turn decreased species asynchrony but increased spatial asynchrony. Decreased β diversity weakened spatial asynchrony. Combining all these indirect pathways, grazing led to increased species stability (total effect size or TES = 0.462), but decreased

community stability at both local (TES = -0.298) and larger (TES = -0.188) spatial scales (Tables S13 and S14).

DISCUSSION

Using a multiscale framework of stability, our study provides, to our knowledge, the first evidence for the scale-dependent effects of grazing on stability (Figure 5). We show that grazing in our system increases local species stability, but it decreases community stability at both local and larger spatial scales. Such scale-dependent effects of grazing can be understood from its negative effects on biodiversity both within local communities and across space, which impair insurance effects by decreasing species asynchrony and spatial asynchrony, respectively (Figure 5).

At the species level, the positive effects of grazing on species stability were mainly attributed to the selective foraging by grazers, which increased the relative abundance of one dominant species, that is *S. grandis*. In general, grazers preferentially forage palatable and nutritious plants. In our study system, *S. grandis* is less palatable and nutritious compared to other plants (Liang et al., 2019). Moreover, *S. grandis* produces long-needle seeds (approximately 1.1 cm long) that can damage animal digestion systems (e.g. tongue and stomach), particularly sheep. These morphological and physiological characters make *S. grandis* more resistant to grazing compared to other plants. Consequently, selective foraging on its more palatable competitors eventually leads to an increase in the relative abundance of *S. grandis* (Figure 4). Enhanced dominance of a more resistant species led to increasing species stability with grazing.

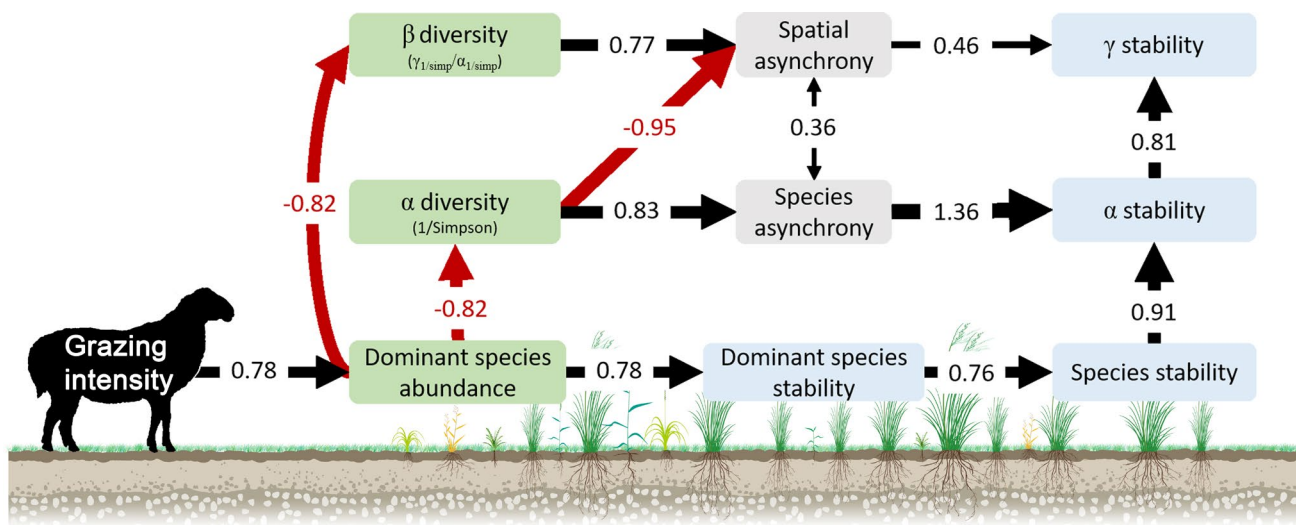


FIGURE 4 The structural equation model (SEM) depicting the direct and indirect effects of grazing intensity on grassland biodiversity and ecosystem stability at multiple scales. Shown are the final SEMs with the standardized path coefficients. Black and red arrows denote positive and negative associations, respectively. Fisher's $C = 69.695$; $df = 64$; $p = 0.292$; $AIC = 157.695$. The dominant species abundance denotes the relative abundance of the dominant species (i.e. *S. grandis*). Information about the priori SEM, the unstandardized path coefficients and the R^2 of individual response variables are provided in Figure S1 and Tables S13 and S14, respectively

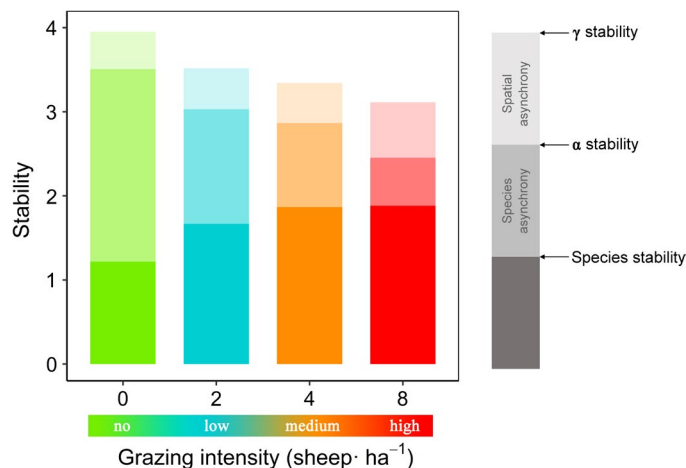


FIGURE 5 Visualized effects of grazing on stability across scales. Shown are the mean values of species stability, α stability and γ stability under four grazing intensities: no- (0 sheep·ha⁻¹), low- (2 sheep·ha⁻¹), medium- (4 sheep·ha⁻¹) and high- (8 sheep·ha⁻¹) intensities. As the grazing intensity increases, species stability increases, but α and γ stabilities decrease due to the reduced insurance effect of species asynchrony. In no-grazing treatment, species asynchrony provided a much stronger insurance effect for γ stability compared to spatial asynchrony. But an increase of grazing intensity reduces biodiversity and its insurance effects, such that in high-grazing treatment, spatial asynchrony provides a relatively stronger insurance effect than species asynchrony

However, by enhancing the dominance of *S. grandis*, grazing decreased plant diversity within local communities and thereby weakened the insurance effect of biodiversity for local community stability (Figure 4). A large body of experimental and theoretical studies have demonstrated the stabilizing role of species diversity in community stability, where both a higher species richness and evenness contribute to stabilizing ecosystem functions (Loreau, 2010; Thibaut & Connolly, 2013; Tilman et al., 2014; Wang & Loreau, 2016). One major mechanism for the stabilizing effect of biodiversity is that different species exhibit asynchronous responses to environmental fluctuations, which compensate for each other and result in a higher stability at the community level (Gonzalez & Loreau, 2009; Tilman et al., 2006). Our SEM confirmed this hypothesis by showing that grazing decreases species asynchrony indirectly via reducing α diversity. This result is consistent with previous findings that anthropogenic drivers (e.g. nitrogen, carbon dioxide, fire, herbivory and water) affect community stability indirectly via biodiversity (Hautier et al., 2015). The negative effects of grazing on species asynchrony suppressed its positive effect on species stability, leading to a decreasing community stability with grazing intensity (Figure 5).

The negative effect of grazing on community stability propagated from local (α) to larger (γ) spatial scales, as α stability at the local community scale was the major driver of γ stability (Figure S10). Yet, the reduction in γ stability was less pronounced than α stability, which was explained by the increase of spatial asynchrony with grazing. Metacommunity theory predicts that asynchronous responses among local communities to environmental fluctuations provide spatial insurance to maintain metacommunity stability (Loreau et al., 2003;

Wang & Loreau, 2014). Theory also predicts that spatial asynchrony among communities increases with β diversity and decreases with α diversity (Wang & Loreau, 2016). Our data supported these predictions and showed that grazing affected spatial asynchrony through two pathways: via changing α and β diversities (Figure 3). On the one hand, grazing decreased local α diversity, which increased spatial asynchrony. This is because a higher α diversity can decrease local community fluctuations via an averaging of species-level stochasticity and drive community-level responses to better track spatially synchronous environmental fluctuations (Wang & Loreau, 2016; Figure S1). On the other hand, due to the selective foraging that increases the dominance of *S. grandis* across the landscapes, grazing decreased β diversity and thus spatial asynchrony. Because the positive pathway via α diversity was relatively stronger than the negative one via β diversity, grazing eventually led to higher spatial asynchrony. Such higher spatial asynchrony compensated to some extent for the reduction in α stability and generated a smaller reduction of γ stability.

From local species to communities at larger scales, asynchrony both among species and across communities provide insurance effects that enhance community stability (Wang et al., 2019b). Recent studies have provided empirical evidence for a greater contribution to the insurance effect by either species asynchrony (Lamy et al., 2019; Wang et al., 2019b) or spatial asynchrony (Thorson et al., 2018). In our study system, species asynchrony provided a much stronger insurance effect for γ stability, compared to spatial asynchrony, in NG systems (Figure 5). However, grazing reversed this pattern by decreasing species diversity, such that spatial asynchrony provided a slightly stronger insurance effect than species asynchrony in high-grazing systems (Figure 5). This is

likely because grazers can have a stronger species preference than a patch preference. These results provide the first evidence that grazing can alter the upscaling patterns of stability by dampening the overall insurance effect of biodiversity and switching the relative importance of species and spatial asynchrony.

We end the discussion with two caveats. First, although our experimental units (i.e. paddocks of $120 \times 120 \text{ m}^2$) are large compared with previous grazing experiments (Beck et al., 2015; Bluthgen et al., 2016; Hallett et al., 2017; Wang et al., 2019a), they are still limited given the large dispersal range of the plants in our system. Thus, the extent of our γ scale should be smaller than that of natural metacommunities or landscapes (Leibold & Chase, 2018). Second, to characterize the paddock, we had sampled five quadrats in a line (Figure 1). Such a sampling design can induce uncertainty due to the small grain size ($1 \times 1 \text{ m}^2$) and the relatively low sampling intensity and linear spatial arrangement. Therefore, while our experimental design provided an opportunity to test the scale dependence of grazing effects, we advocate future larger scale experiments that go beyond ours in terms of the spatial extent, grain size and sampling intensity.

CONCLUSION

Grazing experiments from the past decade provide key insights in understanding the responses of ecosystem stability to grazing pressure. To demonstrate the implication of such experiments for real-world management, we need advanced understanding of whether and in what circumstances the effect of grazing on stability may change across scales. To this end, our study provides an important first step by revealing the effect of grazing on stability at multiple scales and clarifying the role of biodiversity in mediating such effects. In particular, we showed that the grazing-induced biodiversity loss led to increased species stability but simultaneously reduced community stability at both local and larger spatial scales due to the decreased species and spatial asynchrony. Our multiscale approach provides a potential framework to reconcile the idiosyncratic results from studies conducted at a single scale and using different grazing regimes that either increase or decrease biodiversity (Filazzola et al., 2020). Future studies can adopt our approach in the design and analysis of grazing experiments to further resolve the scale dependency of grazing effects, particularly at broader spatial scales. Such insights will be valuable for bridging small-scale ecological research with large-scale management, thus providing useful guides for decision-making in a changing environment.

ACKNOWLEDGEMENTS

This research was supported by the National Key Research and Development Program of China

(2016YFC0500503), the Natural Science Foundation of China (31988102, 31870505) and the Open Project Program of ‘Ministry of Education Key Laboratory of Ecology and Resources Use of the Mongolian Plateau’ (KF2020003). We appreciate fieldwork assistance from Zhiyong Li, Bailing Miao, Yantao Wu, Yabo Shi, Zhiwei Guo, Dongsheng Xie, Xuan Wang, Lei Dong, Zijing Li and the staff members of the National Observing Station of Xilinhot, China.

AUTHOR CONTRIBUTION

ML and SW conceived the idea. ML designed the experiment with CL. ML analysed the data, with help from YH, KW and SW. ML wrote the first draft with SW. All authors contributed to the development of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13826>.

DATA AVAILABILITY STATEMENT

All data used in our study will be uploaded to the Dryad Digital Repository after the manuscript is accepted. <https://doi.org/10.5061/dryad.j0zpc86dw>

OPEN RESEARCH BADGES



This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at: <https://doi.org/10.5061/dryad.j0zpc86dw>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Liang, M., Liang, C., Hautier, Y., Wilcox, K.R. & Wang, S. (2021) Grazing-induced biodiversity loss impairs grassland ecosystem stability at multiple scales. *Ecology Letters*, 24, 2054–2064. <https://doi.org/10.1111/ele.13826>