



RESEARCH ARTICLE

Dominant species determine grazing effects on the stability of herbaceous community production at multiple scales in drylands

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Abstract

1. Sustainable provision of critical ecosystem services in drylands is reliant on their stability under anthropogenic disturbances. Livestock grazing and shrub encroachment are the primary drivers of disturbance that impact their biodiversity and production dynamics. However, the effects of grazing on the stability at multiple scales, particularly following the transition from grass-dominated to shrub-encroached drylands, is still largely unexplored.
2. Here, we conducted comparable sheep-grazing experiments in two types of drylands (grass-dominated vs. shrub-encroached grasslands) on the Mongolia Plateau to explore the effects of grazing and shrub encroachment on biodiversity and stability at multiple scales. We examined how grazing affected the temporal stability of aboveground biomass in herbaceous communities in both grass-dominated and shrub-encroached grasslands, through two potential mechanisms: insurance effects and changes in the population-level stability of individual species.
3. We found that an increase in sheep grazing intensity had significant and negative effects on insurance effects by decreasing both species asynchrony and spatial asynchrony but it had no effects on population stability, consequently leading to reductions in herbaceous community stability of the grasslands. However, grazing-increased insurance effects cancelled out grazing-decreased population stability, contributing to no changes in the community stability of shrub-encroached grasslands. Likely, because grazing-induced reductions in the relative abundance of the dominant species were more noticeable in shrub-encroached grasslands than that of in grasslands. Moreover, the grazing-decreased abundance of dominant species was directly correlated to increases in insurance effects in shrub-encroached grasslands but not in grasslands, despite the positive relationships between population stability and the relative abundance of the dominant species in both grass-dominated and shrub-encroached drylands.
4. *Synthesis and applications.* Our results indicate that grazing can decrease the stability of herbaceous production in drylands but this negative effect is attenuated with the transition from grasslands to shrub-encroached grasslands, suggesting

that grazing effects on herbaceous community stability can be altered by shrub encroachment in drylands. Furthermore, the stability of dominant grasses plays a crucial role in stabilizing herbaceous communities and should be considered in promoting sustainable ecosystem functioning and services in drylands.

KEYWORDS

asynchrony, dominants, grasslands, grazing intensity, insurance effects, population stability, scale-dependence, shrub encroachment

1 | INTRODUCTION

Drylands occupy more than 40% of the global land surface and support nearly 40% of the world's population (Berg & McColl, 2021; Maestre et al., 2012). The provision of ecosystem functions and services from drylands is indispensable for human welfare (Abel et al., 2021; Maestre et al., 2021). Due to its vulnerability and sensitivity to anthropogenic activities, the sustainable delivery of ecosystem functions and services fundamentally relies on the stability of drylands in the face of anthropic pressures (Li et al., 2021; Maestre et al., 2016). Although livestock grazing supporting human demands is one of the major activities in drylands (Herrero et al., 2013), an increase in grazing intensity (GI; i.e. overgrazing) has become the most widespread land-use perturbation with numerous effects on plant diversity (Collins et al., 1998; Koerner et al., 2018), ecosystem functioning and stability (Liang et al., 2021; Milchunas & Lauenroth, 1993). Particularly, by selectively foraging on herbaceous plants, overgrazing can result in shrub encroachment—widely shifting vegetation dynamics and influencing land-use management (Bestelmeyer et al., 2015; Eldridge et al., 2011). To gain a comprehensive understanding of the effects of GI and its consequences, including shrub encroachment, on drylands, further rigorous testing is necessary.

Ecosystem stability is a crucial property of ecosystems as it indicates how they may respond to ongoing, unpredictable anthropogenic disturbances, such as an increase in GI or shrub encroachment. A mathematical framework has been developed to partition the temporal stability at the community level, defined as the ratio of mean biomass production to its interannual standard deviation, into insurance effects (i.e. species asynchrony) and population-level stability of individual species (Loreau et al., 2021; Thibaut & Connolly, 2013; Tilman et al., 2006; Wang et al., 2019). Numerous studies suggest that ecosystem stability at the local scale increases with biodiversity because of asynchronous responses of different species (species asynchrony) through species insurance effects (Hautier et al., 2020; Loreau et al., 2021; Schnabel et al., 2021; Tilman et al., 2006; Yachi & Loreau, 1999). Recent studies also report that ecosystem stability at a larger spatial scale (e.g. metacommunity stability) can increase with species spatial turnover (e.g. β diversity) due to spatial asynchrony among local communities (Hautier et al., 2020; Hautier & van der Plas, 2021; Liang et al., 2022; Qiao et al., 2022; Wang et al., 2021), namely spatial insurance effects (Loreau et al., 2003). Accordingly, community stability increases from local to larger scales because

of the insurance effects from species asynchrony and spatial asynchrony (Hautier et al., 2020; Liang et al., 2022; Wang et al., 2019). Alternatively, population stability reflects the importance of dominant species in regulating community stability (Ma et al., 2017; Sasaki & Lauenroth, 2011; Yang et al., 2017), in line with the mass ratio hypothesis (Grime, 1998). Likely, this is because dominant species are more abundant and resistant to resource fluctuations and their changes have large impacts on population biomass (Grime, 1998; Smith et al., 2020), thereby affecting ecosystem stability (Hooper et al., 2005). In grasslands, grazing can simultaneously affect population stability and insurance effects at multiple scales, fundamentally through grazing-induced shifts of the dominant species abundance in grasslands (Liang et al., 2021). Combined, grazing could either decrease (Liang et al., 2021; Liu et al., 2021; Qin et al., 2019) or increase (Beck et al., 2015; Hallett et al., 2017; Post, 2013) ecosystem stability. Despite earlier studies, the interactions with other associated consequences, such as shrub encroachment, remain largely unknown.

In shrub-encroached grasslands, vegetation may provide limited options for livestock due to the lower availability and production of edible herbaceous species, compared to grass-dominated grasslands (Maestre et al., 2016; Scholes & Archer, 1997). Selective foraging by livestock is likely to interact intensively with interspecific interactions (e.g. grass-shrub relationships). Studies of grazing effects on dominant species have shown that if dominant herbaceous species are palatable and nutritious, increasing GI decreases their abundance because of livestock's selective foraging preferences (Koerner et al., 2018; Milchunas & Lauenroth, 1993). In such cases, shrub species could quickly colonize the habitats and interact with grazing to shift the relative abundance of the dominant herbaceous species (Bestelmeyer et al., 2015). Specifically, the grazing-induced decrease in dominant grass abundance increases resource availability for other plant species, contributing to increasing plant diversity and decreasing individual species abundance of herbaceous communities (Collins et al., 1998; Koerner et al., 2018). It is likely that the effects of grazing on stability in grasslands are primarily dependent on its interactions with ecosystem type, such as grass-dominated versus shrub-encroached grasslands, while changes in dominant species abundance underpin the responses of the diversity-stability relationships to grazing across the transition from grass-dominated to shrub-encroached grasslands (Figure 1a). A grazing-induced decrease in the abundance of palatable dominant herbaceous species might be more pronounced in shrub-encroached grasslands,

compared with grass-dominated grasslands (Figure 1b), and this further leads to an increase in herbaceous diversity caused by decreasing dominant species abundance—more so in grass-dominated grasslands than in shrub-encroached grasslands (Figure 1c). The potential effects of grazing-induced changes in the dominant species on herbaceous community stability were via population stability and insurance effects (species asynchrony and spatial asynchrony) in both the grass-dominated and shrub-encroached grasslands at multiple scales (Figure 1d). (i) If the reduced population stability (by decreasing herbaceous species abundance) overwhelms increasing insurance effects (by increasing herbaceous diversity) under a grazing regime, community stability will be decreased (Figure S1A,D). Alternatively, (ii) if increasing insurance effects overwhelm the reduced population stability, community stability will be increased (Figure S1B,E). (iii) If increasing insurance effects offset reduced population stability, grazing will have neutral effects on community stability (Figure S1C,F).

Here, we conducted two parallel sheep grazing experiments, one in a grass-dominated (grasslands) and the other in a shrub-encroached (shrubby-encroached grasslands) dryland ecosystem, on the Mongolia Plateau. Compared to grasslands, shrub-encroached grasslands have been recognized as the consequence of shrub encroachment after overgrazing disturbance in the grasslands (Bestelmeyer et al., 2015; Eldridge et al., 2011). We set up the same grazing experiments in both the grassland and the shrub-encroached grassland, including no grazing, moderate

GI (2 sheep ha⁻¹ in grasslands; 0.5 sheep ha⁻¹ in shrub-encroached grasslands) and high GI (4 sheep ha⁻¹ in grasslands; 1 sheep ha⁻¹ in shrub-encroached grasslands) treatments, respectively. We calculated the relative abundance of a dominant species (*Stipa glareosa*), plant diversity at local quadrat (α diversity) and larger plot scales (γ diversity), and spatial species turnover (β diversity = γ diversity / α diversity). We also calculated stability metrics (i.e. temporal stability of biomass) at multiple scales, including population stability, and community stability at both local quadrat (α stability) and larger paddock (γ stability) scales (Liang et al., 2021). We hypothesized that: (1) grazing affected α and γ stabilities not only through biological insurance effects (i.e. species and spatial asynchronies) by altering biodiversity but also through population stability by shifting the dominant species abundance in both grasslands and shrublands; and (2) the negative effects of grazing on herbaceous community stability could be altered in shrublands due to grass-shrub interactions.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located at the Urat Desert-grassland Research Station (106°58' E, 41°25' N) in Inner Mongolia, northern China. The region is characterized as a typical continental monsoon

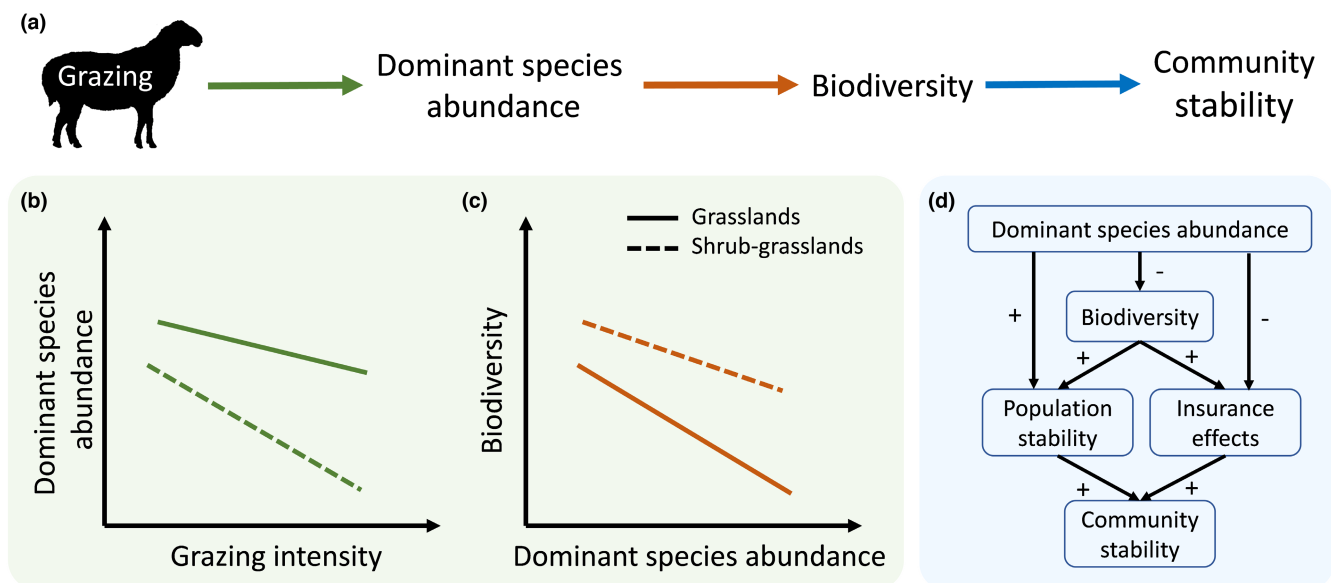


FIGURE 1 A conceptual diagram of grazing-induced changes in herbaceous species dominance regulating biodiversity and stability in drylands. (a) Grazing affects biodiversity and stability by altering the dominant species abundance (e.g. biomass). (b) Since less diverse food for livestock in drylands, the dominant species abundance will decrease when grazing intensity increases; and such trend would be more pronounced in shrub-encroached grasslands, compared with grasslands. (c) Grazing-induced decrease in dominant grass abundance increases resource availability for other plant species, contributing to increasing plant diversity (Koerner et al., 2018). The increase in herbaceous diversity caused by grazing-induced decrease of dominant species abundance is more firmly in grasslands than in shrub-encroached grasslands, due to the “shelters” or “fertilizing islands” under shrub canopy and interspecific competition between grasses and shrubs (Scholes & Archer, 1997). (d) We hypothesize that the effects of grazing-induced changes in the dominant species on herbaceous community stability at larger scales (γ) via population stability and insurance effects (species asynchrony and spatial asynchrony).

climate. The mean annual temperature (MAT) was 5.79°C and the mean annual total precipitation (MAP) was 154.10mm between 1990 and 2020 with 80% falling during the growing season from May to September. During the experimental periods, MAT was 6.07°C and MAP was 169.84mm between 2017 and 2020. Two common types of drylands are present in this region, which are the grass-dominated and shrub-encroached grasslands that have distinct plant compositions and edaphic properties. *S. glareosa* is a widespread perennial grass in this area and has been recognized as the dominant species in the herbaceous communities of both types of drylands. In shrub-encroached grasslands, *Reaumuria soongorica* and *Salsola passerina* are two dominant shrubs (Zuo et al., 2021).

2.2 | Grazing experiments

We conducted similar grazing experiments in both the grassland and the shrub-encroached grassland (Figure S2). We fenced a 350-ha relatively flat area to exclude disturbances from native unmanaged large mammals in 2010. According to the forage production assessment from local herd households, we implemented three GI treatments: no- (NG), moderate- (MG) and heavy-grazing (HG; Du et al., 2019; Zhao et al., 2021). In grasslands, we set no grazing at 0 sheep per plot, moderate grazing at 2 sheep ha⁻¹ (2 sheep per plot), and heavy grazing at 4 sheep ha⁻¹ (4 sheep per plot). By contrast, in shrub-encroached grasslands, due to the low edible grass yield, we set no grazing at 0 sheep per plot, moderate grazing at 0.5 sheep ha⁻¹ (2 sheep per plot) and heavy grazing at 1 sheep ha⁻¹ (4 sheep per plot). The area of control and grazed plots in grassland was approximately 1 ha, while they were approximately 4 ha in shrub-encroached grasslands. In the grassland and the shrub-encroached grassland, each grazing treatment had five replicated plots, so there were 15 plots (15 ha) in the grassland and 15 plots (60 ha) in the shrub-encroached grassland for the grazing experiments (Figure S2). Based on the grazing management practices of local herdsmen in this area, we implemented free sheep grazing in these enclosed plots between June and September. The grazing research reported herein did not require ethical approval.

2.3 | Vegetation survey and sampling design

We carried out vegetation surveys and biomass sampling in August between 2017 and 2021. In both the grassland and the shrub-encroached grassland, we harvested aboveground residual shoot biomass of each herbaceous plant in mid-August in five quadrats (1 × 1 m), distributed at the center and four corners in each plot. Then, the harvested plants were oven-dried at 60°C for 48 h to obtain the biomass (g m⁻²). In total, our plant datasets include more than 4800 plant species biomasses from 750 herbaceous quadrats (2 types of drylands × 15 plots × 5 quadrats × 5 years) between 2017 and 2021.

2.4 | Biodiversity and stability

In our experiment, we considered sampling quadrats as local communities (α) and paddocks as larger-scale communities (γ). Based on the previous equations (Liang et al., 2021), we used the abundance-based metrics (1/Simpson) to calculate α diversity and γ diversity at local and larger scales, respectively. Then we defined species spatial turnover as Whittaker's index: β diversity = γ diversity / α diversity (Whittaker, 1960). According to Wang & Loreau's stability frameworks, we calculated community stability at local quadrats (α) and larger paddocks (γ) scales (Wang & Loreau, 2014, 2016). Using this framework, we can partition γ stability as weighted average α stability and spatial asynchrony among local communities; and α stability can be partitioned as the weighted average population stability and species asynchrony among species within local communities. The stability metrics were defined as the temporal mean biomass over its standard deviation, and the asynchrony metrics were defined as a ratio of the sum of covariances of biomass among species within local communities or among local communities to its total variances accordingly. Details about the equations of the stability are provided in previous studies (Wang et al., 2019). We have calculated:

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

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

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

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 (Liang et al., 2021). In this partitioning, species asynchrony (α stability/population stability) represents the asynchronous dynamics among species and spatial asynchrony (γ stability/ α stability) denotes the asynchronous dynamics among local communities (Wang & Loreau, 2014, 2016). Both species asynchrony and spatial asynchrony can provide insurance effects to enhance γ stability (Liang et al., 2022; Wang et al., 2019). Thus, γ stability may be expressed as the product of species asynchrony, spatial asynchrony and population stability (Hautier et al., 2020; Liang et al., 2021, 2022; Wang et al., 2019).

2.5 | Statistical analyses

To examine the effects of how grazing, year, shrub encroachment and their interactions on the dynamics of community biomass,

dominant species biomass and abundance, we performed a three-way ANOVA with GI (no-, moderate- and heavy-grazing), year (Y: 2017, 2018, 2019, 2020, and 2021) and shrub encroachment (S: grasslands vs. shrub-encroached grasslands). Similarly, we used two-way ANOVA to test the effects of grazing, shrub encroachment and their interactions on stability metrics. The relative abundance (i.e. biomass) of the dominant species, ranging from 0% to 100%, was used as the dominant species abundance. By applying the stability equations, we calculated the stability of the dominant species biomass using its temporal mean over the standard deviation.

To explore the overall effects of dominant species on the metrics of biodiversity and stability, we used linear mixed-effects models (MEMs) using the R package *lme4* (Bates et al., 2015). In these MEMs, the fixed effect was the relative abundance of dominant species and the random effect was GI. Similarly, we implemented the effects of biodiversity on stability using MEMs; for example, α diversity was for population stability, species asynchrony, and α stability; β diversity was for spatial asynchrony; γ diversity was for γ stability. The package of “MuMIn” was used to quantify the proportions of variation explained (Nakagawa & Schielzeth, 2013). For comparable effect sizes, we used natural log-transformed values for all numerical variables.

We used structural equation modelling (SEM) to further explore how changes in dominant species abundance affect population stability and insurance effects (species asynchrony and spatial asynchrony) directly and indirectly through biodiversity at multiple scales using the *piecewiseSEM* package (Lefcheck, 2016). First, we constructed an initial null SEM that characterized the possible effects of grazing on herbaceous community stability at multiple scales in both grasslands and shrub-encroached grasslands (Figure S3), based on key literature on both the theoretical framework (Wang & Loreau, 2014, 2016) and its application to grazing effects (Hautier et al., 2020; Liang et al., 2021; Liu et al., 2021). Second, we fitted the best SEMs using a Fisher's C statistic with $p > 0.05$ and the lowest Akaike information criterion, and then chose the final SEMs using Shipley's test of d -separation without insignificant pathways ($p > 0.05$). All statistical analyses were conducted in R v 4.2.3 (R Development Core Team, 2023).

3 | RESULTS

3.1 | Grazing effects on plant diversity and community biomass

Increasing GI did not affect herbaceous plant diversity (Table 1; Table S1), and the year effect on plant diversity was significant ($p < 0.0001$) and had interactive effects with shrub encroachment, suggesting the annual dynamics of plant diversity varied among grasslands and shrub-encroached grasslands. Plant diversity showed significant inter-annual variability with year explaining the largest proportion of variance (Table 1; Figures S4 and S5). Overall,

herbaceous diversity increased over time in grasslands (Figure S5), and herbaceous diversity (1/Simpson-based metrics) was slightly higher in shrub-encroached grasslands than in grasslands (Figure S6).

Overall, plant community biomass, dominant species biomass (*S. glareosa*) and its relative abundance in herbaceous community were higher in grasslands than in shrub-encroached grasslands (Table 1; Figures S7 and S8). Increasing GI significantly decreased plant biomass in herbaceous community of both grasslands than shrub-encroached grasslands, and these effects were strongest in grasslands. Furthermore, grazing significantly decreased the biomass of dominant species (*S. glareosa*) and its relative abundance—the reduction in relative abundance being strongest in shrub-encroached grasslands. Specifically, compared with no grazing plots, high GI decreased plant community biomass, dominant species biomass, and the relative abundance of dominant species by ~68%, ~59%, and ~11% in grasslands, respectively. In shrub-encroached grasslands, high GI decreased plant community biomass by ~60%, the dominant species biomass by ~77%, and the relative abundance of dominant species by ~41% (Figures S7 and S8).

3.2 | Grazing interacts with shrub encroachment to affect community stability

Grazing decreased the stability of herbaceous community at both quadrat (α) and plot (γ) scales in grasslands but had no effects in shrub-encroached grasslands, suggesting that the effects of grazing on herbaceous community stability change with the shift from grasslands to shrub-encroached grasslands (Figure 2; Table S2). Compared to the ungrazed grasslands, high GI significantly decreased α stability by ~47% and spatial asynchrony by ~26%, which led to a reduction of γ stability by ~62% ($p < 0.05$). However, in shrub-encroached grasslands, high GI did not ($p = 0.083$) decrease population stability nor affect species asynchrony, spatial asynchrony, and γ stability ($p > 0.10$).

Stability metrics across multiple scales were overall lower (~33% in ungrazed plots) in shrub-encroached grasslands than in grasslands, suggesting that shrub encroachment likely decreased the stability of the herbaceous community (Figure 2; Table S2). The lower γ stability in shrub-encroached grasslands was due to the lower species asynchrony, rather than spatial asynchrony and population stability. Also, the stability of the dominant species (*S. glareosa*) was significantly lower in shrub-encroached grasslands than in grasslands (Figure 2f; Table S2, $F_{1,26} = 10.65$, $p = 0.003$).

3.3 | Diversity-stability relationships in grasslands and shrub-encroached grasslands

As the abundance of the dominant species (*S. glareosa*) increased, α diversity ($F_{1,11} = 58.77$, $p < 0.0001$), β diversity ($F_{1,11} = 18.51$, $p = 0.001$) and γ diversity ($F_{1,11} = 155.78$, $p < 0.0001$) all decreased in grasslands (Figure 3a; Table S3). However, the effect sizes (i.e.

TABLE 1 Effects of grazing intensity, shrub encroachment, year and their interactions on biodiversity and ecosystem function in drylands. The results of three-way ANOVA are shown (F -value and contribution percent [i.e. SS_i/SST]) for the effects of grazing intensity (GI, $df_{GI}=2$), shrub encroachment (S, $df_S=1$), year (Y, $df_Y=4$), and their interactive effects on α diversity (1/Simpson), β diversity (γ/α), γ diversity, herbaceous biomass (gm^{-2}), dominant species (*Stipa glareosa*) biomass (gm^{-2}) and the relative abundance of *S. glareosa* (%) in the herbaceous community. SS_i denotes the sum of squares by factors, where i represent GI, S, Y, and their interactions, respectively; SST is the total sum of squares by factors and residuals; the bold values represent significant effects ($p < 0.05$).

	Biodiversity metrics								
	α diversity			β diversity			γ diversity		
	SS/SST	F	p	SS/SST	F	p	SS/SST	F	p
GI	0.10	0.24	0.787	2.28	2.62	0.077	0.23	0.52	0.595
S	0.01	0.04	0.852	2.88	6.61	0.011	0.01	0.03	0.865
Y	36.16	44.58	<0.0001	36.82	21.11	0.0001	44.78	51.04	<0.0001
GI×S	0.57	1.41	0.248	0.24	0.27	0.763	0.50	1.13	0.326
GI×Y	1.90	1.17	0.324	2.24	0.64	0.743	2.27	1.29	0.253
S×Y	35.42	43.67	<0.0001	0.99	0.57	0.683	24.41	27.83	<0.0001
GI×S×Y	1.50	0.93	0.497	2.21	0.63	0.748	1.49	0.85	0.560

	Ecosystem functions								
	Community biomass			Dominant species biomass			Dominant species abundance		
	SS/SST	F	p	SS/SST	F	p	SS/SST	F	p
GI	36.51	140.71	<0.0001	29.44	85.85	<0.0001	5.31	10.09	<0.0001
S	23.10	178.05	<0.0001	18.60	108.47	<0.0001	14.62	55.58	<0.0001
Y	4.98	9.59	<0.0001	13.76	20.07	<0.0001	25.50	24.24	<0.0001
GI×S	7.91	30.50	<0.0001	4.41	12.85	<0.0001	3.77	7.17	0.001
GI×Y	3.70	3.56	0.001	9.36	6.82	<0.0001	3.04	1.44	0.186
S×Y	7.85	15.13	<0.0001	1.15	1.68	0.160	14.87	14.13	<0.0001
GI×S×Y	0.38	0.37	0.936	2.70	1.97	0.056	1.32	0.63	0.756

regression coefficients) were smaller in shrub-encroached grasslands, where the relationship between β diversity and the dominant species abundance was non-significant ($F_{1,11} = 2.47$, $p = 0.145$). Moreover, the effects of dominant species abundance on stability metrics were also different between grasslands and shrub-encroached grasslands (Figure 3a; Table S3). The significantly ($p < 0.05$) negative effects of the abundance of the dominant species on species asynchrony ($F_{1,11} = 7.75$, $p = 0.018$) and spatial asynchrony ($F_{1,11} = 11.96$, $p = 0.005$) were only present in shrub-encroached grasslands, and not in grasslands ($p > 0.1$). The positive effects of the abundance of the dominant species on population stability were relatively small in shrub-encroached grasslands, though the relationships between population stability and the abundance of the dominant species were significant in both grasslands ($F_{1,11} = 14.78$, $p = 0.003$) and shrub-encroached grasslands ($F_{1,11} = 19.73$, $p = 0.001$).

Furthermore, the diversity-stability relationships were also altered by shrub encroachment (Figure 3b; Table S4). Specifically, the relationships between population stability and α diversity were significantly negative in both grasslands ($F_{1,11} = 9.19$, $p = 0.011$) and shrub-encroached grasslands ($F_{1,11} = 14.36$, $p = 0.003$), and the effect size was slightly smaller in the grasslands than that of in the shrub-encroached grasslands. Additionally, the relationship between species asynchrony and α diversity was positive in the

shrubs-encroached grasslands ($F_{1,11} = 4.54$, $p = 0.057$), but not in the grasslands ($F_{1,11} = 0.01$, $p = 0.918$). The relationships between α diversity and α stability, β diversity and spatial asynchrony, and γ diversity and γ stability were insignificant ($p > 0.05$) in both grasslands and shrub-encroached grasslands.

3.4 | Pathways through which grazing affected on community stability

To further distinguish the underlying mechanisms of grazing effects on the stability in both grasslands and shrub-encroached grasslands at multiple scales, we fit two SEMs based on our *a priori* SEM (Figure S3). In grasslands, grazing noticeably decreased α stability and γ stability due to decreasing in species asynchrony (Figure 4a; Tables S5 and S6, total effect size or TES = -0.90) and spatial asynchrony (TES = -0.62). In shrub-encroached grasslands, however, grazing indirectly increased species asynchrony (Figure 4b; Tables S7 and S8, TES = 0.19) and spatial asynchrony (TES = 0.39) by significantly reducing dominant species abundance, which cancelled out the negative effect of grazing on population stability (TES = -0.72), thus leading to grazing having no effect on γ stability. Overall, grazing led to a decrease in herbaceous community stability in grasslands, but the negative effect of grazing was weakened in shrub-encroached grasslands (Figure 5).

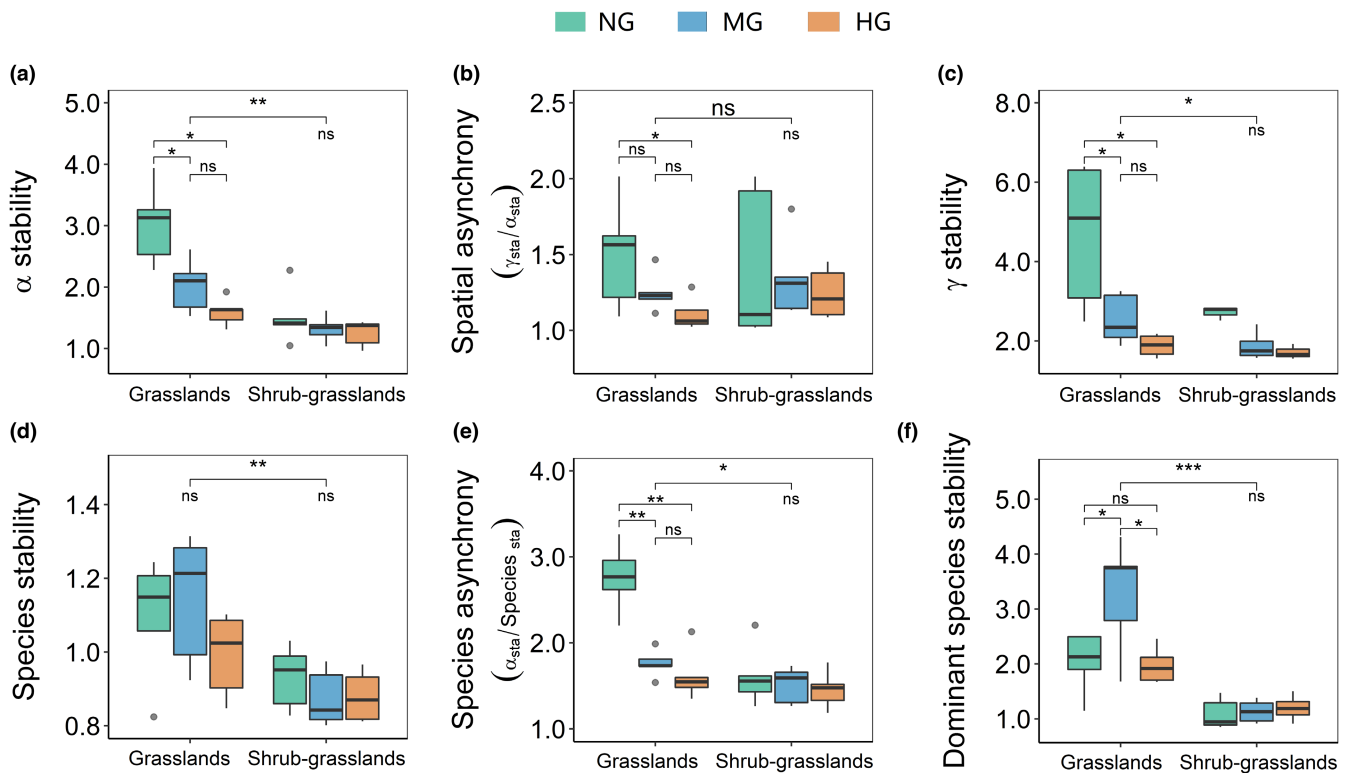


FIGURE 2 Effects of grazing intensity on stability at multiple scales in grasslands and shrub-encroached grasslands. Grazing effects on (a) α stability of local communities, (b) spatial asynchrony among local communities, (c) γ stability of an aggregated community at the larger scales consisting of multiple local communities, (d) population stability, (e) species asynchrony among plant species of local communities and (f) dominant species stability. Sampling size: $N=5$; “ns” and “*” represent insignificant ($p \geq 0.05$) and significant ($p < 0.05$) differences, respectively; significance level: * $p < 0.05$, ** $p < 0.001$ and *** $p < 0.0001$. HG, high grazing intensity (4 sheep ha^{-1} in grasslands; 1 sheep ha^{-1} in shrub-encroached grasslands); MG, moderate grazing intensity (2 sheep ha^{-1} in grasslands; 0.5 sheep ha^{-1} in shrub-encroached grasslands); NG, no grazing. Information about the models is provided in Table S2.

4 | DISCUSSION

Many drylands worldwide are experiencing regime shifts as a result of livestock overgrazing to support the daily needs of ~2 billion people (Berg & McColl, 2021; Li et al., 2021; Maestre et al., 2016). For the sustainable management of dryland ecosystems, we urgently need to understand the effects of grazing on vegetation stability. In this study, we aimed to investigate the effects of GI on herbaceous community stability at multiple scales in both grass-dominated and shrub-encroached grasslands, which share similar climate conditions. Generally, we found that, first, the stability of herbaceous communities is lower in shrub-encroached grasslands at both local and larger scales than those of grasslands but only in the absence of grazing (Figure 2). Second, by reducing local and spatial insurance effects (i.e. species asynchrony and spatial asynchrony), grazing substantially decreases herbaceous community stability in grasslands; however, by preventing insurance effects, shrub encroachment likely alleviates grazing effects on herbaceous community stability (Figure 5). Lastly and most importantly, these effects are primarily associated with changes in the abundance of the dominant species of the herbaceous community.

Our results demonstrate consistently positive associations of dominant species abundance with the stability of herbaceous plant

biomass at both population- and community-levels in grasslands and shrub-encroached grasslands, which are supported by previous findings (Liang et al., 2021; Ma et al., 2017; Sasaki & Lauenroth, 2011; Yang et al., 2017). In our study area, the perennial grass *S. glareosa* is the dominant herbaceous plant in the communities of both grasslands and shrub-encroached grasslands, which is palatable and nutritious compared to unpalatable shrubs and other herbs (Zhao et al., 2021; Zuo et al., 2021). With less-diverse and low forage productions in our drylands, selective grazing results in the primary foraging of the dominant species and reduces its abundance in the herbaceous community (Collins et al., 1998; Koerner et al., 2018; Milchunas & Lauenroth, 1993), which is made more noticeable via shrub encroachment in shrub-encroached grasslands (Figure 4). Thus, the reduced abundance of *S. glareosa* led to decreasing population stability with grazing. Moreover, in agreement with other studies (Hautier et al., 2020; Tilman et al., 2006), increasing plant diversity further contributed to decreasing population stability in both grasslands and shrub-encroached grasslands because of the relatively large temporal variability in biomass of these species. Fundamentally, changes in plant diversity are underpinned by shifts in dominant species abundance in grazing ecosystems (Koerner et al., 2018). Thus, our findings provide robust evidence for the significant stabilizing role of dominant species in drylands (Figure S9).

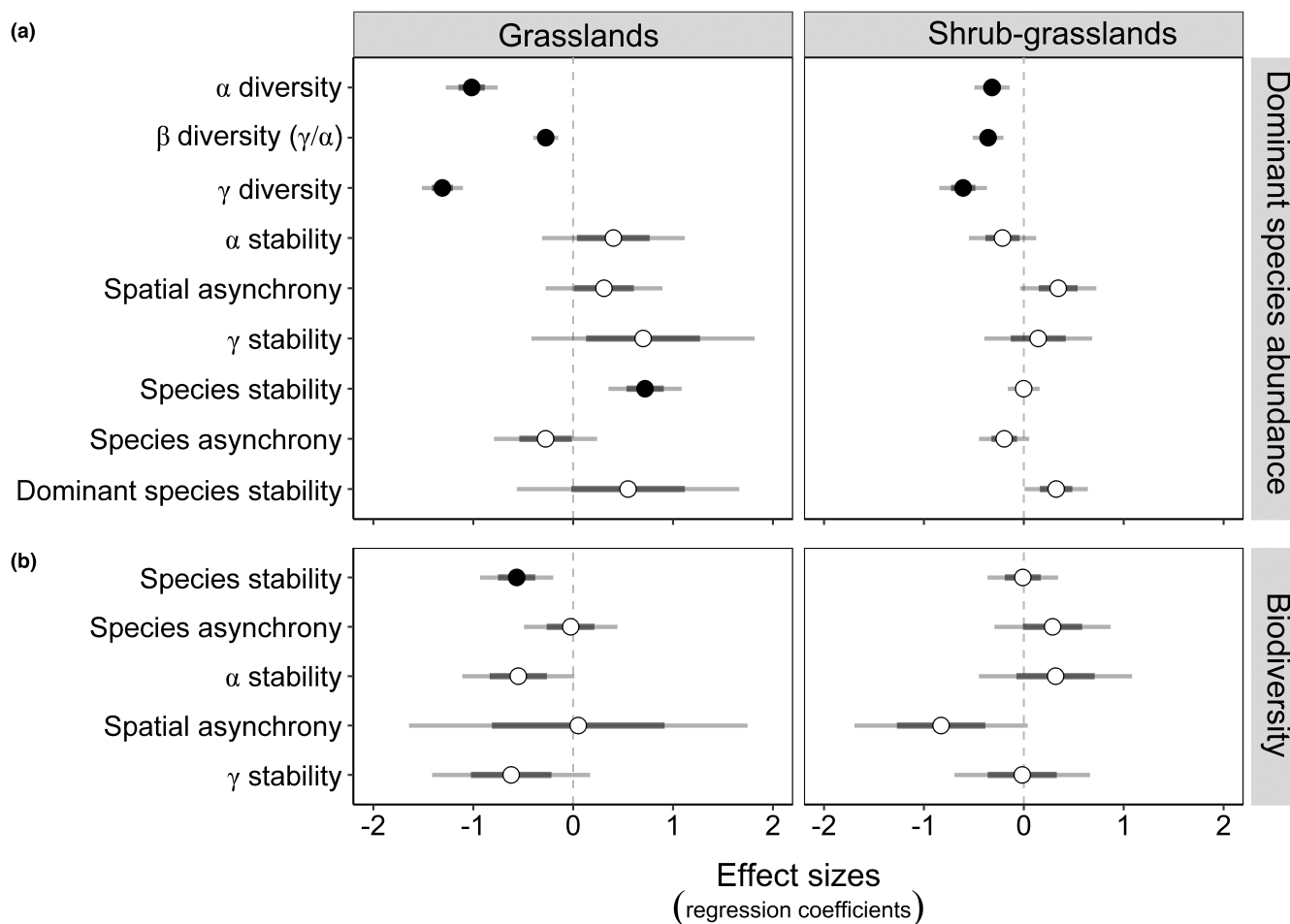


FIGURE 3 Effect sizes of the dominant species abundance and biodiversity on stability at multiple scales in grasslands and shrub-encroached grasslands. Shown are the standardized regression coefficients based on linear mixed-effects models, with “grazing intensity” as a random factor. (a) Both biodiversity and stability metrics were response variables and the relative abundance of the dominant species was a fixed explanatory variable. (b) Stability metrics were response variables and biodiversity metrics at different spatial scales are fixed explanatory variables; α diversity was analysed as a predictor of population stability, species asynchrony, and α stability; β diversity was analysed as a predictor of spatial asynchrony; γ diversity was for γ stability ($N=15$). Filled dots indicate the significant effects ($p < 0.05$). The dark and light bars denote the standard errors and the 95% confidence intervals, respectively. Information about the models is provided in Tables S3 and S4.

In grasslands, our results showed that grazing reduced the stability of herbaceous communities by decreasing biological insurance at both local quadrat and larger paddock scales. At the local scales, grazing directly decreased species asynchrony, likely resulting from the foraging behaviour of grazers. Sheep selectively forage palatable and nutritious plants, which could contribute to a similar dynamic of abundance among herbaceous plants in response to temporal environmental changes (Liang et al., 2021; Liu et al., 2021; Qin et al., 2019). Most of the common species were annual plants in herbaceous communities (Zhao et al., 2021; Zuo et al., 2021), and their asynchronous dynamics are likely associated with interannual variability of rainfall, rather than plant diversity (Hallett et al., 2019). Thereby, with these dramatic variations from year to year, demographic stochasticity is expected to be more pronounced, while the biodiversity effects on community stability through biological insurance could be less apparent (Loreau & de Mazancourt, 2008; Thibaut & Connolly, 2013). Furthermore, likely because such cumulative

effects are also pronounced at larger scales, we also found that grazing decreased spatial asynchrony, which is in contrast to previous findings (Liang et al., 2021). With these idiosyncratic results, we encourage future studies to focus on the interactions of grazing and spatial extents on these effects.

In contrast to grasslands, we found that herbaceous community stability was relatively low and has less been subject to grazing effects in shrub-encroached grasslands (Figure 5). Specifically, grazing indirectly increased both species asynchrony and spatial asynchrony by reducing dominant species abundance in shrub-encroached grasslands. The positive effects of both species asynchrony and spatial asynchrony on herbaceous community stability were offset by the negative effects of grazing on population stability, thus leading to more neutral effects of grazing on herbaceous community stability in shrub-encroached grasslands. These results further suggest that the negative effect of grazing on herbaceous community stability was weakened in shrub-encroached

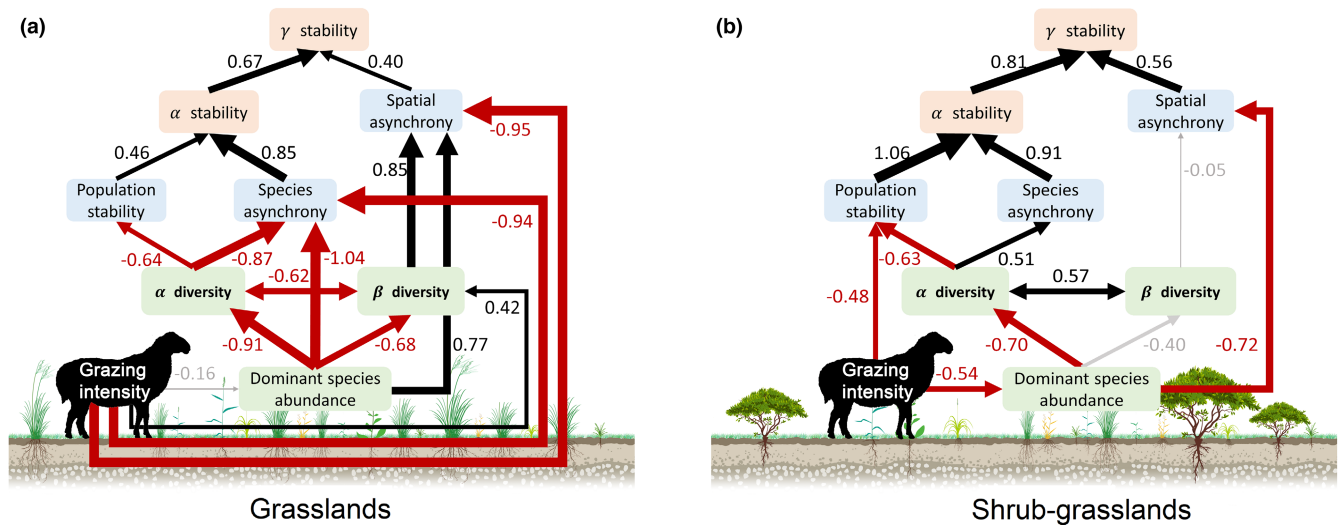


FIGURE 4 The structural equation model (SEM) depicting the direct and indirect effects of grazing intensity on biodiversity and ecosystem stability at multiple scales through the dominant species in grasslands and shrub-encroached grasslands. Shown are the final SEMs in both (a, Fisher's $C=40.13$; $df=40$; $p=0.465$; Akaike information criterion [AIC]=102.13) grasslands and (b, Fisher's $C=52.885$; $df=46$; $p=0.226$; AIC=108.885) shrub-encroached grasslands. The values represent standardized path coefficients; the black and red arrows denote significantly ($p \leq 0.05$) positive and negative associations, respectively; the grey arrows denote insignificant ($p > 0.05$) associations. The dominant species abundance was the relative abundance of the dominant species (*Stipa glareosa*). Information about the unstandardized path coefficients and the R^2 of individual response variables are provided in Tables S5–S8, respectively.

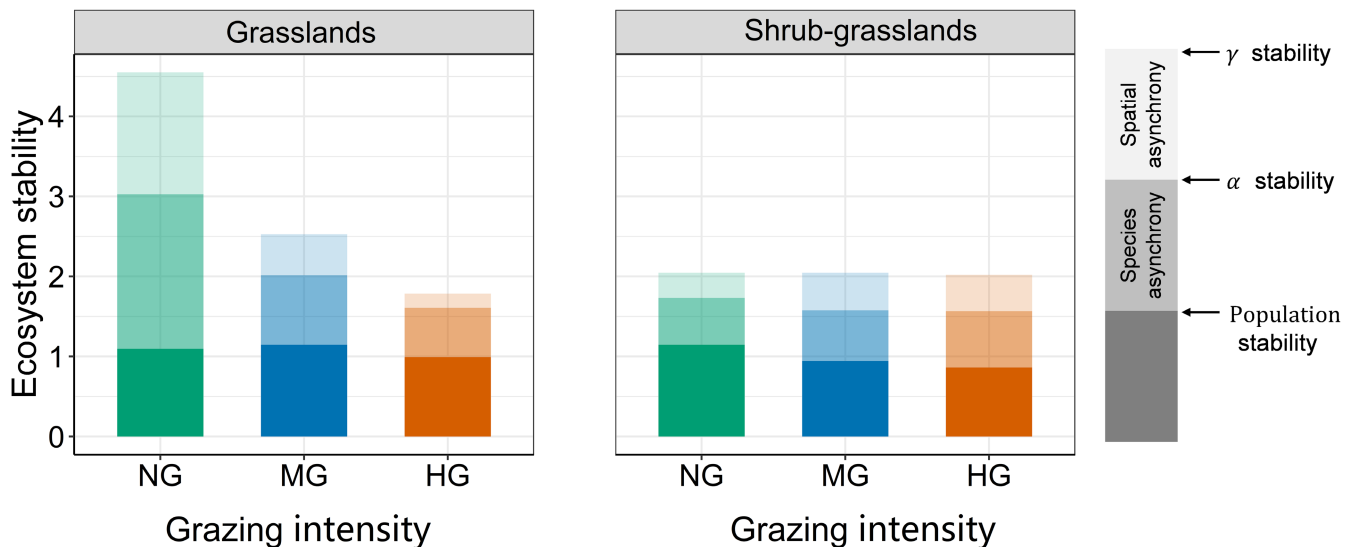


FIGURE 5 Visualized grazing effects on ecosystem stability across multiple scales in grasslands and shrub-encroached grasslands. Shown are the mean values of population stability, α stability, and γ stability under three grazing intensities. HG, high grazing intensity (4 sheep ha^{-1} in grasslands; 1 sheep ha^{-1} in shrub-encroached grasslands); MG, moderate grazing intensity (2 sheep ha^{-1} in grasslands; 0.5 sheep ha^{-1} in shrub-encroached grasslands); NG, no grazing. As the grazing intensity increases, decreases in α and γ stability was due to the substantially reduced insurance effects of both species asynchrony and spatial asynchrony in grasslands. However, shrub encroachment slightly amplified the reduction of population stability but prevented the reductions of insurance effects of both species asynchrony and spatial asynchrony, so that no net changes in α and γ stability occurred in shrub-encroached grasslands.

grasslands at both local quadrat and larger plot scales. Despite the fact that GI was relatively low in our shrub-encroached grasslands, livestock still substantially decreased the relative abundance of *S. glareosa* (Figure S7). Therefore, sheep grazing providing additional resources and spaces for transient plants could promote species spatial turnover and thus insurance effects (e.g. spatial asynchrony, Liang et al., 2021). Additionally, shrubs can also

provide “shelters” or “fertilizing islands” for transient plants under their canopy to prevent livestock foraging (Hulvey et al., 2017; Scholes & Archer, 1997), which possibly increases plant diversity by expanding spatial distributions of these transient species and ultimately promoting insurance effects. In particular, the size of plots in our sites was 4-fold larger in shrub-encroached grasslands than that in grasslands. Livestock grazing could increase spatial

heterogeneity and patchiness of vegetation in these relatively larger paddocks (Adler et al., 2001), and metacommunity theory predicts that such increased spatial heterogeneity could also provide spatial insurance effects to stabilize community dynamics at larger scales (Wang & Loreau, 2014, 2016). With these caveats, we acknowledge that rigorous studies are still needed to explicitly examine these confounding effects.

Overall, our study emphasizes that the stabilizing role of dominant plant species in determining herbaceous community stability may be relatively widespread in arid grassland ecosystems. While our two-site dataset can explore the contrasting effects of grazing on the diversity-stability relationship at multiple scales in grasslands and shrub-encroached grasslands through the fundamental regulation of the dominant species in drylands, one limitation of this study is the relatively few sites that cannot explore the mechanism of how shrub encroachment and its interaction with grazing on community stability. Future empirical work to accurately study their interactive effects on stability across scales is needed to survey multisite plant communities along a shrub encroachment gradient with different intensity grazing, which allows us to explore the generality of our framework. Notably, despite the fact that the negative effect of grazing on herbaceous community stability was weaker in shrub-encroached grasslands than that of grasslands, the shift from the grass- to shrub-dominated states could cause reductions in sustainable delivery of forage productions for livestock, further impacting the economy of grasslands (Bestelmeyer et al., 2015; Eldridge et al., 2011). With increasing anthropic pressures occurring in drylands (Abel et al., 2021; Berg & McColl, 2021; Li et al., 2021; Maestre et al., 2016), integrated management policies are encouraged to consider these interactions for sustaining ecosystem production in larger landscapes. Thus, our findings have important implications for sustainable ecosystem management by considering the influences of land-use pressures (e.g. increasing GI) and biological interactions (shrubs vs. grasses, and plants vs. animals) in drylands.

AUTHOR CONTRIBUTIONS

Xiaoan Zuo and Maowei Liang conceived the study and prepared the data; Maowei Liang contributed to the data analyses; Xiaoan Zuo contributed to collecting the data and led the writing of the manuscript with significant contribution of Maowei Liang; Maowei Liang, Elise S. Gornish, Sally E. Koerner, Fons van der Plas and Shaopeng Wang assisted with the conceptual framework development and paper revision. All authors contributed to the writing process of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data is available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.mpg4f4r54> (Zuo et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The potential scenarios of grazing-induced changes in the dominant species regulating herbaceous community stability via changing population stability and insurance effects in grasslands and shrub-encroached grasslands.

Figure S2. The sampling design and plots distribution map.

Figure S3. A hypothesized full structural equation model depicting potential direct and indirect path effects of grazing intensity on the stability of herbaceous community at multiple scales in drylands.

Figure S4. Dynamics of plant richness of the herbaceous community at multiple scales in drylands under different grazing intensities.

Figure S5. Dynamics of plant diversity (1/Simpson) of the herbaceous community at multiple scales in drylands under different grazing intensities.

Figure S6. Interactive effects of grazing intensity and shrub encroachment on biodiversity of the herbaceous community at multiple scales in drylands.

Figure S7. Dynamics of plant biomass of the herbaceous community in drylands under different grazing intensities.

Figure S8. Interactive effects of grazing intensity and shrub encroachment on plant biomass of the herbaceous community in drylands.

Figure S9. Distinct mechanisms of grazing effects on ecosystem stability across multiple scales in grasslands and shrub-encroached grasslands.

Table S1. Effects of grazing intensity, shrub encroachment, year, and their interactions on richness-based biodiversity metrics in drylands.

Table S2. Effects of grazing intensity, shrub encroachment, and their interactions on the stability at multiple scales in drylands.

Table S3. The mixed-effects of the dominant species (*Stipa glareosa*) for linear mixed-effects models from **Figure 3**, with “the relative abundance of the dominant species” as fixed effects and “grazing intensity” as a random factor ($N=15$); the marginal (R_m^2) and conditional (R_c^2) r^2 represent “fixed effects” and “fixed+random effects” explanations, respectively.

Table S4. The mixed-effects of biodiversity for linear mixed-effects models from **Figure 3**, with “biodiversity” as fixed effects and “grazing intensity” as a random factor ($N=15$); the marginal (R_m^2) and conditional (R_c^2) r^2 represent “fixed effects” and “fixed+random effects” explanations, respectively.

Table S5. Standardized and unstandardized direct effects in our final structural equation model ($N=15$) from **Figure 4a** in grasslands.

Table S6. Individual R^2 of response variables in our final structural equation model ($N=15$) from **Figure 4a** in grasslands.

Table S7. Standardized and unstandardized direct effects in our final structural equation model ($N=15$) from **Figure 4b** in shrub-encroached grasslands.

Table S8. Individual R^2 of response variables in our final structural equation model ($N=15$) from **Figure 4b** in shrub-encroached grasslands.

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