

Article

Temporal Stability of Grazed Grassland Ecosystems Alters Response to Climate Variability, While Resistance Stability Remains Unchanged

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Abstract: Environmental change is a crucial driver shaping grassland biodiversity and stability. Both environmental change and stability contain multiple dimensions. Nonetheless, few studies examined multiple dimensions of stability in response to environmental change, especially under the combined effects of climatic variability and grazing intensity. Here, we conducted a 7-year field sheep grazing experiment, and we evaluated the impacts of grazing intensity (GI) and climate variability (temperature and precipitation variability) on plant community diversity and productivity and multi-dimensional stability using linear and structural equation models. Our results show that increasing grazing intensity significantly decreased temporal stability but did not affect resistance stability. Compared with the non-grazing (NG) treatment, grazing reduced temporal stability by 35.78%. The decline is primarily attributed to the grazing-induced reduction in evenness and weakening of species asynchrony, which in turn impairs insurance effects. The insignificant change in resistance stability was attributed to a trade-off between reduced interspecific competition and direct negative effects. Furthermore, temperature variability and precipitation variability exacerbate and mitigate the effects of grazing on temporal stability (negative) and resistance stability (positive), respectively. Overall, temporal stability is mainly influenced by temperature variability and GI, while resistance stability is mainly affected by GI. Our findings highlight the importance of considering the dimensions of stability and disturbance. Different dimensions of stability may respond differently to disturbance. Multiple disturbances may also interact synergistically or antagonistically on plant community stability.

Keywords: grazing intensity; temperature variability; precipitation variability; temporal stability; resistance stability; asynchrony



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1. Introduction

The investigation of how ecosystem stability responds to environmental change (environmental dependence) and the underlying regulatory mechanisms is a key topic in ecosystem dynamics [1,2]. Ecosystem stability denotes the capacity of an ecosystem to preserve and recover its vegetation structure and function under environmental perturbations [3] and serves as a robust indicator for evaluating grassland ecosystem quality and resilience [3,4]. Natural grasslands deliver many vital ecosystem services, such as carbon storage and crop and livestock production [5]. The long-term persistence of ecosystem functions and services relies on the intrinsic stability of the ecosystem [6]. However, grassland ecosystem productivity and stability are jeopardized worldwide by environmental change, such as climate change and land use change [7–9].

Ecosystem stability encompasses multiple dimensions, including measures of dynamic stability (temporal stability) based on system fluctuations over time, and measures of resistance to change (resilience and resistance stability) based on system responses to perturbations [3]. Despite the recognition of the multidimensionality of stability, most of the current research on the effects of environmental change on stability focused on a single dimension of stability, for various reasons (such as data availability) [4]. Donohue et al. [4] reviewed and reported that this proportion was over 90%. Among the few studies that examined the effects of environmental change on multiple dimensions of stability, a common finding is that different dimensions of stability show divergent responses to disturbances [4,10–12]. For instance, Xu et al. [11] showed that nitrogen addition enhanced the resilience of plant community productivity after drought, but not its resistance, and Ganjurjav et al. [12] demonstrated that grazing decreased the resilience of alpine grassland, but had no significant impact on its resistance. Moreover, the relationship between diversity and stability can vary depending on the definition of stability [13]. Experimental and modeling evidence suggests that diversity can have positive, negative, or neutral effects on different aspects of stability, such as temporal variability, resistance, and resilience [1,14–18]. These examples imply that there could be divergent responses among different dimensions of stability concerning environmental change and biodiversity. Therefore, a multidimensional framework is needed to study stability [4,10]. Focusing on a single aspect of stability may lead to an inaccurate estimation of the potential impacts of disturbance on stability [19,20]. Elucidating how different aspects of stability respond to environmental changes, including changes in plant community attributes induced by environmental change, is crucial for understanding productivity stability [19].

Ecosystems are exposed to multiple disturbances [21]. Nonetheless, more than 80% of experimental and observational research focused on a single disturbance factor, which may lead to biased estimates of the effects of disturbance on ecosystem stability [4]. Grassland ecosystems are currently undergoing climate change (such as changes in temperature and precipitation) and land use change (such as livestock grazing), which may alter their stability [9]. Recent studies showed that grazing can modify productivity stability, either directly or indirectly, through altering plant dominance, species richness, and asynchrony [8,22–24]. Likewise, climate change may also influence grassland ecosystem stability by enhancing niche stability and shifting interspecific competition relationships [25]. There is evidence for negative [26], positive [27], and neutral [28] effects of precipitation on productivity stability. Increased temperature variability was also widely reported to increase community productivity stability (but not always) in temperate grassland [25,28]. Furthermore, studies demonstrated that biodiversity changes induced by environmental change affect ecosystem stability through species asynchrony and species stability [29]. Diversity changes can affect ecosystem functions such as community biomass, and thereby influence stability (over-yielding effect), as well as affect the capacity of ecosystems to buffer stability against environmental fluctuations (insurance effect) [15,30]. In the context of global climate change, the stability of grassland productivity is influenced by grazing in complex and dynamic ways [31]. This leads to inconsistent responses of grazing to stability, with positive [32], neutral [33], and negative [34] effects. Therefore, to understand how grassland productivity stability responds to grazing intensity, it is necessary to consider not only the regulation function of the plant community but also the co-variation in climatic factors [31].

The objective of the study was to elucidate the influence of grazing intensity and climate variability on ecosystem stability, encompassing both temporal and resistance stability, within long-term grazed grassland ecosystems. To accomplish this goal, we conducted a field experiment to manipulate sheep grazing intensity for seven years (2014–2020) on a semi-arid grassland in Inner Mongolia, China. We hypothesized that grazing and climatic factors would have contrasting impacts on productivity stability and that different components of stability would respond differently. To address this hypothesis, we examined the following three questions: (1) How does increasing grazing intensity influence community structure dynamics and productivity stability? (2) How do grazing

intensity, precipitation variability, and temperature variability covary in their effects on different components of productivity stability? (3) What are the environmental drivers of the changes in different components of productivity stability under grazing?

2. Materials and Methods

2.1. Study Site

The site of this study is located at Xilinhot City, Inner Mongolia, China (44°08' N, 116°19' E, 1118 m a.s.l.). Over the past six decades (from 1960 to 2020), the mean annual precipitation was about 279.54 mm, of which nearly 85% occurred during the growing season from May to September. The mean annual temperature rapidly increased by 2.4 °C. The study area is classified as having a temperate semi-arid climate (BSk) according to the Köppen climate classification system. The biota of the site is the typical grassland, which is mainly dominated by *Stipa grandis* P. Smirn (perennial bunchgrass) and *Leymus chinensis* Trin. Tzvel (perennial rhizome grass). Grassland grazing history at the site was low-intensity grazing by sheep (~ 0.5 sheep·day⁻¹·ha⁻¹). Soil is Calciustoll, according to the US soil taxonomy classification.

2.2. Experimental Design and Sampling

2.2.1. Experimental Design

We fenced 12 equal-sized (120 × 120 m) paddocks in 2013 and implemented four grazing intensity treatments from 2013 to 2020, referred to as no grazing (NG: 0 sheep·ha⁻¹·day⁻¹), low grazing (LG: 2 sheep·ha⁻¹·day⁻¹), medium grazing (MG: 4 sheep·ha⁻¹·day⁻¹), and heavy grazing (HG: 8 sheep·ha⁻¹·day⁻¹), respectively [35]. We implemented a randomized block design with three replications of each grazing treatment. A 21-day grazing operation is organized at the beginning of each month during the annual growing season (from June to September), with sheep as the grazing animals.

2.2.2. Sampling

We divided each plot (120 × 120 m) into five subplots (120 × 24 m) virtually and placed one 1 m² quadrat on each. We recorded all vascular plants in each sub-sample plot by species and then mowed and collected all residual living aboveground tissues. Plant tissues were oven-dried at 65 °C for 48 h and then weighed to estimate the biomass of each species (g·m⁻²). We collected these data during the growing seasons (May–September) from 2014 to 2020, with a total of 2100 sample squares (7 years × 5 months × 4 treatments × 3 replicates × 5 sample squares). Further detailed descriptions of the experiments can be found in Liang et al. [8].

2.3. Calculations

2.3.1. Biodiversity, Asynchrony, and Stability

Species richness in each plot was defined as the total number of species detected in the five quadrats. We also calculated the Shannon–Wiener index [36] based on the species richness: $H = -\sum_{i=1}^S p_i \times \ln p_i$, where H denotes the Shannon–Wiener index, p_i denotes the relative biomass of species i in the local community, and S is the number of species in the local community. We defined the Pielou evenness index [37]:

$$Pielou = H/\ln S \quad (1)$$

where H denotes the Shannon–Wiener index, and S denotes the number of species in the local community. The degree of species asynchrony was quantified by the community asynchrony index [38],

$$\text{defined as } asynchrony = 1 - \sigma_{b_T}^2 / \left(\sum_{i=1}^N \sigma_{b_i}^2 \right) \quad (2)$$

where $\sigma_{b_T}^2$ denotes the variance of community biomass, and σ_{bi} denotes the s.d. of biomass of species i in a plot with N species.

In addition, we defined temporal stability [39] as well as resistance stability [40]. We calculated temporal 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. Resistance stability is defined as the ratio of the absolute difference between the mean total biomass under the grazing treatment and the enclosed treatment to the corrected grazing intensity, which characterizes the resistance and sensitivity of ecosystems to stressful disturbances. The mathematical formulas for these definitions are:

$$ts = \sigma / \mu \text{ and } res = (\overline{B_g} - \overline{B_n}) / (\overline{B_g} \times GI), \quad (3)$$

where ts represents temporal stability, μ and σ represent the inter-annual mean and standard deviation of community ANPP for every month of the growing season (May to September) over the seven years, respectively, and res represents resistance stability, GI represents grazing intensity, and $\overline{B_g}$ and $\overline{B_n}$ represent the above-ground biomass of grazing plots enclosed non-grazing plots, respectively.

2.3.2. Climate Data

Furthermore, we quantified climatic variability as the coefficient of variation (CV), which reflects the interannual fluctuations of mean temperature and total precipitation (hereafter denoted as CV_{tem} and CV_{pre} , respectively). Similar to community temporal stability, the inter-annual coefficients of variation were calculated as $\sigma / \mu \times 100$, where μ and σ were the inter-annual temporal mean and standard deviation of mean temperature or total precipitation for May to September across 2014–2020 (Figure A1).

2.4. Statistical Analysis

In this study, all statistics have critical significance levels of $p < 0.05$. We used the Shapiro–Wilk normality test for the normality of variance for each data set. To assess the effects of grazing intensity and grazing month on species asynchrony, temporal stability, and resistance stability, we used repeated measures ANOVA using R package *ez* (*ezANOVA* function). In this analysis, the grazing month was used as a within-subjects factor and grazing intensity as a between-subjects factor. The Tukey’s range test was used to examine differences between grazing intensities. In addition, we conducted repeated measures ANOVA to examine the effects of grazing intensity, grazing duration year (Y: 2014–2020), and grazing month on productivity and the Shannon–Wiener diversity index. Grazing intensity was used as a between-subjects factor, while month and grazing duration year were both used as within-subjects factors.

Furthermore, to assess the effects of climate variability (CV_{tem} and CV_{pre}) on ecosystem stability (species asynchrony, temporal stability, and resistance stability), we fitted a linear mixed model and nonlinear regression. We used grazing intensity as a stochastic intercept to determine the optimal models based on the minimum Akaike information criterion (AIC), while marginal R^2 (R_m^2) and condition R^2 (R_c^2) were calculated for the linear mixed model, and this analysis was conducted in the *lme4* package. Simultaneously, we used multiple regression to determine the main factors influencing ecosystem stability. We used the mean ranking method to determine the relative importance by decomposing R^2 . This analysis was conducted in the R package *relaimpo*.

Finally, we constructed SEM to explore how grazing intensity, monthly mean temperature variability, and precipitation variability impact ecosystem stability by regulating community properties. We hypothesized that grazing intensity, CV_{tem} , and CV_{pre} might directly affect plant diversity and species asynchrony. We also hypothesized that changes in diversity or species asynchrony would further modulate ecosystem temporal stability or resistance stability. First, we used Shipley’s d-separation test to ensure that all meaningful pathways were included ($p > 0.05$). Then, we selected the final SEM according to the

minimum Akaike information criterion (AIC). We calculated the explanatory R^2 for each dependent variable. All SEMs were constructed in the R package piecewise SEM [41]. All analysis and visualization processes were performed in R version 4.0.3.

3. Results

3.1. Effects of Grazing Intensity, Temperature Variability, and Precipitation Variability on Plant Community Diversity and Species Asynchrony, Temporal Stability

Our results show that GI significantly reduced above-ground biomass, diversity, species asynchrony, and temporal stability (Figures 1a,b and A2, Tables 1 and A2). Specifically, compared to the no grazing (NG) treatment, heavy grazing reduced diversity, species asynchrony, and temporal stability by 59.44% and 35.78%, and 35.78%, respectively (Figure 1a,b, Table A1). Furthermore, SEM and linear mixed models indicated that grazing reduced temporal stability indirectly by reducing species asynchrony and dominant functional groups and diversity (Figures 2a,c, 3a, A3a,b,d,e, and A4a).

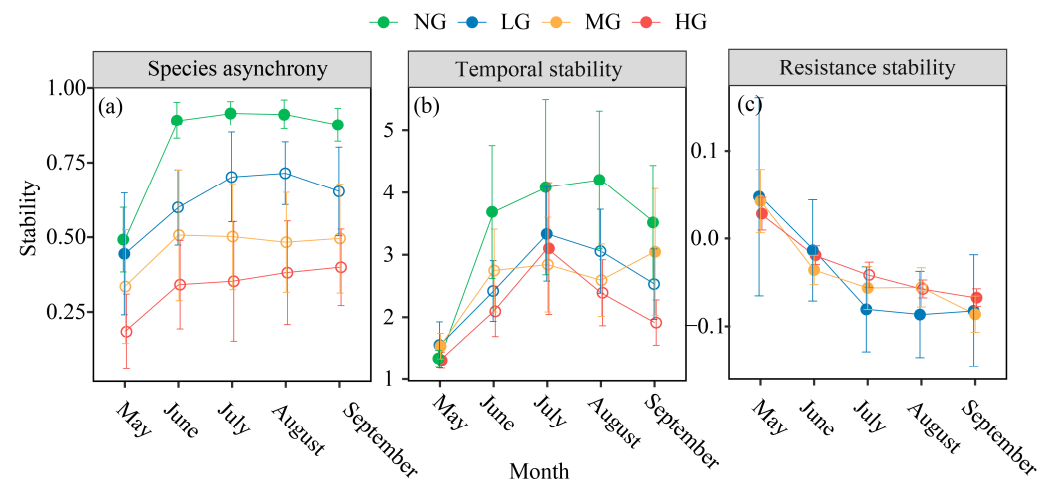


Figure 1. Seasonal dynamics of the effects of different grazing intensity (GI) on species asynchrony and community stability. (a) Figure shows the variable effect of GI on species asynchrony within different months, (b) figure shows the temporal stability of productivity, and (c) figure shows the stability of resistance. Multiple comparisons between different grazing intensities were conducted using the Tukey-test method. Cyan lines and dots represent no grazing (NG), blue represents light grazing (LG), yellow represents moderate grazing (MG), red represents heavy grazing (HG), and hollow dots represent significant differences compared to no grazing ($p < 0.05$).

Table 1. Seasonal dynamics of the effects of different grazing intensity on species asynchrony and community stability.

	GI		M		GI × M	
	F	p	F	p	F	p
Species asynchrony	20.87	<0.001	0.40	0.54	0.60	0.63
Temporal stability	13.19	0.002	0.15	0.71	0.42	0.74
Resistance stability	0.49	0.64	69.08	0.001	0.83	0.48

Note: Grazing intensity was considered as a between-subjects factor and month as a within-subjects factor for repeated measures. GI is grazing intensity, M is month, and GI × M is grazing and month interactions, with values in bold indicating significant difference significance: $p < 0.05$, 95% confidence level, $n = 3$).

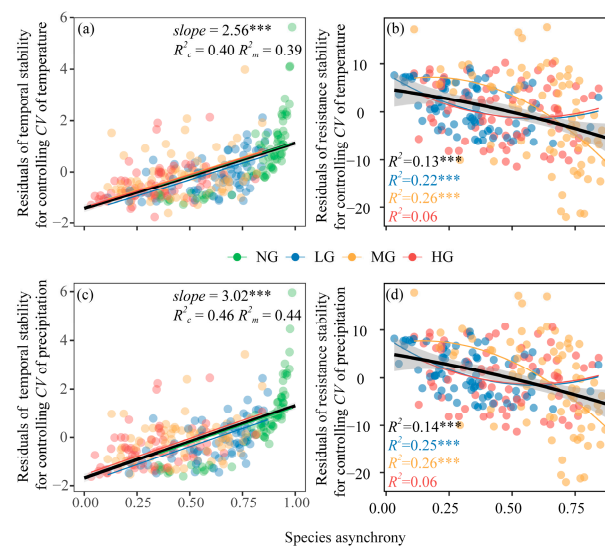


Figure 2. The relationship between species asynchrony and ecosystem stability. The upper panels (a,b) show the relationship between species asynchrony and stability with controlled CV_{tem} , and the lower panels (c,d) show the relationship between species asynchrony and stability with controlled CV_{pre} . The significant level: *** $p < 0.001$.

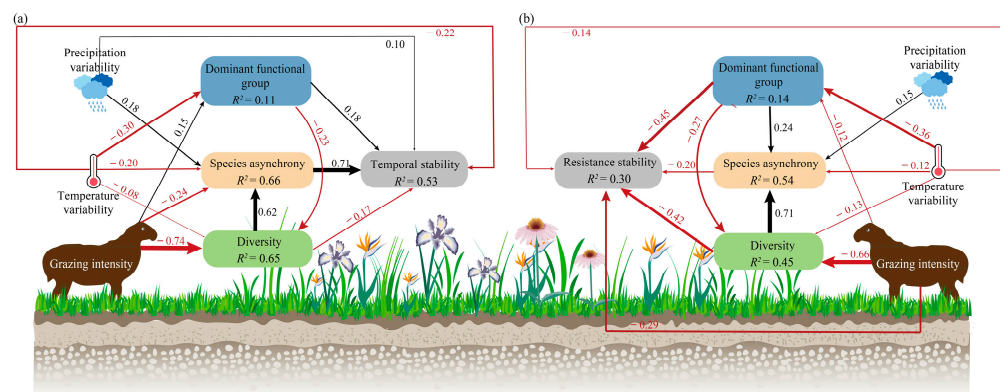


Figure 3. The structural equation model (SEM) depicts the direct and indirect effects of grazing intensity and climate variability on ecosystem stability; (a) figure shows the direct and indirect impact of GI, monthly precipitation variability, and monthly mean temperature variability on temporal stability, and (b) figure shows the direct and indirect impact of GI and climate variability on resistance stability. The black and red arrows denote positive and negative associations, respectively, thicker lines indicate stronger correlations, and the values above the lines indicate standardized impact path coefficients. (a) Model parameters are: Fisher's $C = 4.11$, p -value = 0.66, $Df = 6$, $AIC = 50.11$, and $BIC = 135.30$; (b) model parameters are: Fisher's $C = 10.79$, p -value = 0.21, $Df = 8$, $AIC = 54.79$, and $BIC = 129.94$. Diversity is the alpha diversity PCA1 score and R^2 is the explained percentage. Here, diversity denotes the alpha diversity PCA1 score provided in Figure A1. Information about the direct and indirect effect levels of GI and climate variability on temporal and resistance stability is provided in Figure A5.

Furthermore, CV_{tem} exhibited a negative association with species asynchrony and temporal stability (Figure 4a,b), whereas CV_{pre} showed no significant relationship with these variables (Figure 4d,e). SEM and partial correlation analyses revealed that CV_{tem} directly diminished temporal stability, while indirectly reducing temporal stability by decreasing species asynchrony and dominant functional groups (Figures 3a, 4a,c, and A4a). Conversely, CV_{pre} increased temporal stability both directly and indirectly by increasing species asynchrony (Figures 3a, 4d–f, A3a,b,d,e and A4a). Overall, the relative contributions

of GI, CV_{tem} , and CV_{pre} to temporal stability were 44.39%, 48.95%, and 6.66%, respectively (Figure 5b). Environmental variables together explained 53% of the variation in temporal stability (Figure 3a).

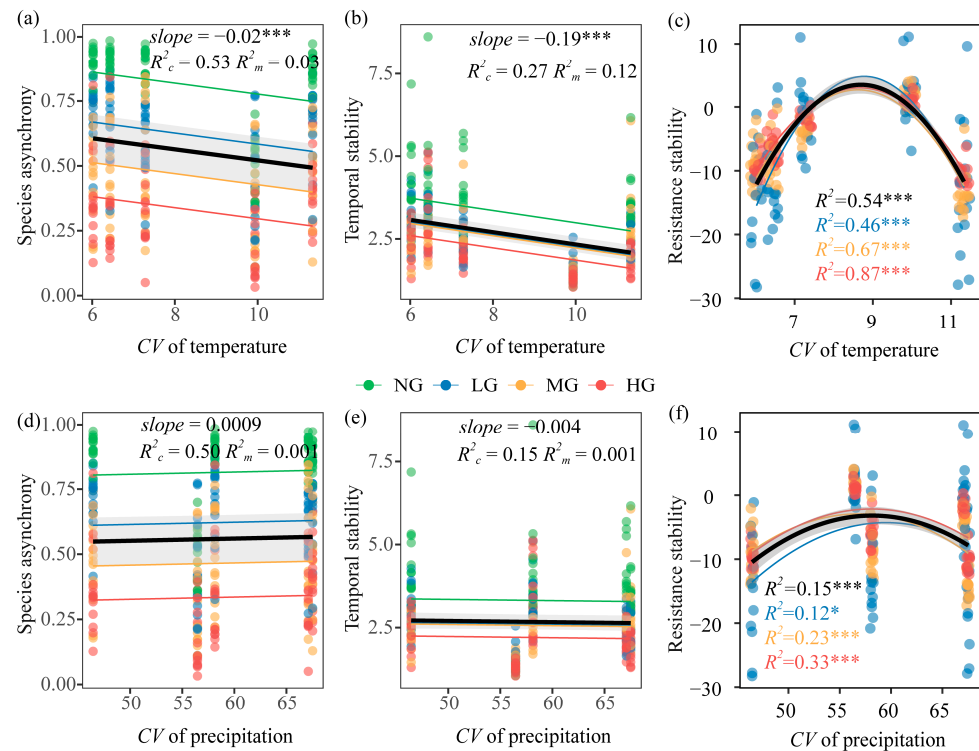


Figure 4. The relationship between climate variability and ecosystem stability. The upper panels (a–c) show the relationship between CV_{tem} and stability, and the lower panels (d–f) show the relationship between CV_{pre} and stability; (a,d) figures show the relationship between species asynchrony and climate variability, (b,e) figures show the relationship between temporal stability of productivity and climate variability, both fitted with a linear mixed model in which GI was used as a random intercept, and (c,f) figures show the relationship between resistance stability and climate variability, fitted with quadratic nonlinear fits. Slope is the slope of the linear mixed model, R^2_c = conditional R^2 and R^2_m = marginal R^2 , cyan lines, and dots represent no grazing (NG), blue represents light grazing (LG), yellow represents moderate grazing (MG), and red represents heavy grazing (HG). The significant level: * $p < 0.05$, *** $p < 0.001$.

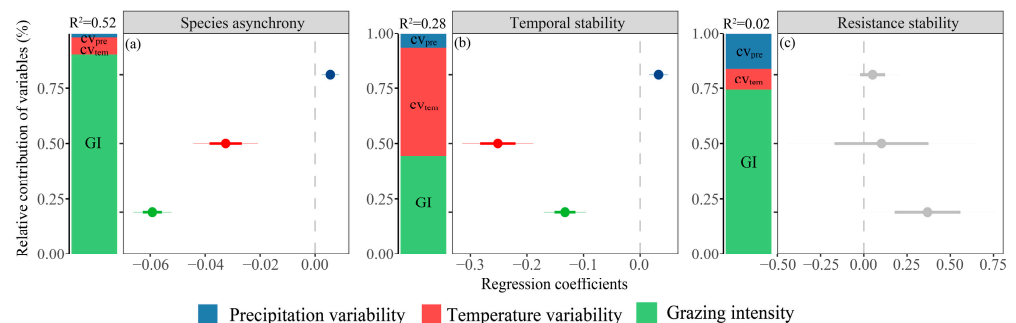


Figure 5. Effects of grazing intensity, precipitation variability, and temperature variability on ecosystem stability; (a–c) show multiple regression coefficients for GI, CV_{tem} , and CV_{pre} and the relative contributions to ecosystem stability. Dark lines indicate standard errors, light lines indicate 95% confidence intervals, colored dots indicate significance ($p < 0.05$), blue represents CV_{pre} , red represents CV_{tem} , and green represents GI. The covariance indices (VFI) for GI, CV_{pre} , and CV_{tem} were 1.00, 1.41, and 1.42, respectively.

3.2. Effects of Grazing Intensity, Temperature Variability, and Precipitation Variability on Resistance Stability

Multiple regression analysis indicated that GI, CV_{tem} , and CV_{pre} exerted positive but nonsignificant influences on resistance stability (Figures 1c and 5, Table 1). Environmental variables together explained 30% of the variation in resistance stability (Figure 3b).

GI represented the major influence on resistance stability, with a relative contribution of 74.39% (Figure 5). It was observed that grazing influences resistance stability through indirect positive effects on diversity and major species functional groups and direct negative effects (Figures 3b and A4b). Remarkably, both CV_{tem} and CV_{pre} showed significant unimodal relationships with resistance stability at all grazing intensities (Figure 4c,f).

4. Discussion

4.1. Grazing Impacts the Temporal Stability of Productivity, Not Resistance Stability

In general, plant community composition is strongly influenced by livestock grazing [42]. Nonetheless, the variation and trend of community composition change depending on the specific grazing conditions [42]. Our experiment observed that under light and moderate grazing, the selective feeding behavior of sheep resulted in the preferential consumption of palatable and nutritionally rich species, such as *L. chinensis*. This led to a further increase in the dominant position of the less palatable dominant species *S. grandis* (Figure A6) [8]. However, under heavy grazing, the increased foraging intensity reduced food selectivity, and the abundance of dominant species such as *S. grandis* and *L. chinensis* decreased. The release of available ecological niches promoted the emergence of rare and annual or biennial species, such as *Salsola collina* and *Dysphania aristata* [22]. Consequently, grazing intensity altered the community structure, shifting the community composition towards more grazing-tolerant species under light and moderate grazing, while heavy grazing diminished the dominance of dominant species and enhanced the colonization of opportunistic species.

Consistent with our hypothesis that grazing intensity affects the stability of production in temperate arid grassland, we found that grazing reduced the stability of ANPP. Specifically, grazing intensity decreased temporal stability but did not affect resistance stability significantly [8,34,43,44]. The detrimental effect of grazing intensity on temporal stability was extensively documented, and asynchrony was identified as a major factor reducing temporal stability across many studies [34,44]. It is noteworthy that our results demonstrate that grazing reduced temporal stability by decreasing mean and increasing SD via modulating species asynchrony (Figures 2, A3 and A7). This implies that grazing impaired productivity temporal stability due to a reduction in asynchrony that impaired insurance effects [16]. Moreover, SEM indicates that grazing diminished the temporal stability of the community by lowering its evenness and weakening the asynchrony among species in response to environmental fluctuations. This outcome supports the theoretical prediction of the synergistic effect of grazing and species asynchrony mediated by evenness [45]. By preferentially consuming palatable species such as *L. chinensis*, sheep increase the competitive advantage of the more grazing-resistant bunchgrass *S. grandis* in the community, resulting in reduced community evenness. Lower community evenness diminishes the asynchronous response of species to environmental fluctuations [8,34,43], and lower species asynchrony reduces the insurance effect of biodiversity on temporal stability [44]. Our findings suggest that species asynchrony associated with plant community evenness is a key factor for maintaining the productivity stability of the grazing grassland ecosystem.

Contrary to temporal stability, grazing only exerted a negligible positive effect on resistance stability, which concurred with the findings of a grazing experiment in alpine grassland [12]. Remarkably, SEM demonstrated that the limited effect can be attributed to indirect positive impacts counterbalancing the direct negative effects of grazing (Figure A4b). It is widely acknowledged that increased grazing pressure can result in a decline in plant cover and biodiversity, thereby reducing the ecosystem's resistance to grazing [32]. Our observations are consistent with this finding. Concurrently, we found that intensified

grazing indirectly enhanced resistance stability by reducing community evenness and dominant functional groups. Firstly, sheep foraging reduced interspecific competition by diminishing evenness and dominance of dominant species [46]. Secondly, the resource release resulting from the decline in the dominance status of the dominant species not only leads to reduced competition for the light within the community and higher regeneration rates, but also promotes resource acquisition and the foraging resistance trait performance of regenerating plants [32]. Thirdly, with increasing grazing pressure, the dominant species *S. grandis* exhibits higher resistance to grazing and drought [47]. Thus, we concluded that the direct negative effects of grazing intensity were counterbalanced by the positive effects of reduced interspecific competition and increased stability of dominant species, leading to only a slight positive effect of grazing on resistance stability. In summary, different stability components displayed varying responses to grazing, with the reduction in productivity stability primarily evident in temporal stability rather than resistance stability.

4.2. Opposing Regulatory Effects of Precipitation and Temperature Variability on Productivity Stability in Grazing Ecosystems

Climate warming and frequent extreme climatic events pose a threat to biodiversity, ecosystem functioning, and stability [28]. Our results demonstrate that temperature variability significantly reduced temporal stability, whereas precipitation variability had no significant effect. The effect of climate variability on temporal stability is consistent with that of a warming and rainfall manipulation experiment on the Tibetan Plateau [28]. Our study area underwent rapid warming in the past 60 years [8], and temperature variability affected temporal stability through two different pathways: on one hand, the increase in temperature variability decreased the asynchronous response of coexisting species to environmental fluctuations by increasing the species extinction rate [48], thereby lowering temporal stability (Figure 3); on the other hand, temperature variability indirectly reduced temporal stability (lower mean) by decreasing the biomass of dominant species (Figure A7) [49]. The precipitation variability and temperature variability have opposite effects on temporal stability (Figure A4a). The mild variation in precipitation amount within the study area could briefly create different ecological niches, and species with different niches could enhance ecosystem temporal stability by responding asynchronously to relative abundance [15,50].

Consistently, our study revealed that temperature and precipitation variability exerted contrasting effects on resistance stability, albeit not statistically significant. Nonetheless, in contrast to temporal stability, mean temperature variation exhibited a weak positive impact on resistance stability, whereas the precipitation variability showed a weak negative influence. Moreover, regression analysis results indicate that mean temperature and precipitation variability had significant unimodal effects on resistance stability, and the relationship was stronger with higher grazing intensity (Figure 4c,f). This finding suggests a consistent synergistic association between climate variability and resistance stability, emphasizing that excessively low or high climate variability does not facilitate the enhancement of resistance stability [51,52]. Smaller climate fluctuations (rare) are unfavorable for the long-term survival of species under superior conditions [51], while heightened climate fluctuations may diminish species persistence by escalating extinction rates [52]. Thus, moderate climate fluctuations promote the improvement of resistance stability, whereas the occurrence of extreme climatic events can significantly undermine resistance stability.

Generally, multiple disturbances exhibit intricate interactions that shape the stability of productivity [10]. In semiarid grassland ecosystems, mean temperature and precipitation variability affected community stability in opposite ways. Temperature variability amplified the effect of grazing intensity on stability, whereas precipitation variability buffered the effect of temperature variability on ecosystems, for both temporal and resistance stability.

4.3. Mechanisms for Maintaining the Stability of Grassland Productivity under Climate Variability

Ongoing climate change, as well as long-term overgrazing, is threatening ecosystem stability in semiarid grassland ecosystems [31]. Our study elucidated the mechanisms

through which grazing intensity and climate variability synergistically impact the stability of grassland productivity. Overall, grazing and climate variability affected stability mainly through temporal stability. On one hand, with increasing grazing intensity, sheep selectivity foraging decreased community evenness, which reduced species asynchrony and lowered productivity stability. On the other hand, climate variability (mainly temperature variability) reduced species asynchrony by increasing species extinction rates, thereby decreasing productivity stability. Conversely, precipitation variability enhanced species asynchrony by increasing species coexistence, albeit weakly. Furthermore, while our investigation did not ascertain significant alterations in resistance stability as a consequence of grazing intensity and climate variability, the persistent response of plant diversity to environmental changes may still engender heightened community resistance stability in the future.

Environmental change-induced shifts in biodiversity are a key determinant of ecosystem stability [2]. Consistent with the prevailing consensus, our results support the positive role of plant communities in temporal stability and the negative role in resistance stability [53,54]. Our experiment demonstrated that species stability (particularly for dominant species) and species asynchrony promote productivity stability [54]. However, high species richness, asynchrony, and abundance of dominant species (biomass, coverage) are frequently accompanied by more intense interspecific competition relationships. This competition exclusion reduces the resistance of ecosystems to risks [22,55]. In grazed grassland ecosystems under climate variability, the biodiversity–productivity stability relationship affects productivity stability through two mechanisms. On the one hand, positive interspecific interactions mitigate the negative deviation of communities from environmental changes; on the other hand, the destructive potential of competitive exclusion among species reduces the risk resistance of communities to environmental changes. Consequently, alterations in interspecific relationships within plant assemblages (the trade-off between competition and cooperation) determine the direction and strength of the diversity–stability relationship.

5. Conclusions

In conclusion, we present novel empirical evidence that in long-term grazed grassland ecosystems, there exist synergistic and antagonistic effects simultaneously between grazing intensity and climate variability (precipitation and temperature) in driving different dimensions of stability. Simultaneously, the main drivers of the diversity–stability relationship differ across stability metrics. These results imply that relying on a single stability metric may lead to inaccurate assessments of productivity stability and underestimate the vulnerability to environmental perturbations. Future studies should assess the response of different dimensions of productivity stability to disturbances. Furthermore, we demonstrate that grazing influences different stability metrics of plant communities directly and indirectly through its impact on biodiversity. Temperature variability exacerbates the effects of grazing on stability, while precipitation variability buffers them. Thus, disentangling the interaction between grazing and climate is essential for understanding the changes in stability attributes in grazed ecosystems. Moderate climate variability enhances ecosystem stability, while excessive grazing may compromise productivity stability.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agronomy13082030/s1>, Table S1: Original dataset employed for data analyses included in the manuscript.

Author Contributions: Conceptualization, Z.L., C.L., J.Z., L.W., Y.W. and Y.H.; methodology, Z.L., Y.W. and Y.H.; software, B.M. and J.C.; validation, Y.W. and Y.H.; formal analysis, Y.W. and Y.H.; investigation, H.L. (Hao Li) and H.L. (Hangyu Li); resources, Z.L. and C.L.; data curation, J.C.; writing—original draft preparation, Y.W. and Y.H.; writing—review and editing, Z.L., C.L., J.Z., Y.W. and Y.H.; visualization, Y.W. and Y.H.; supervision, Z.L., C.L. and J.Z.; project administration, Z.L.; funding acquisition, Z.L. and C.L. All authors have read and agreed to the published version of the manuscript. Y.W. and Y.H. contributed equally to this article.

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Appendix A

Table A1. The effects of grazing intensity on ecosystem stability (i.e., species asynchrony, temporal stability, and resistance stability) for the growing season were analyzed.

Month	GI	Species Asynchrony	Temporal Stability	Resistance Stability
		Mean $\pm$ Std	Mean $\pm$ Std	Mean $\pm$ Std
May	HG	0.18 $\pm$ 0.13 c	1.31 $\pm$ 0.13 b	0.03 $\pm$ 0.019 a
	LG	0.44 $\pm$ 0.20 ab	1.56 $\pm$ 0.37 a	0.05 $\pm$ 0.11 a
	MG	0.34 $\pm$ 0.19 bc	1.54 $\pm$ 0.20 a	0.04 $\pm$ 0.04 a
	NG	0.49 $\pm$ 0.11 a	1.34 $\pm$ 0.13 ab	
June	HG	0.34 $\pm$ 0.15 c	2.09 $\pm$ 0.40 b	−0.02 $\pm$ 0.01 a
	LG	0.60 $\pm$ 0.13 b	2.42 $\pm$ 0.49 b	−0.01 $\pm$ 0.06 a
	MG	0.51 $\pm$ 0.22 b	2.75 $\pm$ 0.66 b	−0.04 $\pm$ 0.02 a
	NG	0.89 $\pm$ 0.06 a	3.69 $\pm$ 1.07 a	
July	HG	0.35 $\pm$ 0.20 c	3.10 $\pm$ 1.06 ab	−0.04 $\pm$ 0.01 a
	LG	0.70 $\pm$ 0.15 b	3.33 $\pm$ 0.75 ab	−0.08 $\pm$ 0.05 b
	MG	0.50 $\pm$ 0.18 c	2.84 $\pm$ 0.76 b	−0.06 $\pm$ 0.02 ab
	NG	0.92 $\pm$ 0.04 a	4.09 $\pm$ 1.41 a	
August	HG	0.39 $\pm$ 0.17 c	2.39 $\pm$ 0.53 b	−0.06 $\pm$ 0.01 a
	LG	0.71 $\pm$ 0.11 b	3.06 $\pm$ 0.67 b	−0.09 $\pm$ 0.05 b
	MG	0.48 $\pm$ 0.17 c	2.59 $\pm$ 0.58 b	−0.06 $\pm$ 0.02 a
	NG	0.91 $\pm$ 0.05 a	4.20 $\pm$ 1.11 a	
September	HG	0.40 $\pm$ 0.13 c	1.91 $\pm$ 0.36 c	−0.07 $\pm$ 0.01 a
	LG	0.65 $\pm$ 0.15 b	2.53 $\pm$ 0.56 bc	−0.08 $\pm$ 0.06 a
	MG	0.50 $\pm$ 0.18 c	3.05 $\pm$ 1.02 ab	−0.09 $\pm$ 0.02 a
	NG	0.88 $\pm$ 0.06 a	3.52 $\pm$ 0.92 a	

Note: Multiple comparisons among grazing intensities were conducted using the Tukey's test (mean $\pm$ std, $n = 3$). Significant differences between any two groups with different lowercase letters were observed at $p < 0.05$. NG refers to no grazing, LG refers to light grazing, MG refers to moderate grazing, and HG refers to heavy grazing.

Table A2. Repeated measures ANOVA table for the effects of grazing, year and month on biodiversity and biomass.

	Biomass		Shannon-Wiener	
	F	P	F	P
GI	39.15	<0.001	12.37	0.002
Y	46.10	<0.001	5.55	0.04
M	195.26	<0.001	2.40	0.16
GI × Y	1.95	0.20	17.47	<0.001
GI × M	37.51	<0.001	1.79	0.23
Y × M	0.35	0.57	64.93	<0.001
GI × Y × M	11.50	0.003	18.95	<0.001

Note: Grazing intensity was considered as a between-subjects factor, and year and month as within-subjects factors for repeated measures. GI refers to grazing intensity, Y refers to year, M refers to month, GI × Y refers to grazing and year interaction, GI × M refers to grazing and month interaction, Y × M refers to year and month interaction, and GI × Y × M refers to grazing year and month interaction, with values in bold indicating significant differences significance: $p < 0.05$, 95% confidence level).

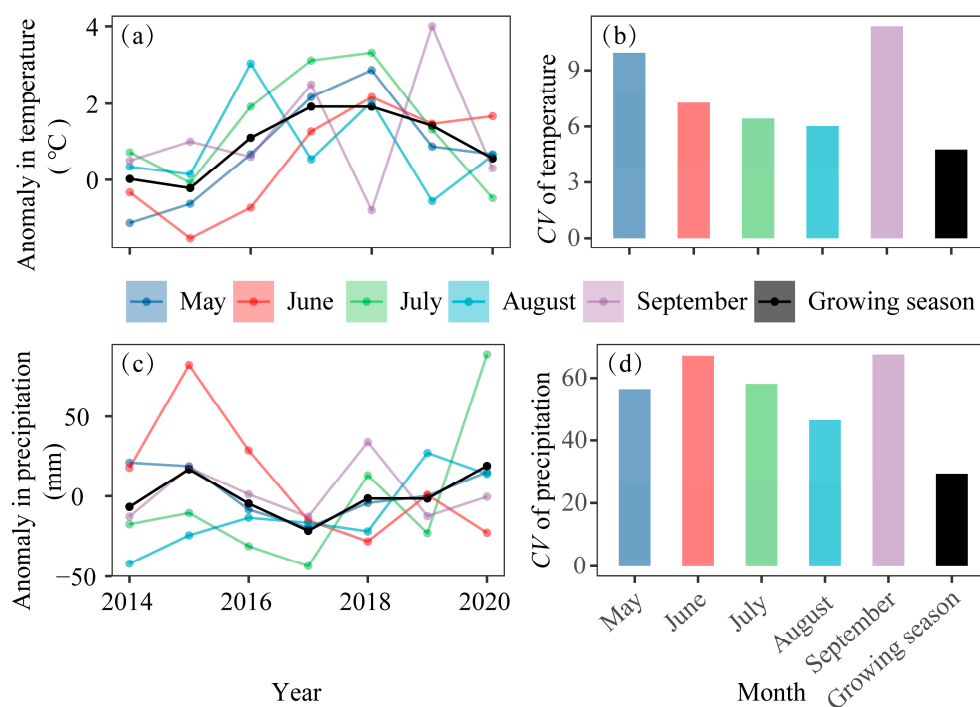


Figure A1. Monthly mean temperature and monthly precipitation anomaly and variance distribution during the growing season from 2014 to 2020. (a) Figure shows the interannual dynamics of monthly mean temperature and growing season mean temperature anomalies between 2014 and 2020, (b) figure shows monthly precipitation and growing season precipitation variability between 2014 and 2020, (c) figure shows interannual dynamics of monthly precipitation anomalies between 2014 and 2020, and (d) figure shows monthly precipitation variability between 2014 and 2020. Blue lines and bars indicate May, red represents June, cyan represents July, light blue represents August, purple represents September, and black represents the whole growing season.

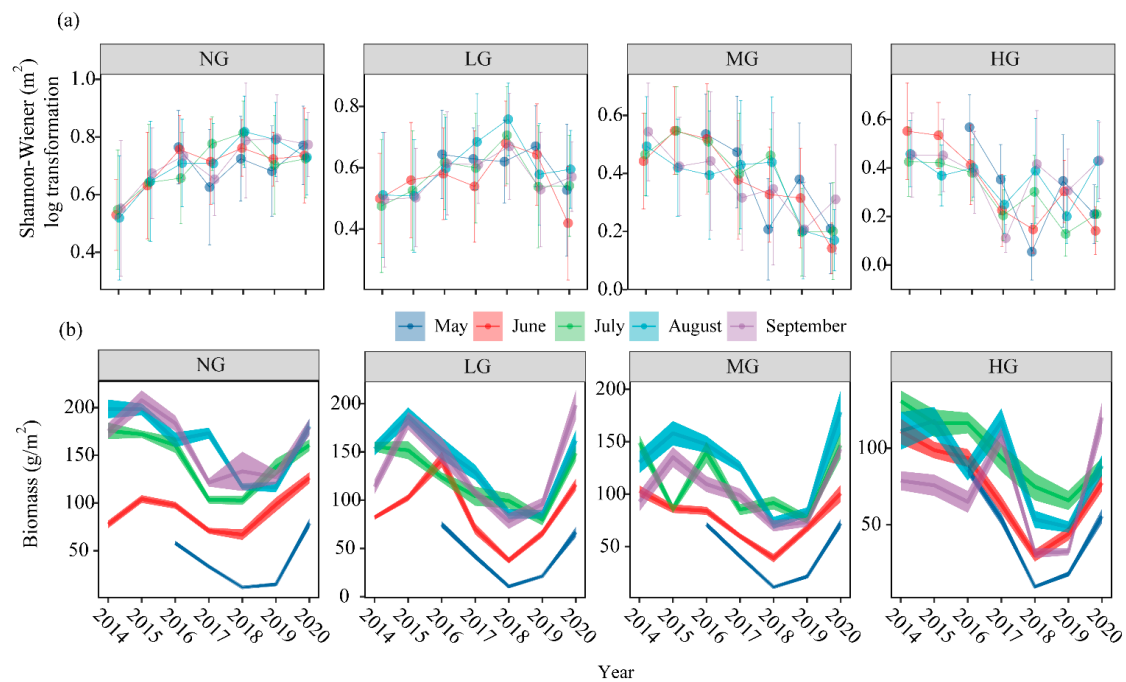


Figure A2. Interannual dynamics of biodiversity and productivity under different grazing intensities in different months. The upper panel (a) shows the interannual dynamics of Shannon–Wiener index for each month under different grazing intensities, and the lower panel (b) shows the interannual dynamics of the above-ground biomass for each month under different grazing intensities, and the multiple comparisons between months were conducted using the Tukey-test method. NG refers to no grazing, LG refers to light grazing, MG refers to moderate grazing, and HG refers to heavy grazing. Hollow dots represent significant differences compared to May (the significant level: $p < 0.05$). Dark blue lines and dots represent May, red represents June, cyan represents July, light blue represents August, and purple represents September.

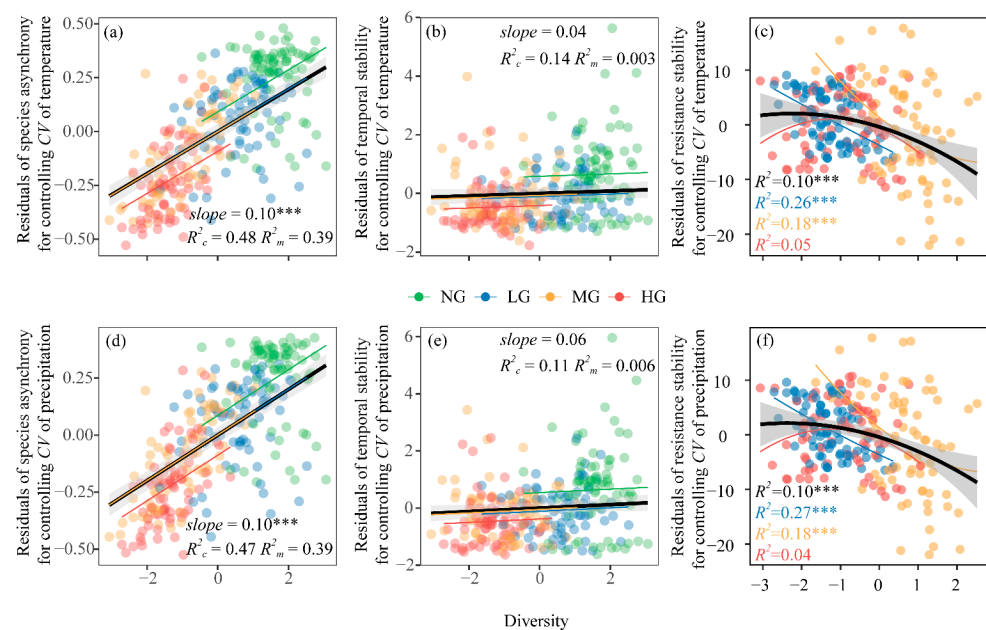


Figure A3. The relationship between diversity and ecosystem stability. The upper panels (a–c) show the relationship between diversity and stability with controlled temperature variation, and the lower panels (d–f) show the relationship between diversity and stability with controlled precipitation variation. The significant level: *** $p < 0.001$.

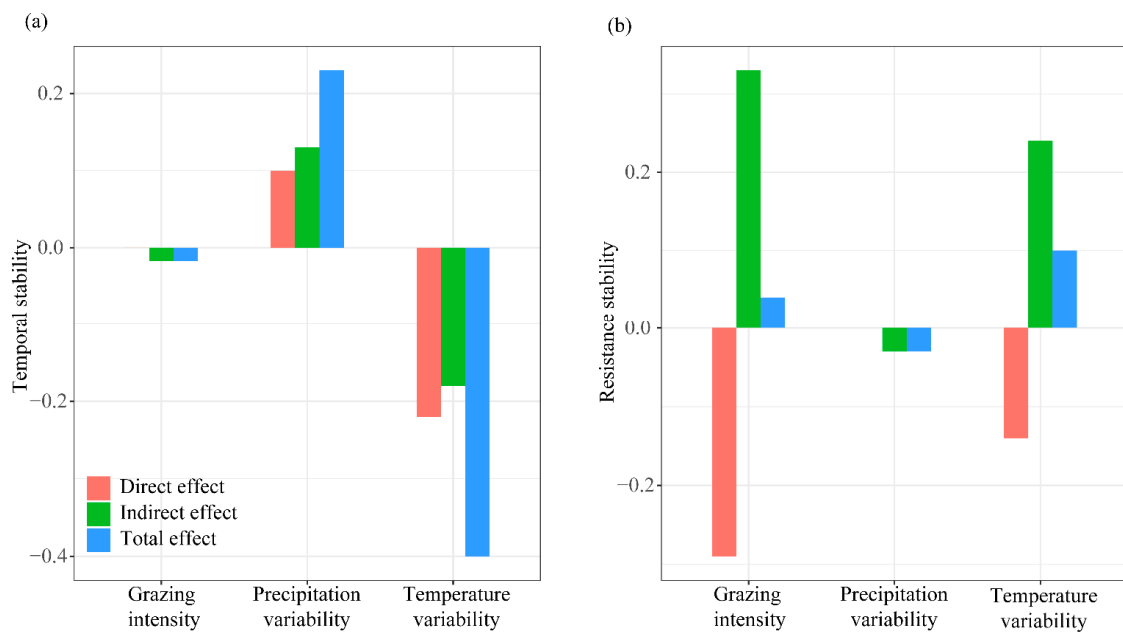


Figure A4. Direct and indirect effects of grazing intensity and climate variability on ecosystem stability. (a) Figure depicting the direct and indirect impact of grazing intensity, monthly precipitation variability, and monthly mean temperature variability on temporal stability. (b) Figure depicting the direct and indirect impact of grazing intensity, monthly precipitation variability, and monthly mean temperature variability on resistance stability. Blue represents the total effect, red represents the direct effect, and green represents the indirect effect.

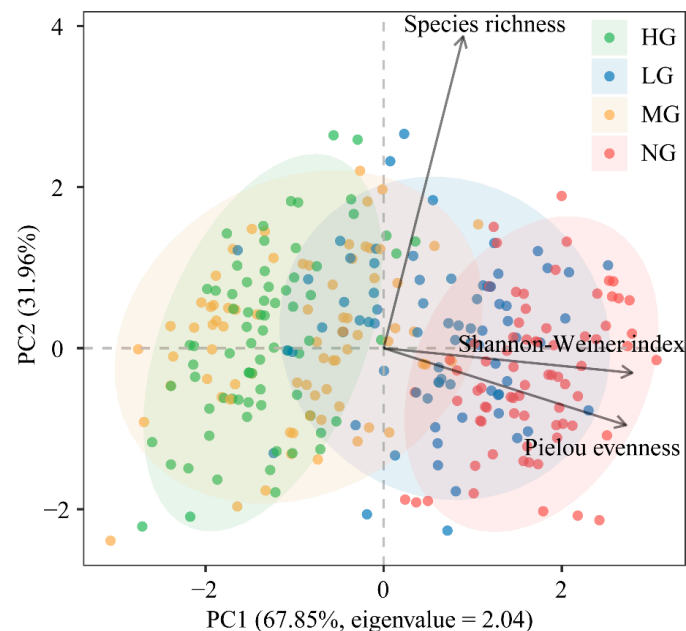


Figure A5. PCA analysis of biodiversity under different grazing intensity, where diversity includes species richness, Shannon–Wiener index, and Pielou evenness. The overall eigenvalue of the model and the explanation ratio of each axis were calculated, cyan dots represent no grazing (NG), blue represents light grazing (LG), yellow represents moderate grazing (MG), and red represents heavy grazing (HG). PCA1 explained 67.35% of the variation in biodiversity and PCA2 explained 32.5% of the variation in alpha diversity, with the Shannon–Wiener diversity index being the main explanatory factor for the PCA1 axis and species richness for the PCA2 axis. Diversity was replaced by PCA1 axis scores.

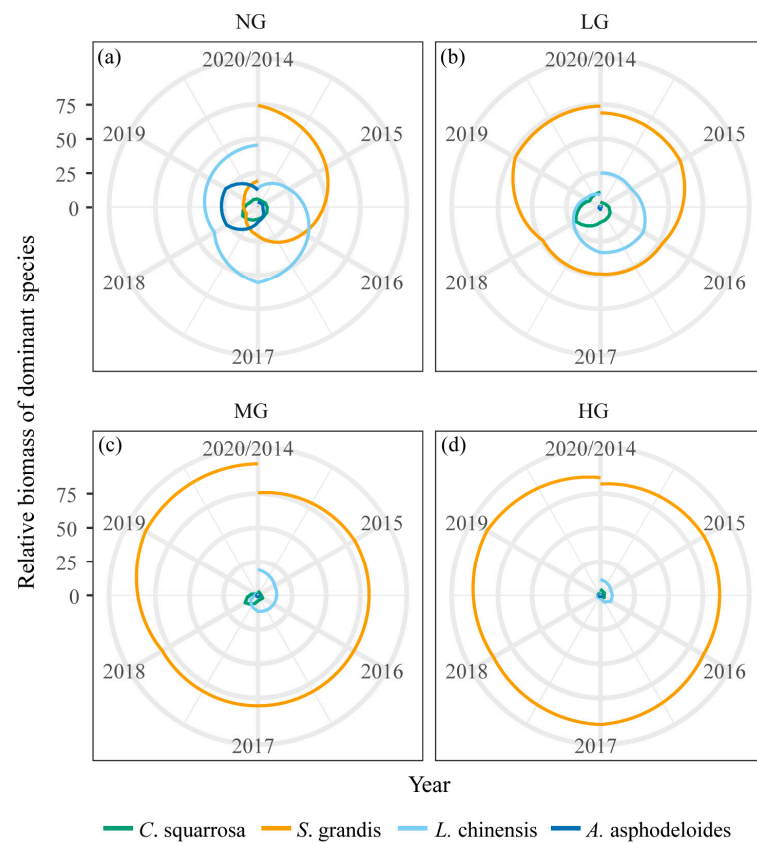


Figure A6. Interannual variation in relative biomass of dominant species under different grazing intensity. (a–d) show changes of the relative biomass of dominant species under NG, LG, MG, and HG from 2014 to 2020, respectively. The green line indicates *Cleistogenes songorica*, the yellow line indicates *Stipa grandis*, the light blue line indicates *Leymus chinensis*, and the dark blue line indicates *Anemarrhena asphodeloides*.

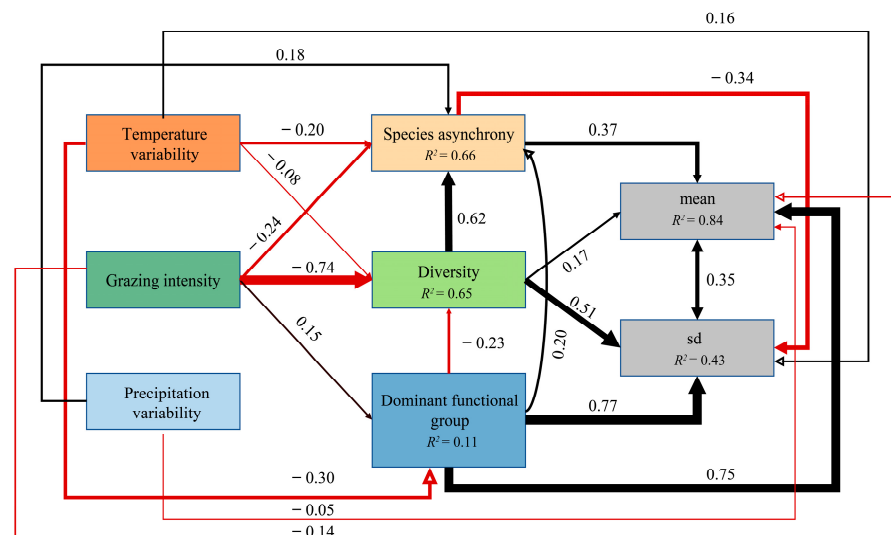


Figure A7. The structural equation model (SEM) depicts the direct and indirect effects of grazing intensity and climate variability on ecosystem temporal stability. Black and red arrows denote positive and negative associations, respectively, thicker lines indicate stronger correlations, and the values above the lines indicate standardized impact path coefficients. Model parameters are: Fisher's $C = 4.11$, p -value = 0.66, $Df = 6$, $AIC = 50.11$, and $BIC = 135.30$. Diversity is the alpha diversity PCA1 score and R^2 is the explained percentage.

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