



## Grazing reduces the temporal stability of temperate grasslands in northern China

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### ABSTRACT

Grazing activity can profoundly influence grassland plant community structure and ecosystem functions. However, our understanding of the effects of livestock grazing on ecological stability across different grassland types remains limited. Based on a 5-year investigation along a precipitation gradient (180 mm in desert steppe, 282 mm in typical steppe and 375 mm in meadow steppe) in temperate grasslands of Inner Mongolia, we examined the responses of the temporal stability of plant community aboveground biomass to grazing intensity at three levels (light grazing, moderate grazing and heavy grazing). We found that grazing intensity at all levels reduced biomass temporal stability across all types of grasslands. Heavy grazing intensity reduced community biomass, species richness and species asynchrony. Structural equation modeling further revealed that grazing decreased community stability mainly by decreasing species asynchrony. In addition, community-level stability was driven by grass species stability in the meadow steppe, but it was affected by the stability of forb species in the desert steppe. These findings suggest that grazing practices may alter the stability properties of grassland plant communities, highlighting the importance of understanding changes in different plant functional groups for predicting community dynamics under grazing management.

### 1. Introduction

Temporal stability, defined as the inverse of variability over time (Pimm, 1984), is a basic attribute of any ecological system. A stable ecosystem is key to providing sustainable ecological goods and services to humanity (Tilman et al., 2014), so understanding the determinants of ecological stability has received much attention in the context of intensive anthropogenic disturbances. The temporal stability of community biomass production has been linked to species diversity (Tilman et al., 2006; Hautier et al., 2015), the degree of species asynchrony (Hautier et al., 2014) and the stability properties of dominant species (Hillebrand et al., 2008). First, increased species diversity may enhance community temporal stability by increasing species compensatory effects (Gonzalez and Loreau, 2009), over-yielding effects (i.e. an increase in ecosystem functions with increasing diversity) (Hector et al., 2010)

and the portfolio effect (Thibaut and Connolly, 2013). Second, variations in the degree of species asynchrony are likely to regulate the responses of community stability to environmental changes (Grman et al., 2010). Finally, the population stability of dominant species could lead to changes in temporal stability at the community level, in particular when a community is dominated by a small number of species (Smith and Knapp, 2003; Hillebrand et al., 2008; Sasaki and Lauenroth, 2011). The relative contribution of these drivers may vary between ecosystems.

Inner Mongolian temperate grassland in northern China, including meadow steppe, typical steppe and desert steppe, is one of the most important components of the Eurasian steppes which have always been exposed to periodical or stochastic disturbances (e.g. grazing and fire) and thus are rather dynamic ecosystems (Nandintsetseg et al., 2018). Temperate grassland is typical in arid and semi-arid regions of the

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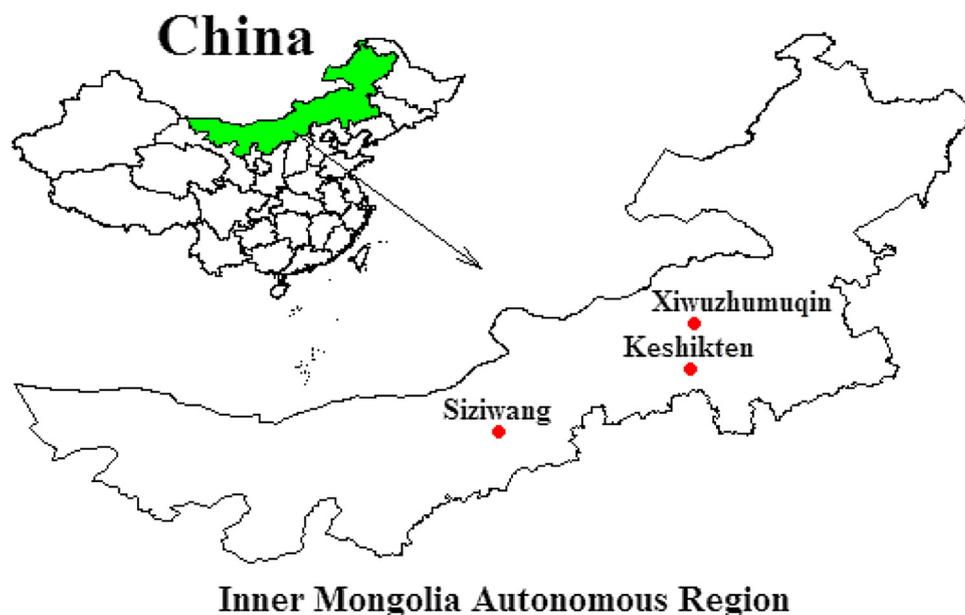


Fig. 1. Geographic locations (red dots) of three study sites in northern China. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Eurasian steppe and stretches across the Eurasian continent. Grasslands not only provide essential goods and services for humans, such as water, medicinal plants and cultural recreation, but also maintain ecosystem services, such as hydrological functions and carbon sequestration, which are reported to be sensitive to environmental disturbances (Kang et al., 2007). However, there are still disputes about the effects of grazing. Household land use rights that are the norm in Inner Mongolia reduce flexibility and force herders to adopt unsustainable grazing practices on their limited land (Liang et al., 2012; Conte and Tilt, 2014). However, complete grazing exclusion is a questionable recommendation and may be seen as a form of “disturbance” in view of the evolutionary grazing history of steppes in Central Asia (Wesche et al., 2016). In Palaearctic grasslands, large areas of former pastures and meadows have been abandoned, leading to succession towards secondary scrublands or forest and the encroachment of competitor grass species, a process associated with a decrease in biodiversity (Valkó et al., 2018). Grazing has been demonstrated to influence the structure and dynamics of vegetation communities (Milchunas and Lauenroth, 1993) and species interactions (Riginos and Young, 2007) that may translate into changes in community stability. Grazing is expected to have positive or negative effects on diversity (Cingolani et al., 2005), depending on resource availability (Proulx and Mazumder, 1998) and grazing intensity, and consequently could lead to shifts in stability. In addition, grazing could promote species level responses that are asynchronous with increasing community stability (Sasaki and Lauenroth, 2011; Wilcox et al., 2017). The effect of grazing on stability can also depend on grazing intensity (Li et al., 2017). Some studies have found that grazing intensity has a significant effect only on species richness (Tóth et al., 2018). Heavy grazing may support ruderals and cause a decline in steppe specialists (Deák et al., 2017). Nico et al. (2016) found that land-use intensity imperils plant and animal community stability through changes in asynchrony rather than diversity in forests and grasslands. Nevertheless, there is a lack of data on whether and how different grazing intensities affect community stability in different types of temperate grasslands. Studies manipulating grazing intensity are vital for assessing grazing effects on community biomass stability and predicting the dynamics of ecosystems under environmental change.

Grazing is the main land-use of natural grasslands across the world (Squires et al., 2018). Nearly a quarter of the global land mass is now

under livestock grazing (Asner et al., 2004). Over the past three centuries, the area of land dedicated to grazing has reached 3451 million hectares, a six-fold increase, due to population growth and colonization (Goldewijk, 2001, 2005). With more than 800,000 km<sup>2</sup> of steppes and drylands, Mongolia hosts one of the world’s largest intact rangeland systems (Batsaikhan et al., 2014). Here, we report on a 5-year grazing investigation conducted to explore the temporal stability of plant biomass production in response to different grazing intensities in the world’s largest remaining temperate grassland in northern China. Structural equation modelling (SEM), an advanced and robust multivariate statistical method, allows hypothesis testing of complex path-relation networks (Grace et al., 2007), which has been widely used to understand the response of grassland ecosystems to environmental changes (e.g. Xu et al., 2015). In the present study, SEM was used to elucidate complex relationships in the grazing-plant-stability system. We aimed to address two questions: 1) How does grazing intensity affect community stability in meadow steppe, typical steppe and desert steppe? 2) What controls the response of the temporal stability of plant biomass production to grazing intensity? We hypothesized that grazing would influence community stability by altering species richness, species asynchrony and population stability (Ren et al., 2018).

## 2. Materials and methods

### 2.1. Study sites

We conducted field investigations in three temperate grasslands in Northern China, including a meadow steppe, a typical steppe and a desert steppe (Fig. 1). The meadow steppe, the typical steppe and the desert steppe are located in Xiwuzhumuqin Banner (43°40’N, 117°45’E; 1090 m), Keshikten Banner (43°26’N, 116°33’E; 1370 m) and Siziwang Banner (41°47’N, 111°53’E; 1450 m) in Inner Mongolia, respectively. There are clear differences in climatic variables between these regions, with mean annual precipitation decreasing from the meadow steppe (MS, 375 mm) to the desert steppe (DS, 180 mm) (282 mm for typical steppe (TS)), whereas mean annual temperature increases from 1 to 3.5°C (1.5°C for typical steppe). Approximately 70–80% of annual precipitation occurs between June and September (i.e. the growing season) in all three grasslands. Various plant community types are found corresponding to changes in climate and soil type in these

regions. The meadow steppe, mostly containing typical kastanozem soils (according to the FAO classification), is dominated by *Stipa baicalensis*, *Leymus chinensis* and *Cleistogenes squarrosa*. The typical steppe on chestnut soil (Haplic Calcisols soil group) is dominated by *Stipa grandis*, *L. chinensis* and *C. squarrosa*. The desert steppe has the lowest level of plant productivity and species richness, dominated by *Stipa breviflora*, *C. songorica* and *Artemisia frigida*, on kastanozem soil.

## 2.2. Experiment design and field measurements

Plots with similar soil types and plant communities with relatively flat topography were selected in each of the three study sites in 2004. Three sheep ranches with similar sized areas were selected in each vegetation type to reflect light, moderate and heavy use. The Household Production Responsibility System (HPRS) has been implemented in Inner Mongolia since the 1980's (Li et al., 2007). Rural households were allocated rights to use the rangelands that surround each village based on their family size (stocking rate = 0.60~1.50 sheep units/ha) (Grazing starts in May and ends in October). Already about 15 years after the implementation of the HPRS, a clear spatial pattern of heavy (degraded) to light (non-degraded) use could be observed around these villages (Pickup and Chewings, 1994). We used this spatial variation in grazing intensity to conduct grazing experiments. The design of our grazing study was modeled after a piosphere in which grazing impacts radiate in a diminishing response away from the centre of each site where livestock shelters and water sources are located (Pickup and Chewings, 1994).

In 2004, we placed a 20 cm × 50 cm quadrat every 50 m along a transect that radiated out from the center of each ranch (one transect per ranch). Plant density, coverage and biomass were determined in August. Cluster analysis was applied to the transect data to classify quadrats into heavy grazing (HG), moderate grazing (MG) and light grazing (LG), which corresponded with their distances from the center points. Grazing intensity was quantified based on the percentage of forage utilization. Grazing intensity was sampled along three replicate transects radiating from the center, with an angle between transects of about 120°. For the MS site, the distances from the center to the boundaries of each grazing intensity zone were 240 m (heavy grazing intensity point), 520 m (moderate grazing intensity point) and 740 m (light grazing intensity point). For the TS site (illustrated in Fig. S1), they were 600 m, 1700 m and 2400 m, and for the DS site they were 180 m, 300 m and 420 m (Han et al., 2008; Tang et al., 2013). The transect data showed significant differences between the three grazing intensity points in 2004, but no clear boundary between adjacent grazing intensity areas. Forage utilization at the grazing intensity points was estimated to be between 65% and 70% for heavy grazing, 40% and 44% for moderate grazing, and 24% to 30% for light grazing.

In 2005–2009, three quadrats (1 × 1 m<sup>2</sup>) were fixed within a 10 m radius of each grazing intensity point in every ranch in mid-August (Li et al., 2008) ( $n_{MS} = 180$ ,  $n_{TS} = 180$ ,  $n_{DS} = 180$ ). The number of species was recorded in every quadrat. Plants of each species were cut at ground level, dried at 60 °C to constant mass and weighed to the nearest 0.1 g. In addition to obtaining biomass data on each species, plants were classified into two different groups (grasses and forbs) based on their functional form, which enabled calculation of functional group biomass.

## 2.3. Data processing and analysis

We quantified the temporal stability of community biomass, grasses and forbs, as the ratio of mean biomass ( $\mu$ ) to its temporal s.d. ( $\sigma$ ) in each plot over the 5-year investigation (2005–2009), as has been done in previous studies (Hautier et al., 2015; Ma et al., 2017; Yang et al., 2017). We defined species richness as the total number of species recorded in the nine quadrats in each vegetation type in a given year. We also calculated Simpson's dominance index based on species biomass

data (Smith and Wilson, 1996).

Repeated-measures ANOVAs were performed to test the effects of grazing intensity on community biomass, species richness, species dominance, the stability of different functional groups and community temporal stability in each steppe. One-way ANOVAs with Duncan's multiple range tests were used to determine the significance of differences among the grazing treatments.

We quantified species asynchrony using the community-wide asynchrony index by species biomass (Loreau and de Mazancourt, 2013). Species asynchrony ( $1 - \phi_x$ ) was calculated as follows:

$$1 - \phi_x = 1 - \sigma^2 / \left( \sum_{i=1}^s \sigma_i \right)^2$$

where  $\phi_x$  is species synchrony, and  $\sigma^2$  is the temporal variance of community aboveground biomass of species  $i$  in a community with  $S$  species (Hautier et al., 2014).

Linear regressions were used to assess how species asynchrony, species dominance, species richness and functional group stability relate to community temporal stability in each of the three steppe types.

We used structural equation modeling (SEM) to estimate the strength of direct and indirect relationships between grazing, species asynchrony, species richness, functional group stability and community stability. In the model, we assumed that grazing had the potential to alter community stability directly, as well as indirectly through changing species asynchrony, functional group stability and species richness. We used the chi-square test, Akaike information criterion and the root mean square error of approximation to evaluate the goodness of fit of the model.

SEM analyses were performed using IBM AMOS 21.0. The remaining statistical analyses were conducted using IBM SPSS Statistics 20.0.

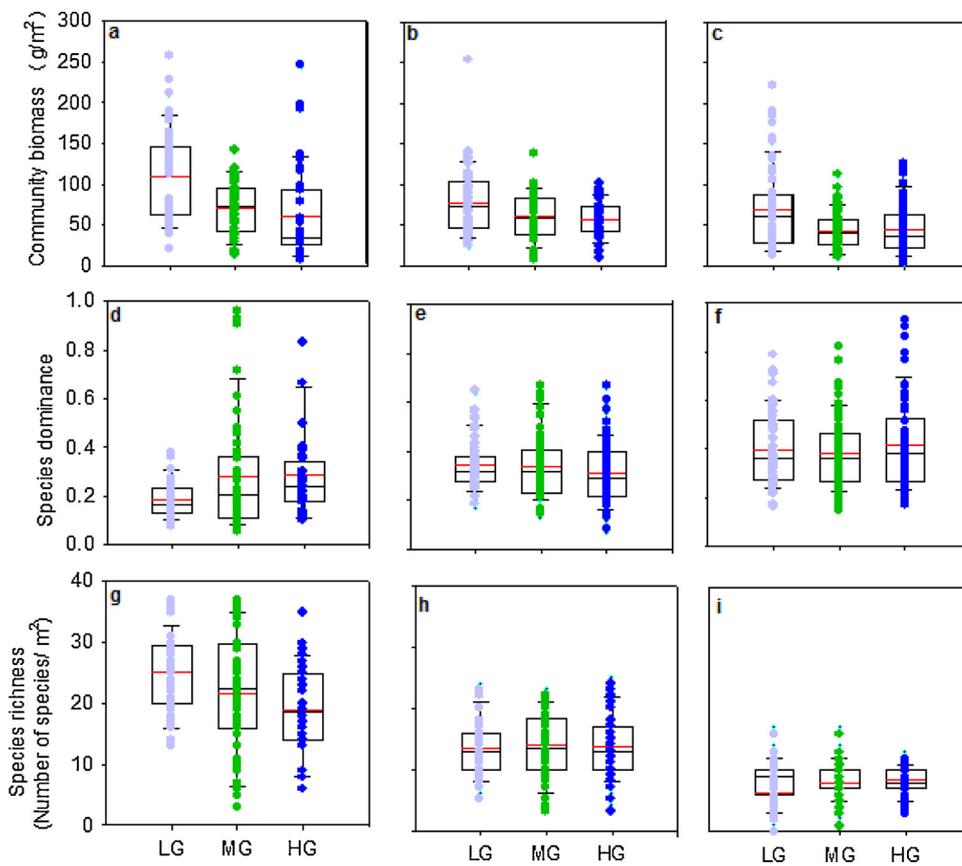
## 3. Results

### 3.1. Effects of grazing intensity on plant community properties

Over the 5-year investigation period, heavy grazing intensity reduced plant community biomass, with a decrease compared to light grazing intensity of 108 g m<sup>-2</sup> (57%) in meadow steppe ( $P < 0.01$ ; Tables S1; Fig. 2a). The reduction in community biomass induced by heavy grazing was not significant in the typical steppe or desert steppe ( $P < 0.01$ ; Fig. 2b, c). Compared to light grazing, species dominance increased by 56% under moderate grazing and heavy grazing in the meadow steppe ( $P < 0.001$ ; Fig. 2d), but showed no significant variation in the typical steppe or desert steppe (Fig. 2e, f). Species richness decreased under heavy grazing in the meadow steppe ( $P < 0.001$ , Fig. 2g), but did not change in the other two steppe types (Fig. 2h, i). Grazing treatments reduced the relative biomass of grasses but enhanced the relative biomass of forbs in typical steppe and desert steppe ( $P < 0.05$ ; Fig. S2b, c). Compared to light grazing, moderate grazing and heavy grazing enhanced the relative biomass of grasses in meadow steppe ( $P < 0.05$ ; Fig. S2a).

### 3.2. Effects of grazing intensity on temporal stability and species asynchrony

Community temporal stability tended to decrease under grazing treatments with an average decrease of 56% in meadow steppe and desert steppe ( $P < 0.05$ ; Table S1; Fig. 3a, c). Heavy grazing significantly reduced the stability of the community in meadow steppe and desert steppe ( $P < 0.05$ ; Fig. 3 a, c), but showed no significant change in the typical steppe (Table S1; Fig. 3b). The temporal stability of grass species decreased by 33% under heavy grazing in the meadow steppe ( $P < 0.001$ , Table S1), but showed no significant change in the typical steppe or desert steppe. Grazing had little effect on the stability of forbs in the three grasslands (Table S1). The effect of grazing intensity on species asynchrony was not significant in the meadow steppe or in the desert steppe ( $P > 0.05$ ; Tables1; Fig. S2a, c). Compared to light

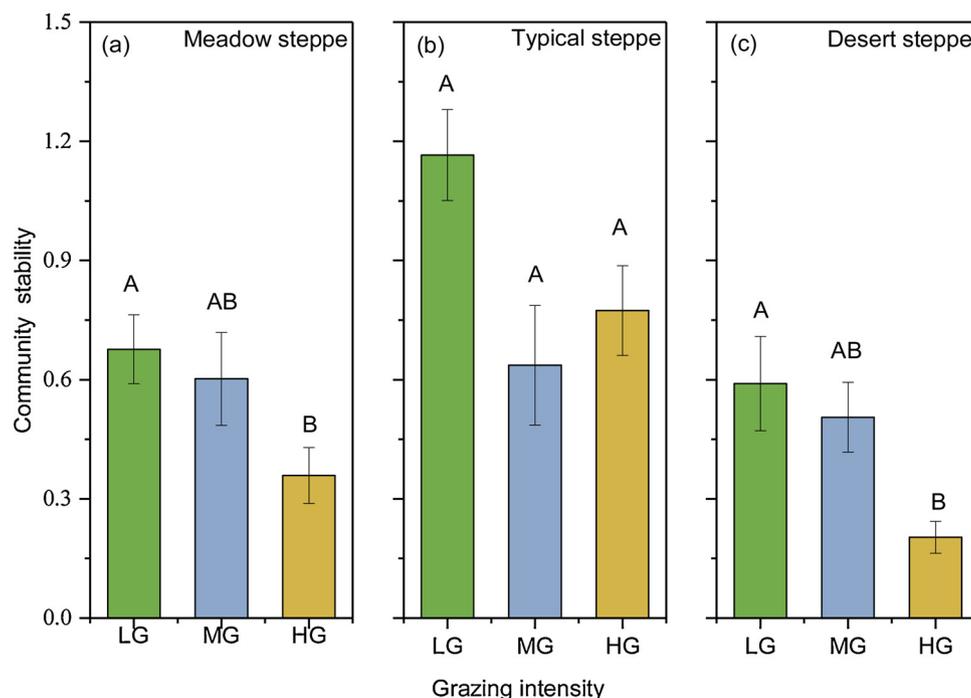


**Fig. 2.** Effects of grazing intensity on (a–c) community biomass, (d–f) species dominance and (g–i) species richness in three grasslands. LG, MG and HG represent light, moderate and heavy grazing intensity, respectively. Error bars show one standard error of the mean. Different letters above bars indicate significant differences according to Duncan’s multiple range test ( $P < 0.05$ ).

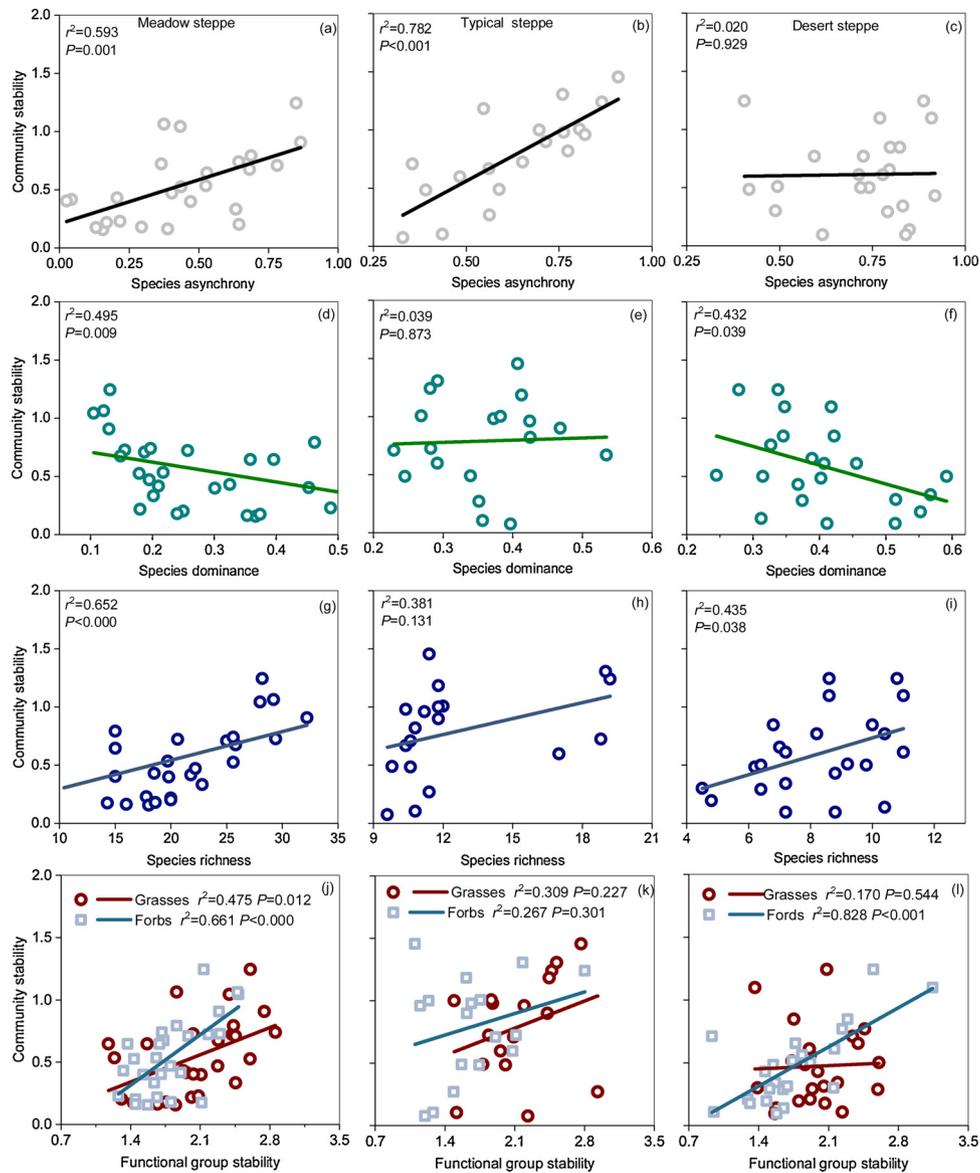
grazing, moderate grazing and heavy grazing reduced species asynchrony, with an average decrease of 36% and 31% in the typical steppe, respectively ( $P < 0.05$ ; Tables1; Fig. S2b).

### 3.3. Factors affecting community temporal stability

Regression analysis showed that in the meadow steppe, community temporal stability was positively correlated with species asynchrony ( $r^2 = 0.593$ ,  $P = 0.001$ , Fig. 4a), species richness ( $r^2 = 0.652$ ,



**Fig. 3.** Effects of grazing intensity on community temporal stability in (a) meadow steppe, (b) typical steppe and (c) desert steppe. LG, MG and HG represent light, moderate and heavy grazing intensity, respectively. Details are as in Fig. 2.



**Fig. 4.** Linear regressions of community temporal stability against (a–c) species asynchrony, (d–f) species dominance, (g–i) species richness and (j–l) functional group stability.

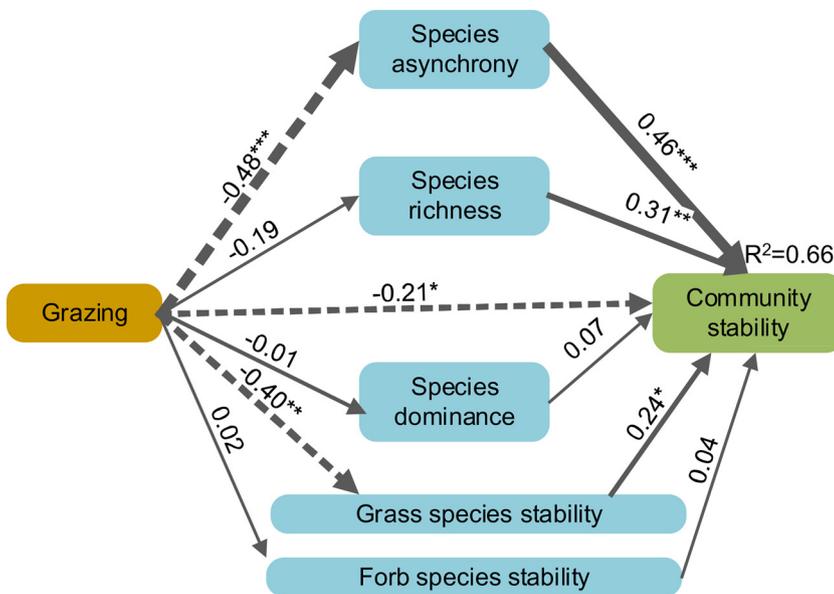
$P < 0.001$ , Fig. 4g), grass species stability ( $r^2 = 0.475$ ,  $P < 0.05$ , Fig. 4j) and forb species stability ( $r^2 = 0.661$ ,  $P = 0.012$ , Fig. 4j), but was negatively associated with species dominance ( $r^2 = 0.495$ ,  $P = 0.009$ , Fig. 4d). Likewise, in the typical steppe, community temporal stability decreased with decreasing species asynchrony ( $r^2 = 0.782$ ,  $P < 0.001$ , Fig. 4b), while no relationship was found between stability and other properties of the typical steppe community ( $P > 0.05$ , Fig. 4e, h, k). In the desert steppe, community stability was found to be associated with species richness ( $r^2 = 0.435$ ,  $P = 0.038$ , Fig. 4i) and the stability of forb species ( $r^2 = 0.828$ ,  $P < 0.001$ , Fig. 4l), but was negatively associated with species dominance ( $r^2 = 0.432$ ,  $P = 0.039$ , Fig. 4f). There were no correlations between stability and other properties of the community in the desert steppe ( $P > 0.05$ , Fig. 4c, l, Fig S3a–c).

Structural equation modeling (SEM) explained 66% of the variation in community stability (Fig. 5). The SEM result (Table S2; Fig. 5) showed that grazing affected community temporal stability indirectly, through changing species asynchrony, species richness and grasses species stability. However, the contribution of species dominance and forb species stability was very limited in these temperate grasslands.

Applied to each steppe type separately, SEM explained 84%, 68% and 88% of the variations in community stability in the meadow, typical and desert steppe, respectively (Fig. S4). First, the SEM result from the meadow steppe (Table S2; Fig. S4a) showed that grazing affected community temporal stability indirectly, through changing species asynchrony, species richness and grasses species stability. In contrast, forb species stability contributed little to community temporal stability. Species dominance was excluded from the SEM model. Second, consistent with the result from the meadow steppe, the SEM model revealed the key role of species asynchrony in regulating the effects of grazing on temporal stability in the typical steppe (Table S2; Fig. S4b). However, the contribution of species richness, grass species stability and forb species stability was very limited. Finally, changes in temporal stability in the desert steppe were influenced mainly by species asynchrony, richness and forb species stability (Table S2; Fig. S4c).

#### 4. Discussion

We set out to explore the responses of community stability to grazing intensity through a 5-year grazing investigation in three



**Fig. 5.** The result of structural equation modeling relating grazing, species asynchrony, species richness, species dominance and functional group stability to community temporal stability. Numbers adjacent to arrows are standardized path coefficients and indicate the effect size of the relation.  $R^2$  represents the proportion of variance in each dependent variable explained in the model. Arrows indicate positive (solid) and negative (dashed) relationships. Arrow width is proportional to the strength of the relationship. Goodness-of-fit statistics for each model are shown below the model. \*\*\* $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$ .  $X^2 = 17.314$ ,  $P = 0.068$ ; RMSEA = 0.105; AIC = 67.314.

temperate grasslands. Three main results emerged: (1) grazing reduced the temporal stability of all types of grassland; (2) decreased stability was associated with decreased species asynchrony; and (3) grazing reduced community stability mainly through altering species asynchrony.

Research findings on the effects of grazing on community stability have been inconsistent. On the one hand, grazing is thought to reduce community stability. For example, Zhang et al. (2016) found that grazing slightly weakened the temporal stability of temperate steppe in Inner Mongolia. This finding is in agreement with our results. On the other hand, grazing has been found to promote community stability by maintaining native plant diversity in an annual grassland (Beck et al., 2015). Our study found that grazing decreased temporal stability in temperate grasslands dominated by perennial plants. The different response patterns between vegetation with different community composition and grassland structure may be ecosystem-dependent.

Several mechanisms may potentially explain the observed changes in community temporal stability. First, grazing can influence diversity (Gross et al., 2014). For instance, Hallett et al. (2017) reported that functional diversity increased stability in a grazed grassland. Second, grazing can affect stability through changes in species asynchrony, which may be driven by environmental changes. Several recent studies have highlighted the important role of species asynchrony in determining community stability (Xu et al., 2015; Ma et al., 2017; Yang et al., 2017). Finally, grazing can result in changes in dominant species that consequently impact community stability. A recent study reported that after six years of grazing, variation in the productivity of dominant plant functional groups contributed more to maximizing stability than species richness (Ren et al., 2018).

In the present study, we suggest that the second mechanism (i.e. species asynchrony) is the most likely factor responsible for the observed pattern of community stability under grazing. Asynchrony in population dynamics across species is a common feature of communities (Ma et al., 2017), and may be caused by asynchronous responses of different species to environmental changes (Loreau and Mazancourt, 2013). In contrast, a community that consists of species with similar traits would result in synchronized population dynamics in response to disturbances (Rocha et al., 2011; Vasseur et al., 2014). We found that grazing reduced species asynchrony, resulting in decreased community biomass stability. Under grazing, a few species, such as *A. frigida* and *Potentilla acaulis*, increased in relative biomass. However, the majority of species, such as *Stipa* sp. and *L. chinensis*, decreased in relative biomass with grazing, leading to less asynchronous population dynamics (Table S3). In contrast to this result, a grazing investigation

using two different grazing practices showed that high grazing intensity enhanced species asynchrony in a continuously grazed system, but exerted no effect in a mixed grazing-mowing treatment (Ren et al., 2018). This difference may be explained by the different grazing practices. Overall, grazing can influence community stability by altering species asynchrony.

Our results indicate that species diversity contributed little to the changes in community temporal stability under grazing in the three temperate grasslands, although a number of studies have shown that increased species diversity tends to promote community stability (Tilman and Downing, 1994; Isbell et al., 2009; Wright et al., 2015). In our study, grazing treatments did not alter species richness in the typical steppe or desert steppe, which was likely due to the relatively low number of species under different grazing treatments (ranging from 14 to 13 species per  $m^2$  for the typical steppe, Fig. 2h; and from 8 to 7 species per  $m^2$  for the desert steppe, Fig. 2i). Another grazing investigation also reported no impact of grazing on species richness (Ren et al., 2018). In addition, species richness did not respond to climate change, such as increased N deposition and warming (Xu et al., 2015; Yang et al., 2017). Such patterns suggest that the contribution of species richness to community stability was very limited in the grasslands studied.

We also considered other potential factors possibly impacting on community stability in response to grazing, such as the stability of plant functional groups. Several previous studies have reported that the stability of functional groups, especially dominant species, has a role in determining community stability (Sasaki and Lauenroth, 2011; Wilsey et al., 2014; Yang et al., 2017). Consistent with their results, we observed significant positive correlations between the stability of functional groups and stability at community level in two grasslands (Fig. 4j, l). SEM analysis further showed that grazing impacted the stability of grasses in the meadow steppe, and the stability of forbs in the desert steppe, consequently leading to variations in community stability. Nevertheless, the responses of functional group stability to grazing varied from ecosystem to ecosystem.

## 5. Conclusion

This study, to our knowledge, is the first to report the negative effect of grazing on the temporal stability of plant community biomass production across three types of grasslands. We found that grazing reduced community temporal stability mainly by altering species asynchrony. In addition, the responses of functional group stability to grazing may be

dependent on ecosystem. These findings suggest that grazing practices can alter the stability properties of communities, and point to the importance of different functional groups for community stability under grazing. As grazing is a widespread practice in grassland management, to provide the evidence base for grazing management recommendations, more experimental evidence is needed to explore how plant functional groups affect stability and thus influence ecosystem functions.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.flora.2019.151450>.

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