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Grazing impairs ecosystem stability through changes in species asynchrony and stability rather than diversity across spatial scales in desert steppe, Northern China

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ABSTRACT

The desert steppe is an important component of arid and semiarid grassland, and plays a crucial role in livestock production. Livestock grazing is a key driver of grassland biodiversity, ecosystem functionality, and stability. However, the effects of grazing on temporal stability of the ecosystem across spatial scales in desert steppe remains unclear. Here, we conducted a five-year sheep grazing experiment encompassing three grazing intensities, namely no grazing (NG), medium grazing (MG), and heavy grazing (HG). This was undertaken at five different spatial scales of 1, 2, 3, 4, and 5 m^2 in a desert steppe, northern China. We tested how grazing has impacted on species diversity, asynchrony, stability, and ecosystem stability across different spatial scales. We found that grazing did not alter the species diversity. However, there was a decrease in ecosystem stability and species asynchrony across spatial scales. MG increased the species stability across spatial scales, while it was reduced under HG. Species asynchrony and stability were negatively associated with diversity. They were positively related to ecosystem stability and formed a negative relationship between species diversity and ecosystem stability across spatial scales. Grazing weakened the negative influence of diversity on species asynchrony, and the insurance influence of asynchrony on ecosystem stability. This reduced the destabilizing effects of species diversity on temporal stability of the ecosystem across spatial scales. Structural equation modeling has shown that grazing indirectly decreased ecosystem stability only through reduction of species asynchrony and stability. This highlights the important regulatory functions of species asynchrony and stability with grazing across spatial scales in desert steppe. We suggest that biodiversity should be balanced against grazing intensity to achieve a high level of ecosystem function and stability with increasing spatial scales in arid grassland.

1. Introduction

Grasslands cover 40.5 % of the Earth's terrestrial land surface and nearly 47 % of semiarid and arid regions and are one of the main resources for livestock production. They have experienced considerable shifts in biodiversity, function, and stability, which has been primarily driven by livestock grazing (White et al., 2000; Asner et al., 2004; Shan et al., 2011). Herbivore activity decreases the spatial heterogeneity of the vegetation due to trampling at fine scales. In addition, it can increase spatial heterogeneity due to an increase in patchness from selective foraging at larger scales (Adler et al., 2001). This can have a pronounced influence on biodiversity as a key community determinant (Schoenbach et al., 2011; Dong et al., 2020; Chen et al., 2021), with potential consequences for stability (Hautier et al., 2014). The maintenance of stability in grasslands depends on how drivers of anthropogenic activities affect biodiversity across spatial scales.

Changes in biodiversity affect ecological services by altering ecosystem functioning and stability in grassland with grazing livestock

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(Aragon et al., 2011; Bardgett and van der Putten, 2014; Angelini et al., 2015; Beck et al., 2015). Increases in grazing intensity decrease grazing diversity or have no effect with increasing spatial scales in arid and semiarid grasslands due to an increased proportion of bare soil (De Bello et al., 2007; Gonzalez et al., 2020). The intermediate disturbance hypothesis suggests that moderate grazing should increase biodiversity in nutrient-rich grassland ecosystems (Milchunas et al., 1988). Ecosystem stability across spatial scales is crucial for understanding ecosystem sustainability and the level of sensitivity to habitat loss (Wang et al., 2017). Ecosystem stability is defined as temporal invariability in the aboveground biomass of a community over a certain period (Lehman and Tilman, 2000; Bluethgen et al., 2016). Species stability is defined as the mean of the population stability for all species in a plot, which is weighted by population abundance using metrics such as density or biomass (Wang and Loreau, 2014). Grazing is likely to decrease the temporal mean of the aboveground biomass and it may have a destabilizing influence on biomass production (Hautier et al., 2014). Moreover, grazing potentially affects ecosystem stability by changing the temporal variance; however, this is less understood (Hautier et al., 2014; Qin et al., 2019; Liang et al., 2021).

The insurance hypothesis predicts that species diversity can increase the stability of grassland ecosystem processes in the context of human disturbance and environmental change (Yachi and Loreau, 1999). Biodiversity predominantly impacts productivity stability through species asynchrony, namely dissimilar responses among species to environmental variability. It quantifies to what extent variability is reduced, which is a potentially important stabilizing mechanism (Aragon et al., 2011; Wang and Loreau, 2016; Wang et al., 2021; Xu et al., 2021). Responses of species asynchrony to environmental fluctuations cause biomass reduction for some species to be compensated for by increases in biomass in other species. This buffers temporal fluctuations in community productivity in grassland ecosystems (Bai et al., 2004; Wang and Loreau, 2014; Hasbagan et al., 2019; Qin et al., 2019; Liang et al., 2021; Wang et al., 2021). Grazing-induced shifts in species diversity affect species asynchrony and potentially affects species stability across spatial scales, which together determine the temporal ecosystem stability (Xu et al., 2021; Liang et al., 2021). There is generally a reduction in mean species stability alongside a reduction in species diversity in most terrestrial grassland ecosystems (Xu et al., 2021; Liang et al., 2021). This is positively related to ecosystem temporal stability because of lower variation in species abundance (Tilman et al., 2014). Dividing the stabilizing role in aggregated ecosystem properties into asynchrony among species and stability within species helps to elucidate their relative importance in regulating temporal ecosystem stability (Thibaut and Connolly, 2013). However, whether grazing affects how species diversity influences ecosystem stability through species asynchrony and stability across spatial scales in arid grassland ecosystems remains unclear.

The species–area relationship (SAR) increases in logarithmic space in most grassland ecosystems (Storch, 2016), which varies with anthropogenic disturbances such as grazing by domestic livestock (Bergholz et al., 2017). Grazing-induced shifts in diversity across spatial scales are affected by the interaction between grazing and the spatial structure of the vegetation (Adler et al., 2001; De Bello et al., 2007). The SAR curves in livestock grazing areas may be less steep than those from areas with no grazing. The invariability–area relationship (IAR) is a new approach to explore the scale dependence of stability (Wang et al., 2017), with an increase with area in logarithmic space (Wang et al., 2017). Only when a proportional change in SAR is caused by the same proportional change in IAR, the diversity–stability relationship remains constant across spatial scales. Otherwise, this relationship becomes scale-dependent in the context of anthropogenic activities (Turner and Tjorve, 2005; Wang et al., 2017). An integrated understanding of whether the strength of the diversity–ecosystem stability relationship changes across spatial scales in grazed grassland ecosystems has practical implications for landscape management.

One appropriate scenario in grassland ecosystems after the theory has been proposed and the experiment has been designed is species diversity and ecosystem stability increasing according to spatial scale. The slope of the species-scale is steeper than that of the stability–scale relationship. Therefore, the slope of the diversity–stability relationship is reduced with increasing scale (Loreau et al., 2003; Loreau and de Mazancourt, 2013; Wang and Loreau, 2016; Wang et al., 2017, 2021; Zhang et al., 2018b; Liang et al., 2021). However, in desert steppe, how grazing has affected the relationships of species–scale, stability–scale, and diversity–stability with increasing spatial scales has not yet been determined. Therefore, using a 5-year grazing dataset (2017–2021) from the field in a desert steppe ecosystem in northern China, we have explored how the relationship of diversity–ecosystem stability with increasing spatial scales has been affected by grazing. We hypothesized that grazing influences ecosystem stability mainly through changing species diversity, asynchrony, and stability across spatial scales. Further, we have hypothesized that grazing can affect the relationship of diversity–ecosystem stability primarily through mediating the relationship of diversity–asynchrony and asynchrony–ecosystem stability across spatial scales (Xu et al., 2021). To test these hypotheses, the following three questions were addressed. (1) How does grazing affect diversity and ecosystem stability across spatial scales? (2) How does grazing influence the diversity–ecosystem stability relationship with increasing spatial scale? (3) Are the influences of grazing on ecosystem temporal stability mediated through diversity, asynchronous dynamics among species, and stability within species across spatial scales?

2. Materials and methods

2.1. Study site

The study was undertaken at the Urat Desert grassland Research Station, Inner Mongolia, China (106°58′N, 41°25′E, 1650 m) (Fig. A2a). From 1971 to 2021 over the last five decades, the mean annual air temperature (MAT) was 6.5 ℃ and the mean annual precipitation (MAP) was 155.6 mm (Zhao et al., 2021). The biome type is desert steppe, which has a typical temperate continental monsoon climate within the moderate temperature zone. There are two plant community types in the region. The shrub community is dominated by *Reaumuria songarica* (Pall.) Maxim. (Tamaricaceae) and the grass community is dominated by *Stipa glareosa* P. A. Smirn. (Graminae) (Zhao et al., 2021). The soil in this study area has been classified as brown and gray brown desert soil (Zhao et al., 2021). The soil properties at the study site have a higher consistency in terms of the soil water content, pH, electrical conductivity and soil Carbon and Nitrogen concentration (Table A1). Moreover, there is relatively little variation in vegetation density across the study site (Table A1).

2.2. Grazing experiment and spatial scales

We fenced an area of approximately 600 m × 1000 m in size in the shrub community encompassing a total of 15 paddocks, each of which were approximately 40,000 m^2. Furthermore, we fenced an area of approximately 750 m × 300 m in size in the grass community, encompassing of 15 paddocks with each one having an area of approximately 10,000 m^2. In 2013, we began a grazing experiment based on the regional distribution of dominant species (Fig. A2b) (Zhao et al., 2021). The grazed paddocks were arranged at random while the control paddocks were set up at random locations outside the grazed paddocks (Fig. A2b). The sheep grazing experiment was undertaken in the shrub and grass community with three grazing intensities, namely no grazing (NG) with 0 sheep·ha^{-1}; medium grazing (MG) with 2 sheep·ha^{-1} in the grass community; and 0.5 sheep·ha^{-1} in the shrub community; heavy grazing (HG) with 4 sheep·ha^{-1} in the grass community and 1 sheep·ha^{-1} in the shrub community (Fig. A2c). The grazing intensities selected for the experiment were based on the grazing capacity for desert steppe in Inner Mongolia, northern China. The grazing experiment was carried out during the growing season from June 1st to September 30th during 2017–2021. There were five replicates per treatment (Zhao et al., 2021) and each paddock contained five plots. More detailed descriptions on sheep grazing experiments can be found in Zhao et al. (2021). We examined five spatial scales from 1, to 2, to 3, to 4, and to 5 m^2 by using a combination of five 1 m^2 plots in each paddock. We also assessed the species diversity and biomass at all five spatial scales (Zhang et al., 2018b).

2.3. Sampling

We conducted vegetation surveys annually in mid-August from 2017 when the standing biomass peaked. At each site, five plots (1 m × 1 m) were dispersedly selected within each paddock, but they were relatively closely connected in space to represent contiguously increasing spatial scales (Zhang et al., 2018b; Liang et al., 2021). All the plant taxa in each plot were recorded to measure the aboveground biomass. We used scissors to clip all the vascular plants in each plot and the plant tissues samples were oven-dried at 65 ℃ for 48 h to measure the biomass of each plant taxon collected ($g{\cdot}m^{-2}$) (Zuo et al., 2020; Liang et al., 2021).

2.4. Diversity, stability, and asynchrony across spatial scales

We used species richness as a measure of diversity based on functional compensation between species and stability theory (McNaughton, 1977; Hautier et al., 2014). Species diversity was all the number of plant taxa recorded in the 1 m^2 plots, that is, the smallest scale, and of the combination of five 1 m^2 plots in each metacommunity (Zhang et al., 2018b). The species richness across spatial scales were averaged across the vegetation datasets collected over five years (Tuomisto, 2010; Wang and Loreau, 2014). We defined temporal ecosystem stability as being temporal invariability in the grassland ecosystem. We defined species stability as the mean of the population stability for all plant taxa in a plot weighted by population biomass abundance. These definitions are calculated using the following mathematical formulas (Wang and Loreau, 2016; Zhang et al., 2018b):

$$\text{Ecosystem stability} = \frac{\mu}{\sigma} \tag{1}$$

$$\text{Species stability} = \frac{\sum_{i,k}\mu_{i,k}}{\sum_{i,k}\sqrt{(\nu_{ii,kk})}} \tag{2}$$

$$\text{Species asynchrony} \ = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^{N}\sigma\right)^2} \tag{3}$$

where μ denotes the interannual mean, and σ denotes the interannual standard deviation of the aboveground biomass over the five years, $\mu_{i,k}$ and $\nu_{ii,kk}$ denote the temporal mean and covariance of the biomass of species i in local community k, respectively. σ^2 is the variance over the five years of the aboveground biomass of species i in a community with N species.

2.5. Statistical analysis

We performed repeated measures analysis of variance (ANOVA) to test whether the effects of grazing or spatial scales on plant species diversity vary according to year. We evaluated how grazing or spatial scales influence species asynchrony, stability, and ecosystem stability using one-way ANOVA ((1) question). We conducted these statistical analyses using SPSS 16. To assess how changes in species diversity mediate the influence of grazing on ecosystem stability at all five spatial scales (1, 2, 3, 4, and 5 m^2) ((2) question), we used linear mixed-effects analysis with the R package lme4 (Bates et al., 2015). The response variables for this analysis were species asynchrony (Fig. 2a) with species diversity as a fixed effect, and stability (Figs. 2b and 3a) with species diversity and species asynchrony as fixed effects, and ecosystem stability (Figs. 2c, 3b, and c) with species diversity and species asynchrony and stability as fixed effects. The random effect used in the analysis was grazing. Based on these correlations, the best structural equation model (SEM) was constructed to estimate the strength of the effects of grazing and spatial scale on ecosystem temporal stability (Qin et al., 2019; Liang et al., 2021) ((3) question). The SEM analysis was performed using IBM AMOS 20.0.

3. Results

3.1. Grazing effects on species diversity and ecosystem stability across spatial scales

Increased grazing intensity did not alter the species diversity at all five spatial scales (Fig. 1a, $F = 0.28$, $p = 0.758$). Medium grazing (MG) increased the dominant species abundance of *S. glareosa* but it decreased under heavy grazing (HG) (Fig. A3b, $F = 159.98$, $p < 0.001$). The HG reduced species stability while MG increased species stability across all spatial scales (Fig. 1b, $F = 6.30$, $p = 0.002$). Increasing grazing intensity decreased species asynchrony (Fig. 1c, $F = 21.57$, $p < 0.001$) and temporal ecosystem stability (Fig. 1d, $F = 29.84$, $p < 0.001$) across all spatial scales. This is because increasing grazing intensity decreased the temporal mean of the aboveground biomass (Fig. A3c, $F = 104.04$, $p < 0.001$) and decreased the temporal standard deviation of the aboveground biomass to a lesser extent (Fig. A3d, $F = 84.98$, $p < 0.001$) across all spatial scales. Grazing was found to explain a large proportion of variance in species asynchrony and ecosystem stability (Table A2). Grazing indirectly decreased ecosystem stability by reducing the species asynchrony and species stability, but not through unchanged species diversity (Fig. 5). Grazing also reduced the temporal standard deviation of the aboveground biomass. However, by decreasing the temporal standard deviation, grazing increased species stability, which led to higher ecosystem stability (Fig. A7d). Considering all the direct and indirect effects, grazing caused a decrease in ecosystem stability (total effect size (as TES) = −0.536, Fig. 5 and A7d).

3.2. Changes in species diversity and ecosystem stability with increasing spatial scale

Species diversity (Fig. 1a, $F = 48.71$, $p < 0.001$) and species stability (Fig. 1b, $F = 2.59$, $p = 0.039$) increased with increasing spatial scales from 1 m^2 to 5 m^2. However, species asynchrony (Fig. 1c, $F = 0.05$, $p = 0.996$) and ecosystem stability (Fig. 1d, $F = 0.25$, $p = 0.911$), did not change with increasing spatial scale. The effects of spatial scale on ecosystem stability were mediated through effects on species diversity, species stability, and species asynchrony. The SEM was used to define the various pathways through which spatial scale influences ecosystem stability. The final SEM demonstrated that spatial scale increased species stability and asynchrony. This led to a higher level of ecosystem stability, except for an increase in species diversity, which led to a lower ecosystem stability (Fig. 5). Increasing spatial scale also increased the temporal standard deviation of the aboveground biomass. However, by increasing the temporal standard deviation, increasing spatial scales decreased species stability, which led to lower ecosystem stability (Fig. A7d). Considering the direct and indirect effects, increasing spatial scales did not alter ecosystem stability (TES = 0.075, Fig. 5 and A7d).

3.3. Grazing effect on diversity–ecosystem stability relationship across spatial scales

Our findings have highlighted the grazing-induced negative species diversity–ecosystem stability relationship across five different spatial scales (Fig. 2). This indicates that temporal ecosystem stability tends to reduce with diversity. Species asynchrony (Fig. 2a, $p < 0.01$) and species

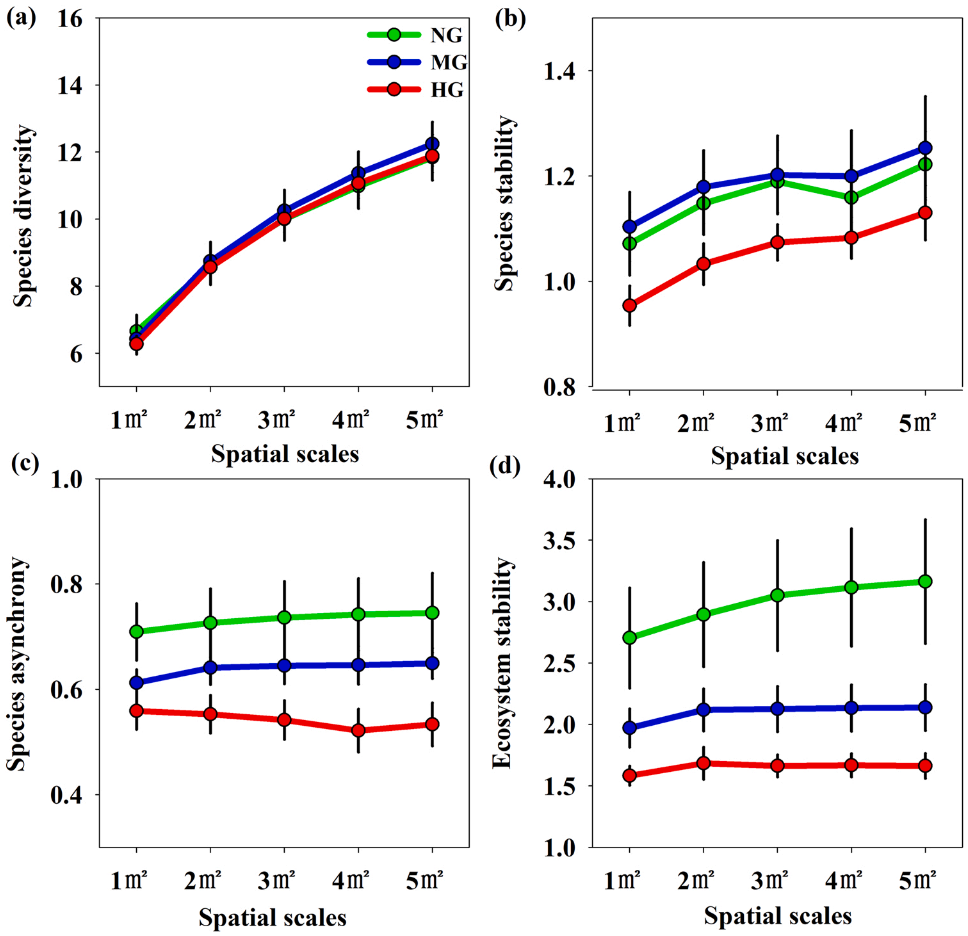

Fig. 1. Grazing effect on species diversity, species stability, species asynchrony, and ecosystem stability at 1, 2, 3, 4, and 5 m^2. The effects of increasing grazing intensity (NG: no grazing, MG: medium grazing, HG: heavy grazing) and spatial scales on (a) species diversity ($F = 0.28$, $p = 0.758$ under grazing; $F = 48.71$, $p < 0.001$ under spatial scales), (b) species stability ($F = 6.30$, $p = 0.002$ under grazing; $F = 2.59$, $p = 0.039$ under spatial scales), (c) species asynchrony ($F = 21.57$, $p < 0.001$ under grazing; $F = 0.05$, $p = 0.996$ under spatial scales), (d) ecosystem stability ($F = 29.84$, $p < 0.001$ under grazing; $F = 0.25$, $p = 0.911$ under spatial scales). The results of analysis of variance under three grazing intensities and five spatial scales, as well as their interactions are provided in Tables A2, A3, and A4.

stability (Fig. 2b, $p < 0.05$) were negatively related to species diversity at all five spatial scales. Ecosystem stability was positively related to species asynchrony (Fig. 3b, $p < 0.001$) and species stability (Fig. 3c, $p < 0.01$) at all five spatial scales. This has resulted in ecosystem stability being negatively associated with species diversity (Fig. 2c, $p < 0.001$) across the five spatial scales. This is because temporal standard deviation of the aboveground biomass is positively correlated with species diversity (Fig. A4b, $p < 0.001$). However, the temporal mean was not related to diversity (Fig. A4a, $p > 0.05$). In contrast, ecosystem stability was negatively associated with the temporal standard deviation at 2 m^2, 3 m^2, 4 m^2, 5 m^2 (Fig. A5b, $p < 0.01$) but positively associated with the temporal mean at 1 m^2 (Fig. A5a, $R^2_m = 0.18$, $F = 6.58$, $p = 0.016$) and 2 m^2 ($R^2_m = 0.16$, $F = 5.61$, $p = 0.025$). Species stability was positively associated with species asynchrony (Fig. 3a, $p < 0.05$) across all five spatial scales.

Grazing generally weakened the negative effects of diversity on ecosystem stability across spatial scales. This is because grazing reduced the ecosystem stability–scale relationship while it did not change the diversity–scale relationship across spatial scales. MG weakened the negative influences of diversity on species asynchrony (Fig. 4a, $R^2_m = 0.73$, $F = 10.96$, $p = 0.045$) and the positive influences of species asynchrony on ecosystem stability (Fig. 4e, $R^2_m = 0.80$, $F = 16.12$, $p = 0.028$) across all spatial scales. This caused MG to weaken the negative influences of diversity on ecosystem stability (Fig. 4c, $R^2_m = 0.84$, $F = 21.38$, $p = 0.019$) across all spatial scales. This is because MG and HG weakened the positive effects of diversity on the temporal standard deviation of the aboveground biomass (Fig. A6a, $R^2_m = 0.92$, $F = 47.65$, $p = 0.006$ under MG; $R^2_m = 0.82$, $F = 18.55$, $p = 0.023$ under HG). HG weakened the negative slopes of temporal standard deviation–ecosystem stability across spatial scales (Fig. A6b, $R^2_m = 0.82$, $F = 17.78$, $p = 0.024$).

3.4. *Changes in the diversity–ecosystem stability relationship with increasing spatial scale*

Our findings have illustrated that the negative relationship of diversity–ecosystem stability increased with increasing spatial scale. The negative slopes of the diversity–species asynchrony relationship (Fig. 4a, $R^2_m = 0.91$, $F = 39.00$, $p = 0.008$) and the diversity–species stability relationship (Fig. 4b, $R^2_m = 0.88$, $F = 29.69$, $p = 0.012$) increased with increasing spatial scales under NG. This resulted in the negative relationship of the diversity–ecosystem stability relationship increasing with increasing spatial scale (Fig. 4c, $R^2_m = 0.87$, $F = 25.73$, $p = 0.015$ under NG). This is also because the positive slope of the diversity–temporal standard deviation relationship (Fig. A6a, $R^2_m = 0.92$, $F = 44.44$, $p = 0.007$) and the negative slope of the temporal standard deviation–ecosystem stability relationship (Fig. A6b, $R^2_m = 0.97$, $F = 118.98$, $p = 0.002$) increased with increasing spatial scale under the NG treatment.

4. Discussion

In our sheep grazing experiments, we first explored the grazing effect on plant species diversity, ecosystem stability, and their relationship across spatial scales in a desert steppe. We found that increasing grazing intensity did not alter the species diversity, but reduced ecosystem stability. This was mediated by a reduction in species asynchrony and by declining species stability. The results showed a consistently negative influence of diversity on temporal ecosystem stability across spatial scales. This has highlighted the distinct destabilizing influences of

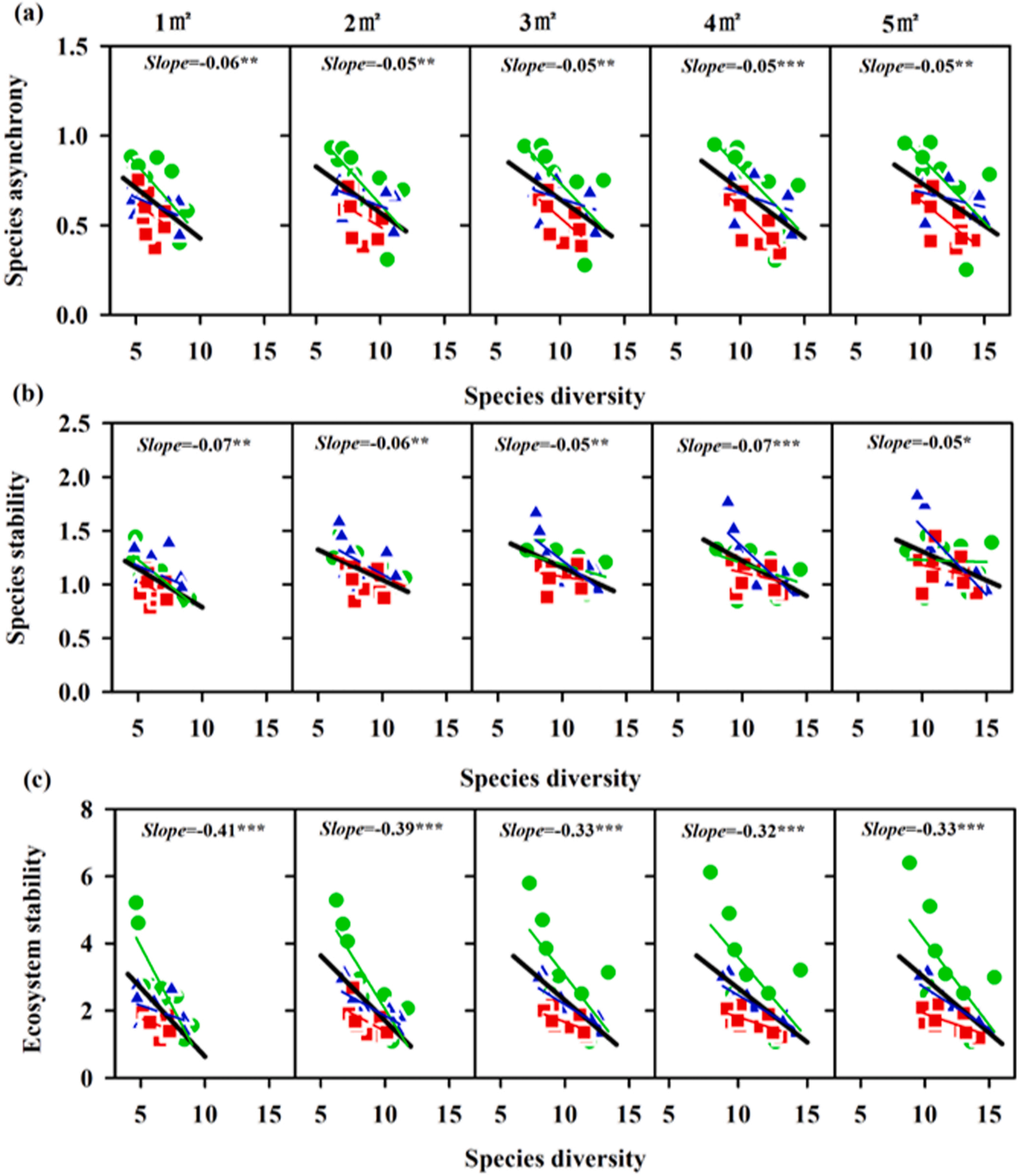

Fig. 2. Relationship between stability and diversity: (a) species asynchrony and species diversity (95 % confidence intervals: −0.086 to −0.021 across spatial scales), (b) species stability and species diversity (95 % confidence intervals: −0.116 to −0.018 across spatial scales), (c) ecosystem stability and species diversity (95 % confidence intervals: −0.591 to −0.168 across spatial scales). Model fit information is provided in Table A5. Points are values for 1, 2, 3, 4, and 5 m^2 with NG shown by green circles, MG is indicated by blue triangles, and HG is indicated by red squares. Black lines represent the overall relationship based on a linear mixed-effects model. Colored lines show random-effect variations for NG, MG, and HG. Significance level: $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

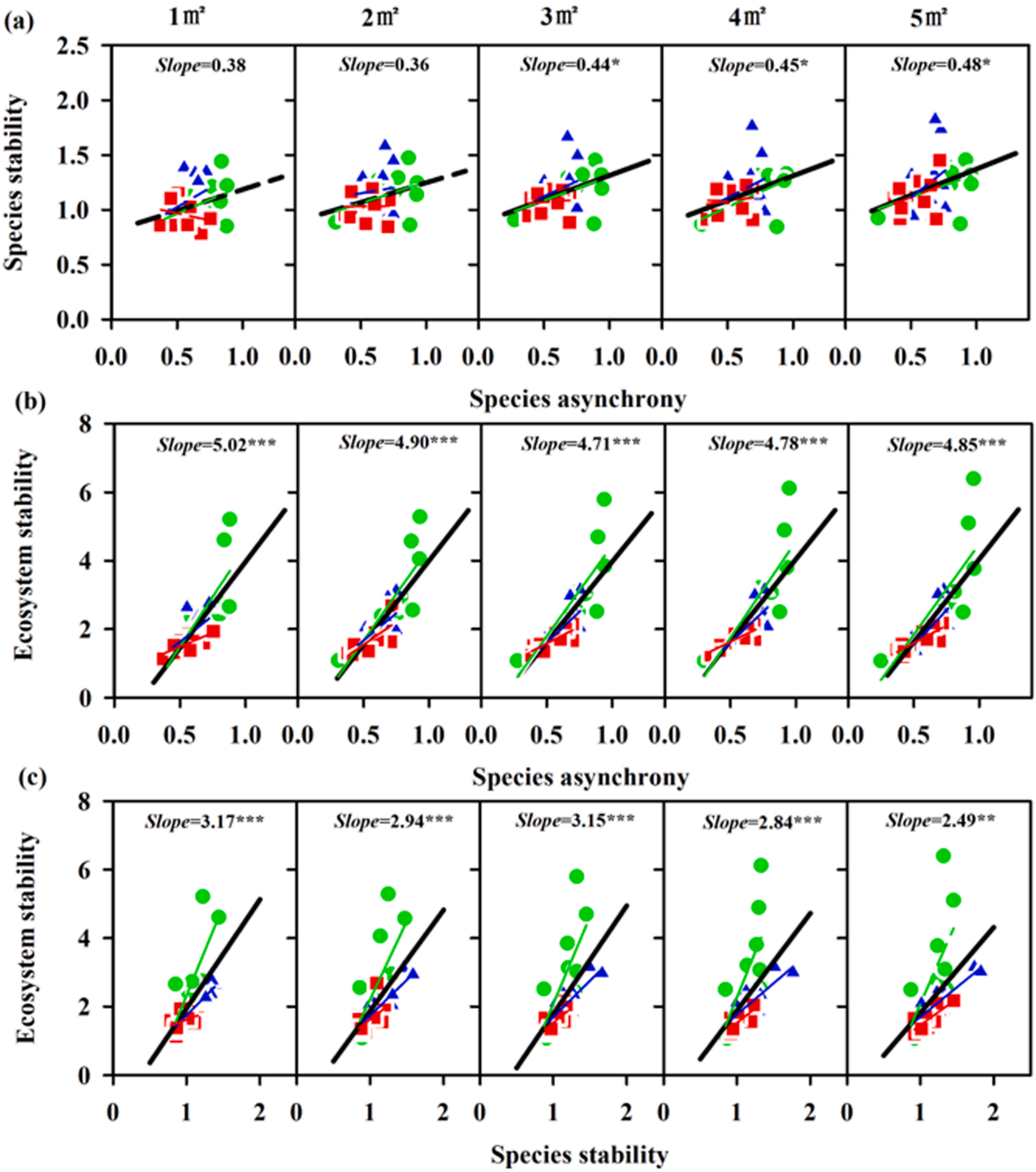

Fig. 3. Relationship between ecosystem stability and species asynchrony. (a) species stability and species asynchrony (95 % confidence intervals: 0.043–0.911 across spatial scales), (b) ecosystem stability and species asynchrony (95 % confidence intervals: 3.303–6.666 across spatial scales), (c) ecosystem stability and species stability (95 % confidence intervals: 1.139–4.483 across spatial scales). Model fit information is provided in Table A5. Points are values for 1, 2, 3, 4, and 5 m^2 for NG (green circles), MG (blue triangles), and HG (red squares). Black lines represent the overall relationship based on a linear mixed-effects model. Colored lines show random-effect variations for NG, MG, and HG. Significance level: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

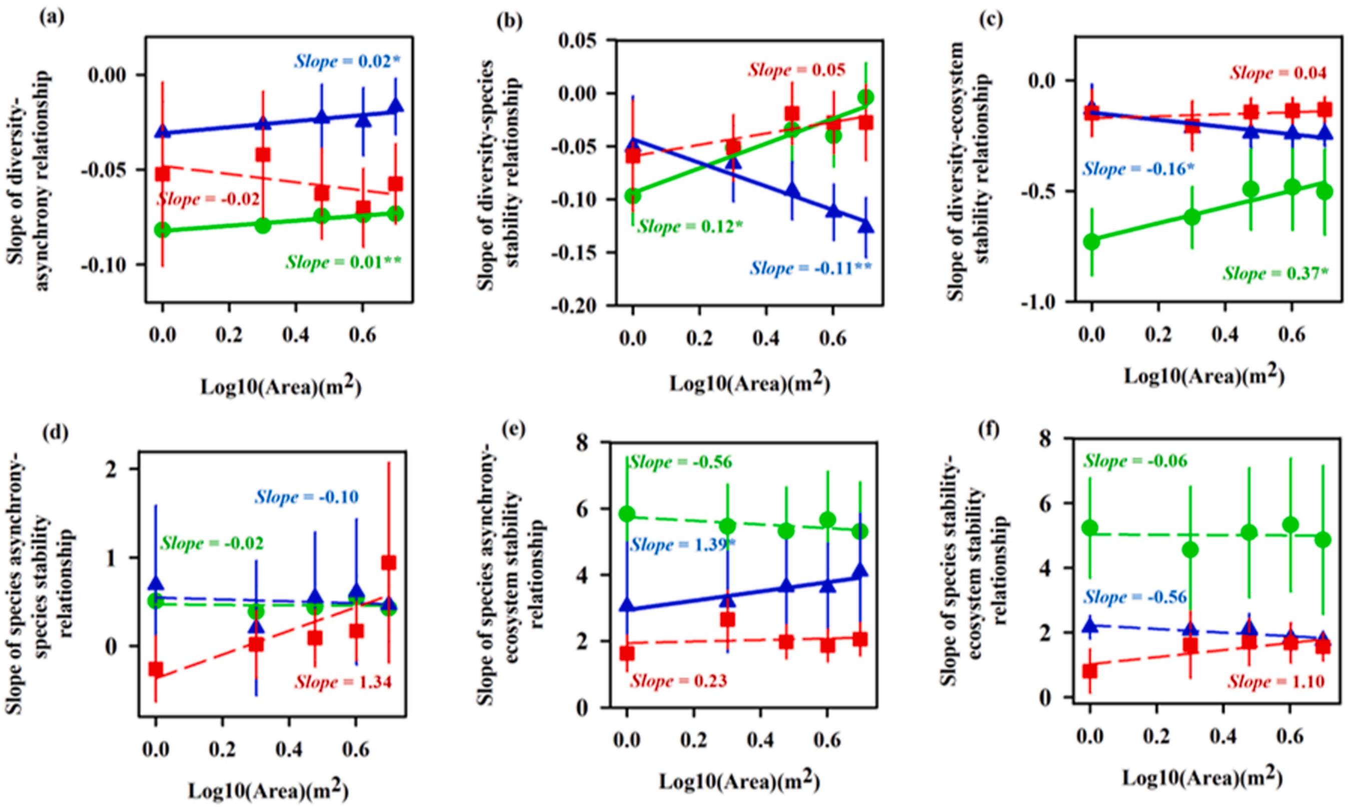

Fig. 4. Grazing effect on the slopes of the diversity–ecosystem stability relationship with increasing spatial scales. (a) Slopes of the diversity–species asynchrony relationship (data from Fig. 2a; $R_m^2 = 0.91$ under NG; $R_m^2 = 0.73$ under MG). (b) Slopes of the diversity–species stability relationship (data from Fig. 2b; $R_m^2 = 0.88$ under NG; $R_m^2 = 0.93$ under MG). (c) Slopes of the diversity–ecosystem stability relationship (data from Fig. 2c; $R_m^2 = 0.87$ under NG; $R_m^2 = 0.84$ under MG). (d) Slopes of the species asynchrony–species stability relationship (data from Fig. 3a). (e) Slopes of the species asynchrony–ecosystem stability relationship (data from Fig. 3b; $R_m^2 = 0.80$ under MG). (f) Slopes of the species stability–ecosystem stability relationship (data from Fig. 3c). Model fit information is provided in Table A6. Points are values for 1, 2, 3, 4, and 5 m^2 for NG (green circles), MG (blue triangles), and HG (red squares). Colored lines show slope variation for NG (green), MG (blue), and HG (red). Significance $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species diversity in ecosystem function. Grazing weakened the negative diversity–ecosystem stability relationship across spatial scales.

4.1. *Grazing and spatial scale affect ecosystem stability as mediated by changing species diversity, asynchrony, and stability*

Grazing did not alter the species diversity across all five spatial scales. Increasing grazing intensity had a similar slope to the SAR, with the curves finally intersecting (Olff and Ritchie, 1998). MG increased species stability at all five spatial scales, which was predominantly attributed to preferential foraging of palatable and nutritious plants by herbivores. This increased the relative abundance of the dominant species *S. glareosa* ($F = 159.98$, $p < 0.001$; Fig. A3b) (Liang et al., 2021). Increasing grazing intensity reduced the species asynchrony and ecosystem stability (Fig. 1c, d). This suggests that species asynchrony is an important driver of grassland ecosystem functionality and stability (Bai et al., 2004; Hautier et al., 2014; Liang et al., 2021). We used the SEM to determine the influences of grazing intensity, species diversity, species asynchrony, and species stability on ecosystem stability (Qin et al., 2019; Liang et al., 2021; Xu et al., 2021). Grazing indirectly

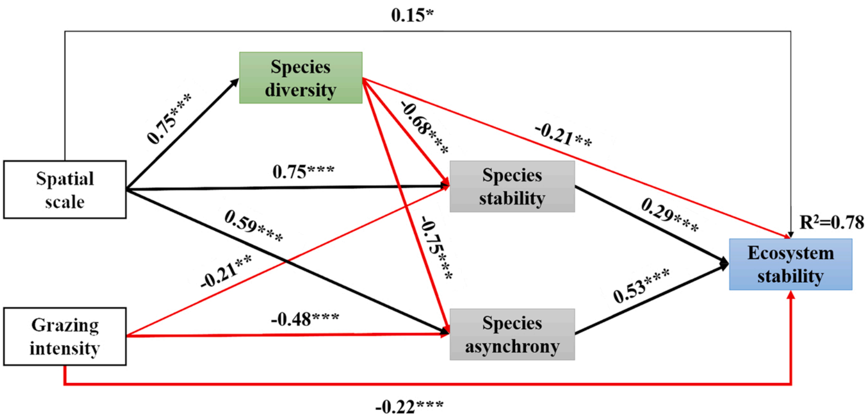

Fig. 5. Structural equation model (SEM) associating grazing, spatial scales, species diversity, asynchrony, and stability with ecosystem temporal stability. The final SEM is presented with the standardized path coefficients. Arrows denote positive (black) and negative (red) relationships, respectively. $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$. $\chi^2 = 0.415$, $p = 0.937$; RMSEA $= 0.000$; AIC $= 48.415$. We provided SEMs fit information including unstandardized path coefficients and R^2 of individual response variables in Table A7 and Table A9 (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

reduces ecosystem stability mainly by decreasing the species asynchronous dynamics far more than by decreasing species stability, but not through species diversity (Fig. 5). This indicates that species asynchrony was the primary factor, and species stability the secondary factor, which is associated with arid grassland biomass production (Liang et al., 2021; Xu et al., 2021). Additionally, it shows that the observed effects of grazing on ecosystem stability are independent of species diversity (Hautier et al., 2014). However, our results are generally in contrast with previous research in semiarid desert steppe, which has shown that species diversity is the main factor associated with ecosystem productivity (Zhang et al., 2018a).

Species diversity increased with increasing spatial scales. Theoretical and experimental studies have also illustrated the positive SAR (Storch, 2016; Zhang et al., 2018b). The changes in SAR were predominantly attributed to spatially distributed patterns of individual species. This has influenced the species asynchrony–area relationship, which has led to variation in the invariability–area relationship (Loreau and de Mazancourt, 2008; Tilman et al., 2014; Wang et al., 2017; Gonzalez et al., 2020). The SEM has demonstrated that increasing spatial scales did not change the ecosystem stability. An increase in ecosystem stability caused by the direct effects of increasing spatial scales was offset by its indirect effects mediated by increasing species diversity, species asynchrony, and species stability (Fig. 5). This was in contrast with research showing that species synchrony decayed exponentially and temporal invariability increased steeply with increasing area (Wang et al., 2017). This was in line with the findings of research in temperate grasslands, which showed that the invariability–area relationship (IAR) did not change with increasing spatial scale (Zhang et al., 2018b). Asynchrony in species biomass fluctuations determines the shape of the IAR. If it decays with distance, the IAR will become disconnected from SAR (Loreau and de Mazancourt, 2008; Thorson et al., 2018).

4.2. Grazing-induced negative effects of diversity on ecosystem stability increased with spatial scale

Our findings have illustrated that ecosystem stability generally reduced with species diversity across spatial scales in grazing arid grassland. Species populations are destabilized with increasing biodiversity in most terrestrial grassland ecosystems (Tilman et al., 2012, 2014). Our findings have also illustrated the destabilizing role of diversity in terms of population stability within species under grazing across spatial scales, which was found to be positively related to ecosystem stability. Higher mean stability within species could stabilize community productivity because of lower variation in species abundance (Tilman et al., 2014). In contrast to the findings of previous studies (Zhang et al., 2018b; Liang et al., 2021), our findings have shown that diversity was negatively associated with asynchronous dynamics among species, which was positively related to ecosystem temporal stability.

The asynchronous dynamics among species would explain the destabilizing influences of diversity on ecosystem function at each of the five spatial scales (Hector et al., 2010; Isbell et al., 2011; Zhang et al., 2018b). Species asynchrony stabilizes species stability and ecosystem temporal stability at all five spatial scales. This is likely because the asynchronous response of coexisting species in the same ecosystem to environmental fluctuations was at fine scales in desert steppe in Inner Mongolian and also at broader scales (Bai et al., 2004; Loreau and de Mazancourt, 2013; Zhang et al., 2018b). The intermediate rates of species dispersal moving among patches of vegetation efficiently trace their environmental optima, promote species persistence, and strongly stabilize productivity in moderate species asynchronous fluctuations (Tilman et al., 2014; Gonzalez et al., 2020). The temporal variance in biomass productivity reduced with biodiversity (Tilman et al., 2014; Ben-Hur and Kadmon, 2020). However, our findings identified a showed positive diversity–variance relationship. The reduction in temporal ecosystem stability with increasing biodiversity can result from a direct denominator increase in temporal variance of the aboveground biomass with biodiversity across spatial scales. This is instead of a marginal and smaller increase in the temporal mean with biodiversity across spatial scales in comparison with temporal variance (Hautier et al., 2014).

The negative slope of the diversity–ecosystem temporal stability relationship was smaller at 1 m^2 (slope = - 0.41) and at 2 m^2 (slope = - 0.39) than that at larger spatial scales (slope = - 0.33) in the grazed steppe. This was mainly due to the interaction between the patch-specific grazing-induced responses at large scales and species-specific grazing-induced responses at fine scales (Adler et al., 2001; Zhang et al., 2018b). Both theories (Loreau and de Mazancourt, 2013; Wang and Loreau, 2016) and long-term experiments in temperate grasslands (Zhang et al., 2018b) have shown that the positive slopes of the diversity–ecosystem stability relationship decrease with increasing spatial scale. However, we found that the negative slopes of the diversity–ecosystem stability relationship increased with increasing spatial scales in desert steppe. This is because the slope of the diversity–spatial scale relationship was higher than that of the ecosystem stability–spatial scales relationship. The result was co-determined by the negative relationship of diversity–species asynchrony and diversity–species stability increasing with increasing spatial scales (Xu et al., 2021). The relationship between biodiversity and ecosystem temporal stability may change based on the spatial scales of observation in grazed grassland (Adler et al., 2001). However, whether the destabilizing effects of diversity on ecosystem temporal stability at the five spatial scales propagated to reduce ecosystem stability at broader spatial scales is not yet clear. How grazing-induced diversity affects the temporal stability of an ecosystem in terms of the continuum of spatial scales, rather than for an isolated scale also requires further research (Adler et al., 2001; Zhang et al., 2018b).

4.3. Grazing weakened the negative diversity–ecosystem stability relationship across spatial scales

Grazing weakened the destabilizing influence of diversity on ecosystem function across spatial scales because the diversity–spatial scale relationship remained unchanged. Meanwhile, the ecosystem stability–spatial scale relationship became less pronounced with increasing grazing intensity. This result was supported by the weakened negative effects of diversity on asynchronous dynamics among species and the insurance effects of asynchronous dynamics on ecosystem stability in grazed steppe (Zhang et al., 2018b; Qin et al., 2019; Liang et al., 2021).

Environmental heterogeneity generally stimulates biodiversity by increasing opportunities for niche partitioning (Tilman et al., 2014; Ben-Hur and Kadmon, 2020). When niche width, dispersal range, heterogeneity, and fragmentation occurs, the effective area per species should be considered. However, the results show that diversity is reduced with an increase in heterogeneity. This may cause a negative influence of diversity on temporal ecosystem stability (Law and Dieckmann, 2000; Turner and Tjorve, 2005; Harpole and Tilman, 2007; Isbell et al., 2011; Bergholz et al., 2017; Zhang et al., 2018b; Ben-Hur and Kadmon, 2020). The effects of biodiversity on the stability of ecosystem function are determined by the resource and physiology limitations imposed by those environments (Harpole and Tilman, 2007; Isbell et al., 2011). The species and their habitat are generally aggregated in patches but are not uniformly distributed across spatial scales. This is because the number of microhabitats and level of heterogeneity increase with increasing spatial scales, which has the potential to create habitat niches for a greater number of species (Law and Dieckmann, 2000; Turner and Tjorve, 2005; Harpole and Tilman, 2007; Bergholz et al., 2017). However, if these species cannot exploit heterogeneous resources effectively, stability at the corresponding scales did not increase through spatial niche complementarity under grazing in desert steppe (Loreau et al., 2003).

5. Conclusions

Our sheep grazing experiment has demonstrated that increases in grazing intensity continuously reduce the temporal stability of the ecosystem across spatial scales in arid grasslands. This study has also highlighted the destabilizing influence of species diversity on ecosystem function across spatial scales in these environments. Grazing has weakened the destabilizing influences of diversity on ecosystem function across different spatial scales. This is because grazing maintained a constant species–scale relationship while the invariability–scale relationship decreased. In our study, we have developed a SEM to explore the relative importance of species diversity, asynchrony, and stability within species in modulating ecosystem stability across spatial scales in arid grasslands. This will have key practical implications for the sustainable management of grassland ecosystems. Future studies should include experiments at scales larger than 5 m^2, particularly encompassing broader spatial scales. This can help to deepen our understanding of the scale-dependance of grazing-induced shifts in species diversity, asynchrony, stability, and ecosystem stability, as well as the associations between them in arid grassland ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108343.

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