

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

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30

31 **Abstract**

32 Livestock grazing is a major driver shaping the functioning and stability of grasslands. Although
33 previous studies have documented the effect of grazing on grassland stability, whether this effect
34 is scale-dependent remains unclear. Here, we conducted a sheep-grazing experiment in a
35 temperate grassland to test grazing effects on biomass stability across scales and organizational
36 levels. We found that an increase of grazing intensity increased species stability, but it
37 substantially decreased local ecosystem stability due to reduced asynchronous dynamics among
38 species. Moreover, grazing reduced ecosystem stability at larger spatial scales, but to a lesser
39 extent. By decreasing biodiversity within and across communities, grazing impairs the insurance
40 effects of biodiversity and hence the up-scaling of stability from species to ecosystem and further
41 to larger scales. Our study provides the first evidence for the context-dependence of grazing
42 effects on grassland stability via shaping biodiversity and contributes to bridging fine-scale
43 experiments and broad-scale ecosystem management.

44

45 **Introduction**

46 Occupying more than one-third of earth's terrestrial land surface and contributing about 40 % of
47 global agricultural domestic products, grassland is the largest coupled human and natural
48 systems on Earth (Herrero *et al.* 2013). The sustainable delivery of functions and services by
49 grassland is critical for human society and wildlife living upon it. However, human activities are
50 altering earth's environment with extreme events becoming more frequent worldwide, which
51 threatens the ability of grassland ecosystems to reliably provide functions and services to
52 humanity (Sloat *et al.* 2018; Liang & Gornish 2019). Understanding the stability of grassland
53 ecosystems in the face of environmental changes is thus critical for sustainable ecosystem
54 management and decision-making.

55 Livestock grazing is the most intensive land-use activity in grasslands, which presents a
56 major driver shaping the functioning and stability of grasslands (Fetzel *et al.* 2017; Wang *et al.*
57 2019a; Filazzola *et al.* 2020). Recent studies experimentally testing the effect of grazing on
58 grassland ecosystem stability revealed differential effects at different spatial scales (Post 2013;
59 Beck *et al.* 2015; Hautier *et al.* 2015; Bluthgen *et al.* 2016; Hallett *et al.* 2017; Ganjurjav *et al.*
60 2019; Qin *et al.* 2019). At smaller spatial scales (e.g., ~tens of m²), studies have shown that
61 herbivore exclusion decreases the temporal stability of productivity or cover in grassland
62 communities (Post 2013; Beck *et al.* 2015; Hautier *et al.* 2015; Hallett *et al.* 2017), indicating
63 that herbivory could promote community stability. At intermediate scales (e.g., from ha to km²),
64 two recent studies found that livestock grazing did not affect the stability of total plant cover
65 across European grasslands (Bluthgen *et al.* 2016) or aboveground plant biomass on the Tibetan
66 Plateau (Ganjurjav *et al.* 2019). At even broader scales (e.g., ~hundreds of km²), studies in
67 temperate grasslands found that livestock grazing decreased the stability of plant community

68 productivity (Qin *et al.* 2019). These results suggest that the effect of grazing on stability might
69 be scale dependent. Yet, previous studies have mostly focused on a particular scale, and whether
70 grazing effects differ across scales remains to be tested.

71 The impact of grazing on stability may be mediated by its effect on plant species diversity. A
72 large body of experimental and theoretical work has demonstrated that biodiversity can provide
73 insurance effects to enhance ecosystem temporal stability (Loreau 2010; Tilman *et al.* 2014).
74 While these studies have mostly been conducted at small spatial scales, recent studies started to
75 understand whether these results can be extended to understand biodiversity and stability at
76 larger spatial scales, where landscape heterogeneity and habitat structures may interact with
77 biodiversity patterns (Donohue *et al.* 2013; Isbell *et al.* 2017; Kefi *et al.* 2019; Gonzalez *et al.*
78 2020). Such a potential scale dependency is particularly relevant in grazing systems, which often
79 exhibit greater heterogeneity as grazing area increases (Adler *et al.* 2001). Moreover, herbivore
80 behavior (e.g., foraging selectivity and trampling) is an important mechanism impacting plant
81 diversity in grassland ecosystems (Collins *et al.* 1998; Koerner *et al.* 2018) with scale-dependent
82 effects on plant species diversity (Olf & Ritchie 1998; de Bello *et al.* 2007; Tonn *et al.* 2019).
83 However, to our knowledge, no study has explored whether changes in plant diversity with
84 grazing intensity mediate its impact on stability across spatial scales.

85 Recently, a new theoretical framework has been developed to study ecological stability
86 across scales (Wang & Loreau 2014, 2016). This framework proposes consistent measures of
87 temporal stability (i.e. the inverse of temporal variability) across organizational levels and spatial
88 scales (Fig. 1). Specifically, in a landscape consisting of a number of communities, γ stability is
89 defined as the temporal stability of total ecosystem function at large spatial scales (i.e. a
90 landscape or aggregation of communities), α stability is defined as a weighted average of

91 temporal stability across local communities, and *species stability* is defined as a weighted
92 average of local population stability across species within local communities (Fig. 1). Theory
93 predicts a consistent increase of stability from species to local communities and further to larger
94 spatial scales, with the amounts of increase determined by *species asynchrony* and *spatial*
95 *asynchrony*, respectively (Wang *et al.* 2019b). Specifically, γ *stability* can be expressed as the
96 product of species stability, species asynchrony, and spatial asynchrony. Thus, asynchronous
97 responses among species and local communities to environmental fluctuations provide species
98 and spatial insurance, respectively, to maintain the stability of ecosystem function at larger
99 organizational level and spatial scales (Yachi & Loreau 1999; Loreau *et al.* 2003). Recent studies
100 showed that local species diversity (α diversity) and spatial turnover (β diversity) could
101 contribute to increasing species and spatial asynchrony, respectively (Wang & Loreau 2016;
102 Hautier *et al.* 2020; but see Wilcox *et al.* 2017; Zhang *et al.* 2019). Thus, grazing may regulate
103 ecosystem stability at larger scales by altering local and spatial turnover of biodiversity, but this
104 hypothesis has not been tested previously.

105 In this study, we conducted a grazing experiment to quantify the impact of grazing intensity
106 on stability at multiple scales and assess whether these effects are mediated by changes in plant
107 diversity. Specifically, we asked the following questions: (1) Does grazing affect the stability of
108 plant biomass at species, local communities, and large spatial scales? (2) Does grazing affect
109 species and spatial insurance effects by changing plant diversity at multiple spatial scales? Our
110 analyses revealed context-dependent effects of grazing on stability, which shifted from a positive
111 effect on species stability to negative effects on community stability at both local and larger
112 spatial scales. Such effects were modulated by grazing-induced decreases in both α and β
113 diversity. Our findings provide novel insights for a mechanistic understanding of grassland

114 ecosystem stability across scales and have useful implications for landscape-scale ecosystem
115 management.

116

117 **Material and methods**

118 *Study site*

119 The study site is located at the Xilin Gol Grassland Nature Reserve, Inner Mongolia, China
120 (44°08'N, 116°19'E, 1 129 m) (Fig. S1a). The biome type is the typical steppe grassland, which
121 is dominated by rhizome grass (*Leymus chinensis* (Trin.) Tzvel.) and bunchgrass (*Stipa grandis*
122 P. Smirn) (Liang *et al.* 2019). Soil taxonomy was classified as the Calcic-Orthic Aridisol based
123 on USDA soil classification. The study area is characterized as the semiarid climate (BSk) in the
124 Köppen climate classification. During the past six decades, the mean annual air temperature was
125 2.6 °C and mean annual precipitation (MAP) was 266.9 mm, with more than 90 % the
126 precipitation falling in the growing season (<http://data.cma.cn/>).

127 *Grazing experiment*

128 In 2011, we fenced 12 equal-sized (120 m × 120 m) paddocks to exclude natural grazing
129 activities and implemented four grazing intensity treatments from 2013 to 2018, including 0, 2,
130 4, and 8 sheep·ha⁻¹, referred to as no- (NG), light- (LG), medium- (MG), and heavy-grazing
131 (HG), respectively (Fig. S1b). Each treatment had three replicates. We implemented sheep-
132 grazing in four bouts during the growing season of each year, from June through September.
133 Each bout was exposed to some grazing treatment for 21 days. Species biomass data was
134 collected in the last week of each month after grazing since June 2014. More detailed
135 experiments descriptions can be found in Liang *et al.* (2019).

136 *Plant sampling strategies*

137 We regarded each 120 m × 120 m paddock as a community at the large scale, which consisted of
 138 five subplots (120 m × 20 m) (Fig. S1c). For each subplot, we used scissors to clip the residual
 139 living aboveground tissue of all vascular plants (i.e., green plant biomass) above the soil surface
 140 in a 1 m × 1 m quadrat, which was used to represent the community at local spatial scale. After
 141 these tissues of plants has been oven-dried at 65 °C in 48 hours, we weighted them and estimated
 142 the biomass for each species (g·m⁻²). We collected the data in June, July, August, and September
 143 between 2014 and 2018. In total, we measured more than 7, 000 plant species biomass values in
 144 1, 200 quadrats from 2014 to 2018, i.e. five years × four months (or bouts) × four treatments ×
 145 three replicates × five quadrats.

146 *Biodiversity, stability, and asynchrony across scales*

147 We used abundance-based metrics to calculate species diversity across scales (Fig. 1 and Fig.
 148 S1c). At the local spatial scale (e.g., a local community l), we calculated the Simpson index:

149 $\phi_l = \sum_i^S p_{il}^2$, where p_{il} represents the relative biomass of species i in the local community l and S is

150 the number of species in the local community l . We then defined α diversity as the inverse of the

151 weighted average of Simpson index: $\alpha_{simp} = 1 / \sum_{l=1}^5 \omega_l \phi_l$, where ω_l is the ratio of total biomass of

152 the local community l to that of the aggregate community (i.e. aggregation of the five quadrats)

153 at the large scale (Wang & Loreau 2016). The γ diversity was defined as: $\gamma_{simp} = 1 / \sum_i P_i^2$, where

154 $P_i = \sum_{l=1}^5 \omega_l p_{il}$ denotes the relative abundance of species i in the aggregate community at the large

155 scale. β diversity was defined multiplicatively, i.e. $\beta_{simp} = \gamma_{simp} / \alpha_{simp}$. To test the robustness of our

156 results, we also calculated the Bray-Curtis dissimilarity among the five quadrats in each plot as
 157 an alternative measure of β diversity. Besides, we also calculated species richness at the local
 158 quadrat (α_{rich}) and larger (γ_{rich}) scales, and the multiplicative beta diversity as: $\beta_{\text{rich}} = \gamma_{\text{rich}} / \alpha_{\text{rich}}$.

159 Furthermore, we defined the species stability, as well as community stability at α and γ
 160 scales (Wang & Loreau 2014; Wang *et al.* 2019b). For the stability metrics, we calculated its
 161 temporal stability by the inverse of coefficient of variation (i.e. the ratio of mean to standard
 162 deviation). Species stability was defined as the weighted average of local species stability across
 163 species and local communities; α stability was calculated as the weighted average of community
 164 stability across local communities; γ stability was calculated as the community stability at large
 165 spatial scale (Fig. 1). The mathematical formulas for these definitions are (Wang *et al.* 2019b):

$$166 \quad \text{Species stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sum_{i,k} \sqrt{v_{ii,kk}}} \quad (1)$$

$$167 \quad \alpha \text{ stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sum_k \sqrt{\sum_{i,j} v_{ij,kk}}} \quad (2)$$

$$168 \quad \gamma \text{ stability} = \frac{\sum_{i,k} \mu_{i,k}}{\sqrt{\sum_{i,j,k,l} v_{ij,kl}}} \quad (3)$$

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

171 The spatial stability framework clarified that asynchrony among lower-level components
 172 (e.g. species or communities) are key to the scaling of stability (Lamy *et al.* 2019; Wang *et al.*
 173 2019b). In light of this framework, we defined *species asynchrony* as the ratio of α stability to
 174 species stability, which captures the incoherence in population dynamics among species within

175 local communities; we then defined *spatial asynchrony* as the ratio of γ stability to α stability,
176 which captures the incoherence in community dynamics among local communities. We also
177 defined *total asynchrony* as the product of *species asynchrony* and *spatial asynchrony*, which
178 quantifies the total insurance effect provided by species and spatial asynchrony from local
179 species to communities at larger spatial scales. More details about the equations of the stability
180 and synchrony indices can be found in Wang et al. (2019b).

181 *Statistical analysis*

182 To assess the effects of grazing on biodiversity and stability of plant communities at multiple
183 scales, we ran mixed-effects models (MEMs) using the R package ‘*lme4*’ (Bates *et al.* 2015). In
184 these models, the fixed effect was “*grazing intensity*” and random effects were “*month/year*” and
185 “*month*” for examining biodiversity and stability, respectively. We used the Fligner-Killeen Test
186 to test homogeneity of variances among four grazing intensities; if homoscedasticity was not
187 met, we added weights for EMMs using *gls()* function in R (Zuur *et al.* 2010). Considering the
188 autocorrelations among observations through time, we compared models without autocorrelation
189 structure to the mixed-effects models including a first-order autoregressive model (AR (1)); all
190 these MEMs gave similar results; thus, we chose the best fit model according to the lowest
191 Akaike Information Criterion (AIC). To facilitate comparison of effect sizes of grazing intensity
192 gradient on these biodiversity and stability metrics, we used the natural log-transformed response
193 variables. In addition, we ran similar MEMs using “*grazing intensity*” as a factorial variable (GI:
194 no-grazing (NG), low-grazing (LG), medium-grazing (MG), and high-grazing (HG)), and
195 compared grazing effects among different grazing intensities using Tukey’s-range test. We also
196 performed the repeated-measures ANOVA to test whether the main effects of “*grazing intensity*”
197 on these variables vary with “*year*” and “*month*”, or any interactions. “*grazing intensity*”

198 explained the largest proportion of variance in total of biodiversity (except for plant richness)
199 and stability metrics (Table S1, Table S2, Table S3, Table S4, and Table S5). Here, we used the
200 non-transformed response variables to quantitatively compare their changes under different
201 grazing intensities.

202 To address our second question of how biodiversity influence stability at different scales, we
203 examined the relationships between biodiversity and stability using MEMs, with “*grazing*
204 *intensity*” and “*month*” as random factors. In particular, we tested the relationships of species
205 asynchrony with α diversity, of spatial asynchrony with α and β diversity, and of total
206 asynchrony with γ diversity. For the relationship of spatial asynchrony with α and β diversity, we
207 ran partial linear mixed-effects models (p-MEMs). Specifically, we first ran a MEM between
208 spatial asynchrony and β diversity (or Bray-Curtis dissimilarity), we then extracted the residuals
209 of spatial asynchrony and tested their relationship with α diversity using MEMs, with “*grazing*
210 *intensity*” and “*month*” as random factors. Similarly, we tested the relationship between β
211 diversity (or Bray-Curtis dissimilarity) and the residuals from the MEM of spatial asynchrony
212 with α diversity.

213 Furthermore, to explore how an increase of grazing intensity directly and indirectly impact
214 the hierarchical stability and asynchrony via regulating biodiversity (Fig. S12), we employed a
215 structural equation modeling (SEM) to quantify the different pathways between grazing intensity
216 (as a continuous variable) and γ stability using the R package ‘*piecewiseSEM*’ (Lefcheck &
217 Freckleton 2016). The piecewise SEM could generate a single structural model by piecing
218 multiple linear mixed-effects models (e.g., “*month*” is a random factor). In light of recent
219 metacommunity theory, we constructed a hypothesized SEM that characterized the effect of
220 grazing on species stability, species asynchrony, and spatial asynchrony via altering α and β

221 diversity (Wang *et al.* 2019b). We used Shipley's test of d-separation to ensure that we did not
222 miss any potential pathways between variables (natural log-transformed), and chose the final
223 model that had the lowest AIC. All analyses were programmed in R v 3.6.0 (R Development
224 Core Team 2019).

225

226 **Results**

227 Increasing grazing intensity decreased plant species diversity at both local (α diversity; $F_{1,10} =$
228 22.58, $P = 0.0008$) and larger (γ diversity; $F_{1,10} = 23.50$, $P = 0.0007$) scales (Fig. 2 and Fig. S2a).

229 Grazing also reduced β diversity (Fig. 2a, $F_{1,10} = 20.12$, $P = 0.0012$), regardless of the metrics
230 used (Fig. S4). Compared to the no-grazing treatment, α , β , and γ diversity were decreased on
231 average by 41 %, 12 %, and 49 %, respectively, in the heavy-grazing treatment (Fig. S2). The
232 reduction of plant species diversity was due to a shift in species composition under grazing, but
233 not to a reduction in the number of species (Fig. S3). Specifically, grazing increased the relative
234 abundance of the dominant species, i.e. *Stipa grandis* across the study area (Fig. S4a, $F_{1,10} =$
235 16.09, $P = 0.003$), which decreased α diversity and β diversity due to spatial homogenization.
236 We also found that biodiversity metrics exhibited temporal variations that are potentially driven
237 by environmental fluctuations, but overall grazing intensity alone explain the largest proportion
238 of variance in plant diversity (Table S2 and Table S3).

239 Grazing had context-dependent effects on stability (Fig. 2 and Table S5). At the species
240 level, increasing grazing intensity increased the stability of the dominant species (Table S5, $F_{1,10}$
241 = 10.38, $P < 0.0001$) and thus species stability (Fig. 2c, $F_{1,10} = 16.01$, $P = 0.003$), as grazing did
242 not affect the temporal mean biomass of the dominant species (Fig. S5c, $F_{1,10} = 1.33$, $P = 0.277$)
243 but reduced its temporal standard deviation (Fig. S5d, $F_{1,10} = 11.38$, $P = 0.007$). However,

244 grazing decreased community stability at both local (α stability: $F_{1,10} = 27.50$, $P = 0.0004$) and
245 larger (γ stability: $F_{1,10} = 10.17$, $P = 0.010$) scales (Fig. 2c). Compared to those in no-grazing
246 treatment, species stability was on average 55 % higher (i.e., $\frac{\bar{V}_g - \bar{V}_c}{\bar{V}_c} \times 100\%$), α stability was 29
247 % lower, and γ stability was 24 % lower in heavy-grazing treatment (Fig. S8). Such context-
248 dependent grazing effect on stability was mediated by its effect on asynchrony (Fig. S9 and
249 Table S11). Grazing significantly decreased species asynchrony (Fig. 2b, $F_{1,10} = 27.35$, $P =$
250 0.0004) while increasing spatial asynchrony (Fig. 2b, $F_{1,10} = 12.81$, $P = 0.005$). Specifically,
251 species asynchrony was 55 % lower and spatial asynchrony was 13 % higher in heavy-grazing
252 treatment, compared to those in no-grazing. From local species to communities at larger spatial
253 scales, species and spatial asynchrony together contributed to enhancing stability by 242 % in
254 no-grazing treatment, but their contribution was only 69 % in heavy-grazing treatment (Fig. S7f).

255 We found that species asynchrony was positively related to α diversity (Fig. S10a, $R^2_m =$
256 0.68 , $F_{1,35} = 44.83$, $P < 0.0001$), and spatial asynchrony was associated with both α and β
257 diversity (Fig. S11). Specifically, spatial asynchrony was negatively related to α diversity after
258 the effect of β diversity was controlled (Fig. S11a, $R^2_m = 0.11$, $F_{1,35} = 5.51$, $P = 0.025$), and it was
259 positively related to β diversity after the effect of α diversity was controlled (Fig. S11c, $R^2_m =$
260 0.06 , $F_{1,35} = 3.18$, $P = 0.083$). These relations were robust to different metrics of β diversity (Fig.
261 S11). Moreover, total asynchrony was positively related to γ diversity (Fig. 3, $R^2_m = 0.48$, $F_{1,35} =$
262 22.90 , $P < 0.0001$). Therefore, by decreasing species diversity at different scales, grazing could
263 impair species and spatial asynchrony and thus insurance effects for community stability at
264 larger scales.

265 We used a structural equation model (SEM) to disentangle the direct and indirect pathways
266 through which grazing influenced γ stability. Specifically, we examined how grazing affected the
267 three components of γ stability (= species stability \times species asynchrony \times spatial asynchrony)
268 by altering species diversity (Fig. S12). Our final SEM showed that an increase of grazing
269 intensity increased the abundance of the dominant species, which led to a higher stability of the
270 dominant species and the average species stability (Fig. 4). However, by increasing the dominant
271 species abundance, grazing decreased both α and β diversity. The decreased α diversity in turn
272 decreased species asynchrony but increased spatial asynchrony, whereas the decreased β
273 diversity weakened spatial asynchrony. Combining all these pathways, grazing led to increased
274 species stability (total effect size or TES = 0.462), but decreased community stability at both
275 local (TES = -0.298) and larger (TES = -0.188) spatial scales (Table S7 and Table S8).

276

277 **Discussion**

278 By quantifying stability across organizational levels and spatial scales in a grassland ecosystem,
279 our study provides, to our knowledge, the first evidence for the context-dependent effects of
280 grazing on stability (Fig. 5). Our results demonstrate that grazing increases species stability but
281 decreases community stability at both local and larger spatial scales. Such context-dependent
282 effects of grazing can be understood from its influence on species and spatial asynchrony (Fig.
283 5), which are in turn explained by herbivory selective foraging that significantly alters species
284 diversity patterns including the dominant species abundance, species diversity, and spatial
285 heterogeneity.

286 At the species level, the positive effects of grazing on species stability are mainly attributed
287 to the selective foraging by grazers that increases the relative abundance of one dominant

288 species, i.e. *S. grandis*. In general, gazers preferentially forage palatable and nutritious plants. In
289 our study system, *S. grandis* is less palatable and nutritious compared to other plants, thanks to a
290 long evolutionary history of plant-herbivore interactions under the nomadic pastoralism on the
291 Mongolia Plateau (Sanjmyatav 2012). As a tussock grass, livestock browsing does not damage
292 the basal meristem of *S. grandis*, which may lead to tiller development via increasing light
293 penetration (Borer *et al.* 2014). Moreover, *S. grandis* produces long-needle seeds (approximately
294 1.1 cm long) with a barb that can hook on animal fur, and its barb could damage animal's
295 digestion system (e.g., tongue and stomach), particularly for sheep. These morphological and
296 physiological characters make *S. grandis* more resistant to grazing compared to other plants.
297 Consequently, selective foraging on its more palatable competitors eventually led to an increase
298 of abundance of *S. grandis* (Fig. 4). Thus, the grazing-induced dominance by a more resistant
299 species increases stability at the species level. Increasing species stability might in part be
300 attributed to our sampling design. Clipping quadrats with shifting locations through time might
301 accounts for spatial variation in species biomass. More specifically, because grazing decreases
302 spatial turnover (i.e. β diversity; Fig. 2) and thus spatial variation in species biomass, higher
303 species stability may be simply due to the artificial effect of our sampling approach. To evaluate
304 this possibility, we tested the relationships of the stability of *S. grandis* with its abundance and β
305 diversity. Our results showed that whereas both factors are significantly related to dominant
306 species stability, dominant species abundance provided a much better explanation and β diversity
307 became insignificant after the effect of the dominant species abundance was accounted for (Fig.
308 S13, Fig. S14, Table S13, and Table S14). Thus, the increasing species stability with grazing
309 should be mainly explained by the increased dominance of *S. grandis*, rather than the artificial
310 effect of sampling.

311 By enhancing the dominance of *S. grandis*, grazing decreases plant diversity within local
312 communities and thereby weakens the species insurance effect for community stability (Fig. 4).
313 A large body of experimental and theoretical studies have demonstrated the stabilizing role of
314 species diversity in ecosystem stability (Loreau 2010; Tilman *et al.* 2014). One major
315 mechanism for the stabilizing effect of biodiversity is that different species exhibit asynchronous
316 responses to environmental fluctuations, which compensate for each other and result in a higher
317 stability at the community level (Tilman *et al.* 2006; Gonzalez & Loreau 2009). Our SEM
318 confirmed this hypothesis by showing that grazing decreases species asynchrony indirectly via
319 reducing α diversity. This result is consistent with previous findings that anthropogenic drivers
320 (e.g., nitrogen, carbon dioxide, fire, herbivory, and water) affect ecosystem stability indirectly
321 via biodiversity (Hautier *et al.* 2015). The negative effects of grazing on species asynchrony
322 suppress its positive effect on species stability, leading to a decreasing community stability with
323 grazing (Fig. 5).

324 The negative effect of grazing on community stability propagate from local (α) to larger (γ)
325 spatial scales, as α stability at the local community scale is the major driver of γ stability (Fig.
326 S8). Yet, the reduction in γ stability was less pronounced than α stability, which was explained
327 by the increase of spatial asynchrony with grazing. Metacommunity theory predicts that spatial
328 asynchrony among communities increases with β diversity and decreases with α diversity (Wang
329 & Loreau 2016). Our data supported these predictions and showed that grazing affected spatial
330 asynchrony through two pathways via changing α and β diversity (Fig. S11). On the one hand,
331 grazing decreases local α diversity and increased spatial asynchrony. On the other hand, due to
332 the selective foraging that increases the dominance of *S. grandis* across the landscapes, grazing
333 decreases β diversity and thus spatial asynchrony. Because the positive pathway via α diversity is

334 relatively stronger than the negative one via β diversity, grazing eventually leads to higher spatial
335 asynchrony. Such higher spatial asynchrony compensates to some extent for the reduction in α
336 stability and generates a smaller reduction of γ stability.

337 From local species to communities at larger scales, asynchrony among species and across
338 communities provide insurance effects that enhance ecosystem stability (Wang et al. 2019). In
339 such a context, recent studies provided evidence for a stronger insurance effect by either species
340 asynchrony (Lamy et al. 2019; Wang et al. 2019) or spatial asynchrony (Thorson *et al.* 2018). In
341 our study system, species asynchrony provides a much stronger insurance effect for γ stability,
342 compared to spatial asynchrony, in no-grazing systems (Fig. 5). However, grazing can reverse
343 this pattern by decreasing species diversity, such that spatial asynchrony provides a slightly
344 stronger insurance effect than species asynchrony in high-grazing systems (Fig. 5). This is likely
345 because grazers have a stronger species preference than a patch preference in our study system.
346 These results provide the first evidence that grazing can alter the up-scaling patterns of stability
347 by dampening the overall insurance effect and switching the relative importance of species and
348 spatial insurance.

349

350 **Conclusion**

351 Our findings contribute to an in-depth understanding of the scaling property of ecological
352 stability and how it may be influenced by disturbances like livestock grazing. In particular, our
353 results demonstrate general destabilizing effects of grazing on grassland ecosystems across
354 scales, but the strengths of these effects depend on the study scale. Our multi-scale approach
355 provides a potential framework to reconcile previous findings of varying grazing effects across
356 scales (Post 2013; Beck *et al.* 2015; Hautier *et al.* 2015; Bluthgen *et al.* 2016; Hallett *et al.* 2017;

357 Qin *et al.* 2019). Moreover, future studies should extend our approach to even larger scales,
358 particularly those ecosystem management is applied at. Such insights will be valuable for
359 bridging small-scale ecological research with large-scale management, thus providing useful
360 guide for grassland management and decision-making in a changing environment.

361

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369

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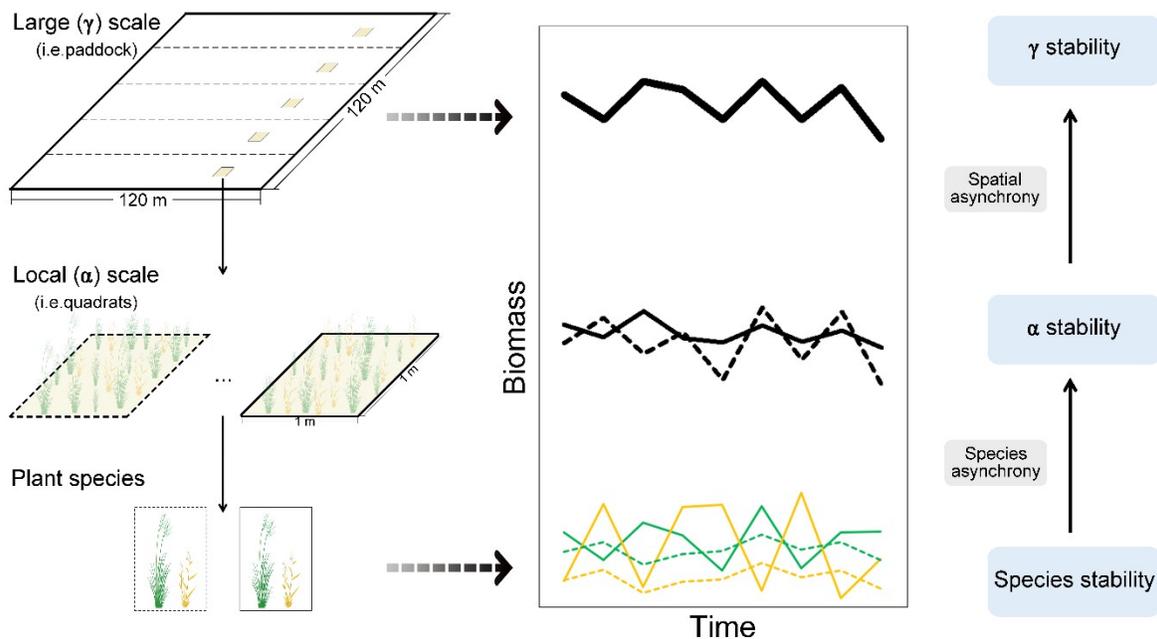
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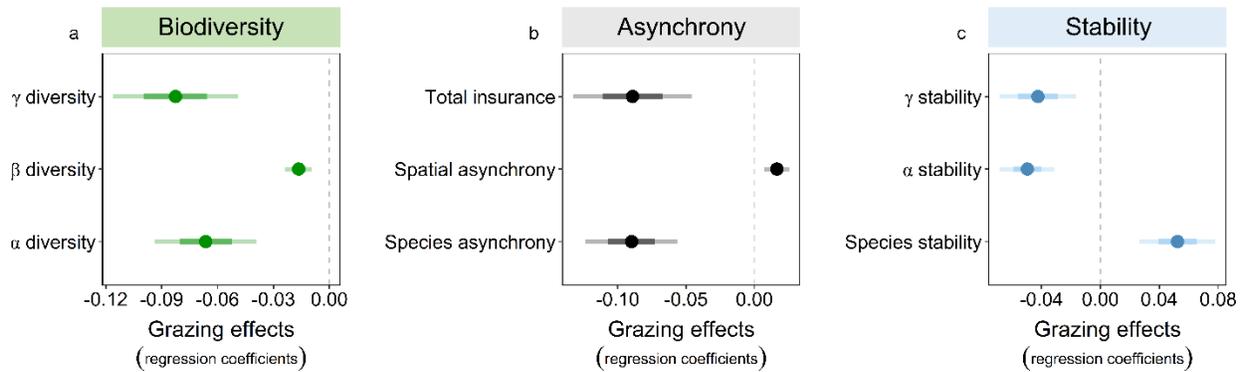
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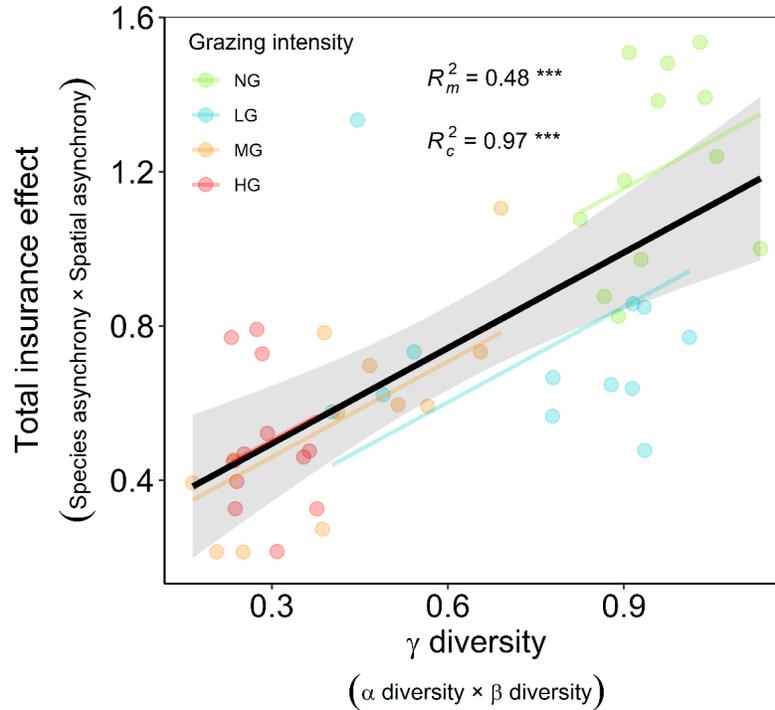
470

471 **Figure 1** A theoretical framework of ecological stability across scales illustrated with our
 472 experiment. Within each paddock ($120 \times 120 \text{ m}^2$), five local communities (1 m^2 quadrats) were
 473 sampled. We regard each quadrat as the local (α) scale, and aggregation of the five quadrats as
 474 the larger (γ) scale. Ecosystem stability is defined as the mean of an ecosystem function divided
 475 by its standard deviation through time across organizational levels (i.e. from species to
 476 community) and spatial scales (i.e., from local to larger spatial scales). Theoretically, stability at
 477 larger spatial scale (γ stability) is determined by three components, namely *species stability*,
 478 *species asynchrony*, and *spatial asynchrony*. At the local scale (i.e. quadrats), asynchronous
 479 dynamics among species (solid green and yellow lines) leads to a high α stability (solid black
 480 line), despite the low *species stability*; in contrast, synchronous dynamics among species (dashed
 481 green and yellow lines) leads to a low α stability (dashed black line), despite the high *species*
 482 *stability*. At the large spatial scale (i.e. paddock), asynchronous fluctuations between local
 483 communities (spatial asynchrony) contribute to increasing γ stability.



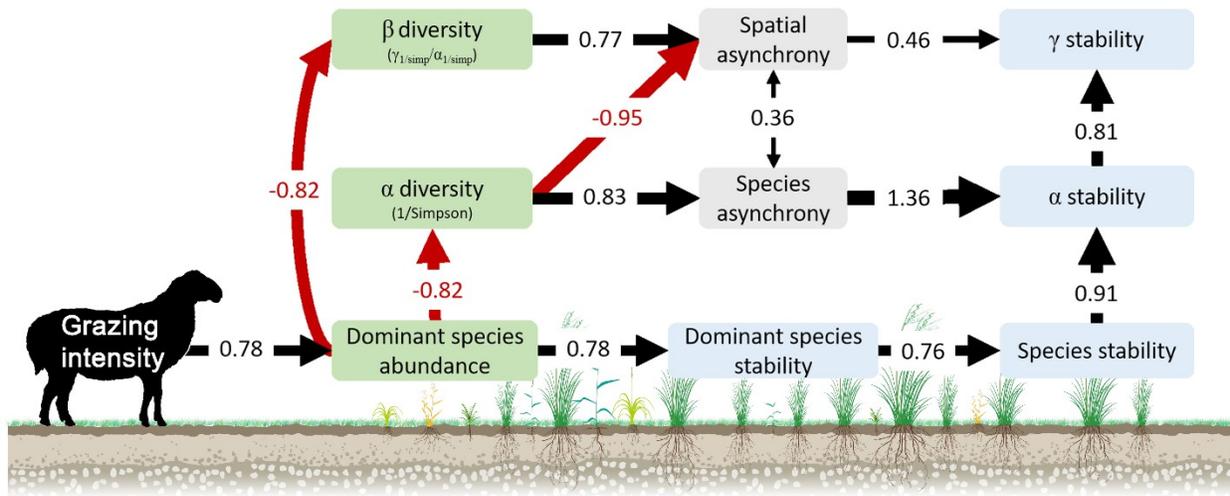
484

485 **Figure 2** Grazing effects on biodiversity, asynchrony, and stability at multiple scales. Shown are
 486 the regression coefficients from linear mixed-effects models, which quantify the effects of
 487 increasing grazing intensity on (a) biodiversity (α diversity in 1 m² quadrats, $F_{1,10} = 22.58$, $P =$
 488 0.0008; γ diversity in 120 × 120 m² paddock, $F_{1,10} = 23.50$, $P = 0.0007$; β diversity (γ / α), $F_{1,10} =$
 489 20.12, $P = 0.0012$), (b) asynchrony metrics (species asynchrony, $F_{1,10} = 27.35$, $P = 0.0004$;
 490 spatial asynchrony, $F_{1,10} = 12.81$, $P = 0.005$; total insurance = species asynchrony × spatial
 491 asynchrony, $F_{1,10} = 16.27$, $P = 0.002$), and (c) stability metrics (species stability, $F_{1,10} = 16.01$, $P =$
 492 0.003; α stability, $F_{1,10} = 27.50$, $P = 0.0004$; γ stability, $F_{1,10} = 10.17$, $P = 0.010$). The darker bar
 493 denotes the standard error and the lighter bar represents the 95 % confidential interval. Here,
 494 species diversity was defined by the reverse of Simpson index that incorporates both the number
 495 and abundance of species (see ‘Methods’). The repeated-measurement ANOVA and Tukey’s-
 496 range test for multiple comparisons under four grazing intensities are provided in Table S2,
 497 Table S5, Fig. S2, Fig. S7, and Fig. S8, respectively.



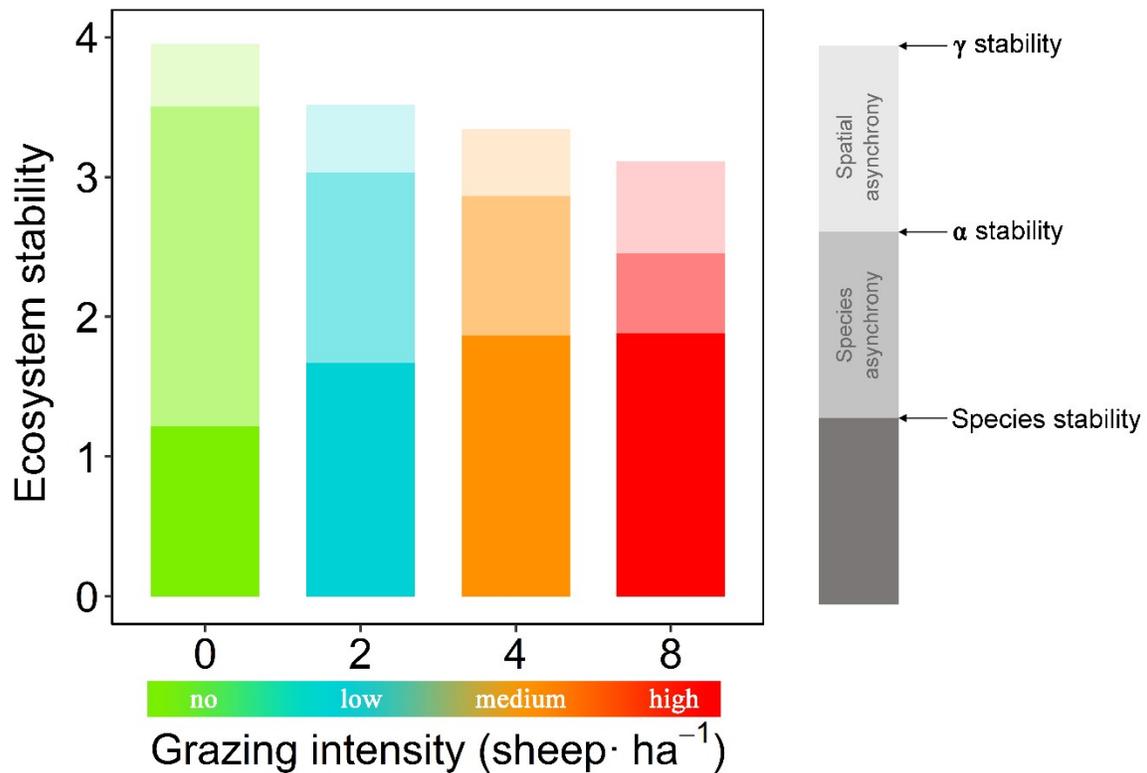
498

499 **Figure 3** Relationship between total insurance effect and γ diversity. Each point represents
500 values for a paddock at a given grazing intensity and particular month. Black line represents the
501 overall relationship ($F_{1,35} = 22.90$, $P < 0.0001$) from a linear mixed-effects model (with the
502 shaded areas denoting the 95 % confidence intervals), and the colored lines indicate random-
503 effect variations for no grazing (NG, green), low grazing (LG, blue), medium grazing (MG,
504 orange), and high grazing (HG, red) intensity. The marginal (R_m^2) and conditional (R_c^2) r-squared
505 represent “fixed effects” and “fixed + random effects” explanations, respectively. The significant
506 level: “*”: $P < 0.05$; “**”: $P < 0.001$; “***”: $P < 0.0001$.



507

508 **Figure 4** The structural equation model (SEM) depicting the direct and indirect effects of
 509 grazing intensity on grassland biodiversity and ecosystem stability at multiple scales. Shown are
 510 the final SEM with the standardized path correlation coefficients. Black and red arrows denote
 511 positive and negative associations, respectively. Fisher's $C = 69.695$; $df = 64$; $p = 0.292$; $AIC =$
 512 157.695 . Information about the priori SEM, the unstandardized direct effects, and the R^2 of
 513 individual response variables are provided in Fig. S12, Table S7, and Table S8, respectively.



514

515 **Figure 5** Visualized effects of grazing on stability across scales. Shown are the mean values of
 516 species stability, α stability, and γ stability under four grazing intensities: no- (0 sheep·ha⁻¹), low-
 517 (2 sheep·ha⁻¹), medium- (4 sheep·ha⁻¹), and high- (8 sheep·ha⁻¹) grazing intensity. As the grazing
 518 intensity increases, species stability increases, but α and γ stability decrease due to the reduced
 519 insurance effect of species asynchrony. In no-grazing treatment, species asynchrony provided a
 520 much stronger insurance effect for γ stability compared to spatial asynchrony. But an increase of
 521 grazing intensity reduces biodiversity and its insurance effects, such that in high-grazing
 522 treatment, spatial asynchrony provides a relatively stronger insurance effect than species
 523 asynchrony.