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# Herbivores safeguard plant diversity by reducing variability in dominance

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# Herbivores safeguard plant diversity by reducing variability in dominance

## Abstract

1. Reductions in community evenness can lead to local extinctions as dominant species exclude subordinate species; however, herbivores can prevent competitive exclusion by consuming otherwise dominant plant species, thus increasing evenness. While these predictions logically result from chronic, gradual reductions in evenness, rapid, temporary pulses of dominance may also reduce species richness. Short pulses of dominance can occur as biotic or abiotic conditions temporarily favor one or a few species, manifested as increased temporal variability (the inverse of temporal stability) in community evenness. Here, we tested whether consumers help maintain plant diversity by reducing the temporal variability in community evenness.

2. We tested our hypothesis by reducing herbivore abundance in a detailed study of a developing, tallgrass prairie restoration. To assess the broader implications of the importance of herbivory on community evenness as well as potential mechanisms, we paired this study with a global herbivore-reduction experiment.

3. We found that herbivores maintained plant richness in a tallgrass prairie restoration by limiting temporary pulses in dominance by a single species. Dominance by an annual species in a single year was negatively associated with species richness, suggesting that short pulses of dominance may be sufficient to exclude subordinate species.

4. The generality of this site-level relationship was supported by the global experiment in which inter-annual variability in evenness declined in the presence of vertebrate herbivores over timeframes ranging in length from 2-5 years, preventing declines in species richness. Furthermore, inter-annual variability of community evenness was also negatively associated with pre-treatment species richness.

5. Synthesis: A loss or reduction of herbivores can destabilize plant communities by allowing brief periods of dominance by one or a few species, potentially triggering a feedback cycle of dominance and extinction. Such cycles may not occur immediately following the loss of herbivores, being delayed until conditions allow temporary periods of dominance by a subset of plant species.

## Keywords

Determinants of plant community diversity and structure, Nutrient Network (NutNet), light, biomass, *Chamaecrista fasciculata*, Plant–herbivore interactions, Plant–plant interactions

## Disciplines

Ecology and Evolutionary Biology | Plant Sciences | Terrestrial and Aquatic Ecology

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13 **HERBIVORES SAFEGUARD PLANT DIVERSITY BY REDUCING VARIABILITY IN**  
14 **DOMINANCE**

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## 45 **Summary**

46 **1.** Reductions in community evenness can lead to local extinctions as dominant species exclude  
47 subordinate species; however, herbivores can prevent competitive exclusion by consuming  
48 otherwise dominant plant species, thus increasing evenness. While these predictions logically  
49 result from chronic, gradual reductions in evenness, rapid, temporary pulses of dominance may

50 also reduce species richness. Short pulses of dominance can occur as biotic or abiotic conditions  
51 temporarily favor one or a few species, manifested as increased temporal variability (the inverse  
52 of temporal stability) in community evenness. Here, we tested whether consumers help maintain  
53 plant diversity by reducing the temporal variability in community evenness.

54 **2.** We tested our hypothesis by reducing herbivore abundance in a detailed study of a developing,  
55 tallgrass prairie restoration. To assess the broader implications of the importance of herbivory  
56 on community evenness as well as potential mechanisms, we paired this study with a global  
57 herbivore-reduction experiment.

58 **3.** We found that herbivores maintained plant richness in a tallgrass prairie restoration by  
59 limiting temporary pulses in dominance by a single species. Dominance by an annual species in  
60 a single year was negatively associated with species richness, suggesting that short pulses of  
61 dominance may be sufficient to exclude subordinate species.

62 **4.** The generality of this site-level relationship was supported by the global experiment in which  
63 inter-annual variability in evenness declined in the presence of vertebrate herbivores over  
64 timeframes ranging in length from 2-5 years, preventing declines in species richness.  
65 Furthermore, inter-annual variability of community evenness was also negatively associated with  
66 pre-treatment species richness.

67 **5. Synthesis:** A loss or reduction of herbivores can destabilize plant communities by allowing  
68 brief periods of dominance by one or a few species, potentially triggering a feedback cycle of  
69 dominance and extinction. Such cycles may not occur immediately following the loss of  
70 herbivores, being delayed until conditions allow temporary periods of dominance by a subset of  
71 plant species.

72 **Key-words:** Determinants of plant community diversity and structure; Nutrient Network  
73 (NutNet); light; biomass; *Chamaecrista fasciculata*; Plant–herbivore interactions; Plant–plant  
74 interactions

## 75 **Introduction**

76 Changes in relative abundance within plant communities may occur in response to factors such  
77 as disturbance (Yuan et al., 2016), climate (Post and Pedersen, 2008; Kaarlejärvi et al., 2013;

78 Post, 2013; Pardo et al., 2015; Sullivan et al., 2016), disease (Creissen et al., 2016), the loss or  
79 appearance of mutualists or enemies (Morris et al., 2007), or a sudden resource pulse (Hillebrand  
80 et al., 2007; Yang et al., 2008; Kaarlejärvi et al., 2013), as well as interactions among these or  
81 other factors. Such environmental factors may allow temporary periods of increased dominance  
82 by one or a few species (hereafter referred to as “pulses” of dominance).

83 Sufficiently strong pulses of dominance can lead to losses of subordinate species (Wilsey and  
84 Polley, 2004; Hautier et al., 2009) that can persist for multiple growing seasons depending on the  
85 colonization rates of extirpated species (Cadotte, 2006) and the priority effects imposed by  
86 remaining species (Fukami, 2015). Moreover, decreased plant diversity can further destabilize  
87 communities by reducing resistance and/or resilience to disturbance (*e.g.*, McNaughton, 1985;  
88 Duffy, 2002; Caldeira et al., 2005; Isbell et al., 2015), potentially increasing the probability of  
89 future pulses of dominance. Losses in plant diversity are also associated with decreased stability  
90 of plant community biomass (McNaughton, 1985; Caldeira et al., 2005; Tilman et al., 2006;  
91 Isbell et al., 2009; Eisenhauer et al., 2011; Hautier et al., 2015), suggesting increased variability  
92 in competition for light (*e.g.*, Borer et al. 2014b). This potential feedback of decreased stability  
93 leading to species loss, which in turn further reduces stability, could contribute to an “extinction  
94 cascade” (*sensu* Valiente-Banuet and Verdú, 2013; Fig. 1).

95 Herbivores may prevent these losses in diversity by restraining dominance during temporary, as  
96 well as prolonged (*e.g.*, persistent nutrient additions as in Borer et al., 2014b), periods when  
97 conditions favor potentially-dominant species (Fig. 1). Indeed, herbivores can reduce mean plant  
98 biomass while also increasing the temporal stability of the plant community (Eisenhauer et al.,  
99 2011), potentially limiting periods of increased competition for light (Gibson, 1988; Stevens and  
100 Carson, 2002; Hautier et al., 2009; Borer et al., 2014b). This maintenance of species diversity at  
101 the local scale may affect plant richness at larger scales by conserving beta diversity and  
102 associated opportunities for migration between plots. Therefore, herbivory may play an  
103 important role in maintaining plant diversity during brief periods of dominance.

104 We propose that herbivores maintain plant diversity, in part, by limiting strong, yet temporary,  
105 pulses of dominance that would otherwise exclude subordinate species. We tested this  
106 hypothesis by experimentally reducing herbivore abundances in communities of high and low  
107 diversity within a developing grassland in the U.S. Midwest, further assessing the generality and

108 potential mechanisms influencing the relationships between herbivory, stability, and diversity in  
109 a global herbivore reduction experiment. We predict that:

- 110 1. Reduced herbivore abundance allows pulses of increased dominance by one or a few  
111 species (Fig. 1a), manifested as increased inter-annual variability (the inverse of stability)  
112 of community evenness, that is associated with a loss of species (Fig. 1c-d).
- 113 2. Losses in species diversity following herbivore reductions are associated with increased  
114 variability in biomass and light (Fig. 1b-e).
- 115 3. If species richness moderates temporal variability (McNaughton, 1985; Isbell et al., 2009;  
116 Eisenhauer et al., 2011), then initial plant richness is negatively associated with inter-  
117 annual variability, potentially leading to a positive feedback (Fig. 1b-h).
- 118 4. Herbivore loss drives spatial homogenization through lower species richness across plots  
119 (*i.e.*, beta diversity). Such declines in richness across plots could limit potential  
120 colonizers from the species pool, further limiting plant richness following pulses of  
121 dominance. Alternatively, it is possible herbivore loss may increase beta diversity if  
122 different species increase in dominance in different locations.

## 123 **Materials and methods**

### 124 RESTORATION EXPERIMENT

125 The Oakridge Research and Education Prairie is a 1.6 ha tallgrass prairie restoration in Ames,  
126 Iowa, U.S.A. (42.035°, -93.664°), that was managed for row crops for at least 100 years before  
127 its planting in March of 2012. Prior to planting, we established eight 32 x 32 m blocks, fencing  
128 off four blocks to reduce the abundance of mammalian herbivores including white-tailed deer  
129 (*Odocoileus virginianus*), prairie voles (*Microtus ochrogaster*), and meadow voles (*M.*  
130 *pennsylvanicus*). Fences consist of two strands of electric fencing running ~0.4 and 1 m above  
131 ground level that are both set 1 m outside a third strand running 0.75 m above ground level  
132 following the design by Hygnstrom et al. (1994). The inner fence also consists of 1.3 cm (0.5 in)  
133 mesh hardware cloth extending 0.5 m above and 0.4 m belowground to discourage burrowing.

134 We trapped and removed voles from fenced areas at least three times from May-October each  
135 year with trapping periods spaced at least one month apart. The only exception to this trapping  
136 pattern was in the first year of the experiment (2012) when we only trapped twice. We placed



137 7.6 x 8.9 x 22.9 cm Sherman Live Traps (H.B. Sherman Traps, Tallahassee, Florida) in an even,  
138 4 x 4 grid within each fenced block, spacing traps ~9 m apart and ~2 m from the fence. We  
139 baited traps with oats, locking them open for at least two days before setting to allow habituation.  
140 Trapping continued for at least three consecutive nights during each period, extending longer  
141 when needed to reduce numbers. All voles trapped inside fenced blocks were relocated >4 km  
142 away to minimize reentry, and breeches in the fences were patched whenever detected. The  
143 number of voles removed from fenced treatments is available in Table S2. Trapping and  
144 handling of animals was conducted in accordance with ethical standards approved by a local  
145 IACUC committee.

146 We sowed both high and low diversity plant communities within each of the eight experimental  
147 blocks. High diversity treatments include 51 species in a circular area (19.2 m diameter) in the  
148 center of each block. One species in each of the high diversity communities was unique to that  
149 block to monitor long distance dispersal (not reported here). We sowed the remainder of the  
150 field with a subset of 14 species from the high diversity treatment. The number of species used  
151 in the low and high diversity communities approximate diversities in most prairie restorations  
152 and remnants, respectively (*e.g.*, Martin et al., 2005). Species in the low-diversity treatment  
153 were selected to represent all major functional groups (forb, legume, C3/C4 grass; see Table S1  
154 in Supporting Information for full species list).

155 We annually measured diversity and community composition at peak biomass in early fall in  
156 permanent 1 x 1 m plots in each high (n = 3 plots/block) and low (n = 4 plots/block) diversity  
157 treatment per block. We visually estimated cover using a modified Daubenmire method  
158 (Daubenmire, 1959), estimating cover to the nearest 1%. We calculated species richness (S) as  
159 the number of plant species present in a plot and evenness as  $H/\ln(S)$ , where H is Shannon's  
160 diversity. We measured beta diversity across plots as the mean Bray-Curtis dissimilarity  
161 between a plot and its treatment median in a multi-dimensional analysis of species abundance  
162 (Anderson et al., 2006). Greater distances from the median indicate greater differences among  
163 plots in terms of community composition. We calculated Bray-Curtis distances in R 3.2.3 (R  
164 Core Team, 2015) using the `vegdist` function from the `vegan` package (Oksanen et al. 2016). We  
165 calculated inter-annual variability for evenness as the coefficient of variation (standard  
166 deviation/mean) across all years within a plot.

167 We tested the effects of the herbivore reduction and the diversity treatments on all measures of  
168 diversity, inter-annual variability of community evenness, and cover of a single dominant  
169 species, *Chamaecrista fasciculata* (Michx.) that was only sown in high-diversity treatments. We  
170 selected *C. fasciculata* as this was the only species in any treatment or year to achieve a mean  
171 cover of >50% per plot (Fig. S1). Additionally, we compared *C. fasciculata* abundance to  
172 species richness in the high diversity treatments. For all tests, we treated our analysis as a  
173 repeated measure, split-plot design by applying mixed-effects ANOVA, or ANCOVA when  
174 comparing *C. fasciculata* abundance to species richness, with year as a fixed effect and plot  
175 nested within block as random effects. We controlled for temporal autocorrelation among plots  
176 with an autoregressive correlation of order 1 following Pinheiro and Bates (2000). We made *a*  
177 *priori* contrasts showing the effect of herbivore reductions in each diversity treatment by year  
178 using Bonferroni corrections for multiple comparisons. Repeated measures models were run in  
179 R using the nlme package (Pinheiro et al. 2016) and all other models were run using the lmerTest  
180 (Kuznetsova et al., 2016) and lme4 packages (Bates et al., 2015). Denominator degrees of  
181 freedom were estimated using the Satterthwaite approximation (Satterthwaite, 1946).

## 182 GLOBAL GRASSLANDS EXPERIMENT

183 In the global experiment, we used data from 40 sites in the Nutrient Network, not including the  
184 restoration experiment described above. These Nutrient Network sites represent six continents  
185 and 13 countries, ranging in species richness from 2-37 species and in evenness from 0.07-1  
186 (Fig. 2, Table S3). In addition to manipulating nutrient additions to grasslands, the Nutrient  
187 Network also tests the effects of experimentally reducing vertebrate herbivores. The  
188 experimental design of the herbivore reduction treatment and data collection procedures have  
189 previously been described in detail (Borer et al., 2014a; Borer et al., 2014b), so we only briefly  
190 review the methods here.

191 Sites are divided into 2-6 blocks with one 5 x 5 m control and herbivore reduction plot per block.  
192 Herbivore reduction plots are surrounded by 1 m tall wire mesh with four strands of wire spaced  
193 in 0.3 m increments above the mesh. Wire mesh extends 0.3 m outward from the base of the  
194 fence to discourage burrowing. Herbivores excluded at each site were reported by site managers  
195 and are listed in the supporting information (Table S4). Plant cover, biomass, and light  
196 penetration measurements were collected annually at peak biomass for 2-8 years at each site,

197 depending on site age (Table S4). Plant cover was estimated as in the restoration experiment in  
198 one permanent 1 x 1 m subplot per plot. Total biomass was measured by collecting living  
199 aboveground biomass rooted and plant litter lying within two 0.1 x 1 m strips located outside the  
200 cover subplot, drying at 60°C for 48 hours, and weighing. Photosynthetically active radiation  
201 (PAR) was measured above the plant canopy and at ground level from opposite corners of the  
202 cover subplots within 2 hours of solar noon using a linear quantum light sensor (MQ-301,  
203 Apogee Instruments, Logan, Utah). Light penetration was calculated as the proportion of PAR  
204 reaching the soil surface.

205 We calculated plant diversity using the same metrics as in the restoration experiment. Changes  
206 in richness were calculated as the log response ratio (LRR) compared to pre-treatment values.  
207 We calculated inter-annual variability of evenness, biomass, and light penetration as the  
208 coefficient of variation across years for each plot. We also calculated variability as the standard  
209 deviation across years for a plot, but results using this approach were not qualitatively different  
210 from using the coefficient of variation and so are not reported here. We calculated variability  
211 across a variable, moving window of 2-7 years depending on treatment duration at each site.  
212 Consequently, a single plot may have multiple measures of variability for each window of  
213 duration beginning with two-year increments, building to a single measure of variability for the  
214 duration of the treatment with a single exception. We did not calculate variability across the  
215 longest possible timeframe of eight years in the oldest sites as this would have eliminated  
216 variation in treatment duration, a covariate in our models. Including this longest window of  
217 variability in a simplified model without treatment duration did not qualitatively affect our  
218 results and so is not reported here.

219 We made all comparisons using mixed-effects models as in the restoration experiment with  
220 block nested within site as a random effect. We tested the indirect effect of herbivores on  
221 changes in plant diversity with two sets of models. In the first, we tested the effects of  
222 herbivores on inter-annual variability for evenness, plant biomass, and light penetration with pre-  
223 treatment plant richness and treatment duration as a covariate. Second, we examined the  
224 relationship between inter-annual variability of evenness (which may vary independently of  
225 richness; Wilsey et al., 2005), biomass, or light penetration and the LRR of plant richness at the  
226 end of the window of variability considered with herbivore treatment as a fixed effect and

227 treatment duration as a covariate. As variation in evenness was positively correlated with  
228 variation in both light penetration ( $F_{1,85.5} = 5.92$ ,  $P = 0.017$ ) and biomass ( $F_{1,90.6} = 10.38$ ,  $P =$   
229  $0.001$ ), we tested the relationship between these factors and the LRR of plant richness separately.

230 We also examined the indirect relationships between herbivores and species richness using  
231 piecewise structural equation models (SEM), allowing inclusion of random effects (Lefcheck,  
232 2016). However, results from this approach were consistent with the mixed-effects models  
233 described above and so are not reported here.

## 234 **Results**

### 235 RESTORATION EXPERIMENT

236 The diversity treatment increased plant richness, but not evenness, across herbivore treatments in  
237 the restoration experiment (Table 1, Fig. 3). By comparison, herbivores that were affected by  
238 our fencing treatment (hereafter “herbivores”) did not affect species richness or evenness when  
239 considered in the aggregate (Table 1). However, the effects of herbivores on plant richness  
240 differed significantly by year (herbivore x year, Table 1). Pre-planned contrasts between  
241 herbivore treatments indicate that in the third year of the experiment, herbivores prevented a  
242 significant decrease in evenness within plots (Fig. 3b, e) and beta diversity among plots (Fig. 3c,  
243 f) while marginally increasing richness (Fig. 3a, d). These effects occurred even though vole  
244 populations were lower during this year of the experiment than other years (Table S2),  
245 suggesting that herbivores can have significant effects at low abundance. The positive effect of  
246 herbivores on beta diversity persisted into the fourth year while other effects were marginal or  
247 absent. Reductions in diversity were paralleled by increased dominance of a single species.

248 Herbivores prevented a strong pulse of dominance by a single species in the third year of the  
249 experiment. High-diversity communities were seeded with *Chamaecrista fasciculata* (Michx.),  
250 an annual sown only in the high-diversity treatment. *C. fasciculata* increased in abundance  
251 significantly in the third year of the experiment, with the greatest increase coinciding with  
252 herbivore reductions (Table 1, Fig. 4a, Fig. S1), and was associated with reduced richness during  
253 this period of dominance (cover:  $F_{1,85.75} = 5.23$ ,  $P = 0.025$ ; cover x year:  $F_{3,78.20} = 6.71$ ,  $P =$   
254  $0.004$ ; Fig. 4b). The absence of species capable of achieving the same level of dominance as *C.*

255 *fasciculata* during this experiment (Fig. S1) precluded similar effects in the low-diversity  
256 treatment.

257 Neither herbivores nor the diversity treatment significantly affected inter-annual variability,  
258 measured as the coefficient of variation, in evenness in the restoration experiment (herbivores:  
259  $F_{1,52} = 1.13$ ,  $P = 0.2925$ ; diversity:  $F_{1,52} = 3.90$ ,  $P = 0.0536$ ; herbivores x diversity:  $F_{1,52} = 0.13$ ,  
260  $P = 0.7226$ ), though variability was marginally greater in the high than the low diversity  
261 treatment (high diversity:  $0.131 \pm 0.014$ , least squares mean  $\pm$ SE; low diversity:  $0.094 \pm 0.012$ ).  
262 However, our relatively small sample size at this site ( $n = 56$  plots) limited our power to detect  
263 an effect of herbivores on inter-annual variations in evenness as seen at the global scale of the  
264 Nutrient Network (power = 0.278).

## 265 GLOBAL GRASSLANDS EXPERIMENT

266 Herbivores indirectly support plant diversity in grasslands across the globe by reducing inter-  
267 annual variability in evenness. Herbivores significantly reduced inter-annual variability in plant  
268 community evenness and light penetration when variability was calculated over windows  
269 ranging in duration from 2-6 years (Fig. 5a) and 2-5 years (Fig. 5c), respectively. In contrast,  
270 herbivores did not affect the inter-annual variability of community biomass at any temporal scale  
271 measured here (Fig. 5b). Herbivore effects on variability were not due to persistent, directional  
272 changes as herbivores did not significantly affect mean evenness, though they did increase mean  
273 light penetration (Table 2); however, this latter effect did not vary with treatment duration (*i.e.*,  
274 herbivores x treatment duration interaction, Table 2). Inter-annual variability in evenness was  
275 negatively associated with initial richness when variability was calculated over windows ranging  
276 in duration from 3-5 years (Fig. 5d). Despite this relationship, inter-annual variability of light  
277 penetration and community biomass were not significantly related to initial richness (Fig. 5e, f).

278 Inter-annual variability in evenness was associated with losses in plant richness. The log  
279 response ratio of richness declined significantly as inter-annual variability of evenness increased  
280 over the preceding 2-5 years of the experiment (Fig. 6a). By comparison, changes in richness  
281 were not significantly associated with inter-annual variability in community biomass (Fig. 6b) or  
282 light penetration (Fig. 6c). The direct effect of herbivores was positively, though only  
283 occasionally significantly, associated with the log response ratio of richness, depending on the  
284 timeframe used to calculate variability and the other factor (evenness, biomass, or light) included

285 in the model (Table S6). However, by reducing inter-annual variability in community evenness,  
286 herbivores had a positive, indirect effect on richness.

## 287 **Discussion**

### 288 *Herbivores maintain diversity by limiting pulses of dominance*

289 Herbivores indirectly maintain plant richness by reducing the intensity of temporary pulses of  
290 dominance (Fig. 1a-g). In the restoration experiment, herbivores prevented temporary reductions  
291 of evenness and beta diversity caused by the dominance of a single, annual species. Such  
292 temporary periods of dominance may be sufficient to exclude subordinate species, as suggested  
293 by the negative relationship between *C. fasciculata* cover and species richness. The global  
294 experiment demonstrated the generality of this relationship: herbivores reduced inter-annual  
295 variability in evenness in grasslands across the globe, thus preventing, or at least minimizing,  
296 temporary periods of dominance associated with species loss. This effect of herbivores via inter-  
297 annual variation complements previously described patterns showing that herbivores may also  
298 influence species richness through changes in mean dominance, community biomass, and light  
299 availability (Borer et al., 2014b). Thus, herbivores may maintain plant richness through both  
300 persistent and ephemeral effects on community dominance.

301 The mediating effect of dominance between herbivores and plant richness suggests that plant  
302 species may not be lost immediately following reductions in herbivory. Pulses of dominance, as  
303 observed in our experiments, may occur as annual climates, disturbance, or other conditions  
304 change to favor one or a few species in a plant community. Consequently, the full effect of  
305 herbivores on plant richness may not be observed until environmental conditions provide a  
306 “window of opportunity” (Balke et al., 2014) for a potentially dominant species to increase in  
307 relative abundance. For example, caribou (*Rangifer tarandus*) and muskox (*Ovibos moschatus*)  
308 grazing appeared to have no effect on a grassland community in Greenland prior to experimental  
309 increases in temperature, but after warming, grazing increased stability and prevented losses in  
310 forb richness (Post and Pedersen, 2008; Post, 2013). In a Spanish grassland, livestock grazing  
311 did not strongly affect community structure until an unusually dry period when herbivores  
312 prevented shifts in dominance among grass species (Pardo et al., 2015). The effects of  
313 herbivores on limiting dominance also extend to species that are potentially invasive under  
314 certain conditions (Post and Pedersen, 2008; Kaarlejärvi et al., 2013). These delayed effects of

315 herbivore loss on plant richness may lead to an “extinction debt” that will not be fully realized  
316 until environmental conditions shift to favor a potentially dominant species.

317 Even partial losses in the herbivore community may be sufficient to allow losses in plant  
318 diversity. Mono- or oligotrophic herbivore guilds may be ill-equipped to respond to shifts in  
319 plant dominance across or within seasons, thus promoting inter-annual variability and species  
320 loss. For example, domestic livestock can increase inter-annual variability in plant evenness and  
321 diversity while decreasing mean diversity (Aguilar and Sala, 1998; Bertiller and Bisigato, 1998;  
322 Hanke et al., 2014). Alternatively, diverse herbivore guilds may better support plant diversity as  
323 different herbivores will be able to respond to different dominant species at any given time  
324 (McNaughton, 1985; Duffy, 2002).

325 While we have focused on increases in dominance as a result of increased abundance, it is  
326 possible that dominance can result from decreases in the abundance of other species. The latter  
327 case may occur when conditions disfavor rather than favor a suite of species. However, in either  
328 case, the competitive environment shifts in favor of one group of species. Such conditions may  
329 then allow the favored group to exclude other species through increased abundance or cause rare  
330 species to go locally extinct via ecological drift. Thus, we predict that variability in community  
331 evenness will decrease plant richness regardless of whether environmental conditions lead to an  
332 increase of potentially dominant species or a decrease of potentially subordinate species.

333 Decreased richness in our studies is more likely to have followed brief changes in evenness,  
334 measured as inter-annual variability, than *vice versa*. If low richness led to a decrease in  
335 evenness, one may expect that evenness would remain low until community richness recovered.  
336 However, we found that following a partial recovery in evenness, community richness remained  
337 low. Therefore, we suggest that increased variability in community evenness reduces  
338 community richness rather than low richness prompting pulses of dominance.

### 339 *Mechanisms of diversity in stable communities*

340 The exact mechanisms by which herbivores indirectly maintain plant diversity via increased  
341 community stability are unclear. Light availability (*e.g.*, Olf and Ritchie, 1998; Bakker et al.,  
342 2006; Schmitz, 2006; Borer et al., 2014b) and community biomass (*e.g.*, McNaughton, 1985;  
343 Duffy, 2002; Bakker et al., 2006; Eisenhauer et al., 2011), the most commonly studied effects of

344 herbivores on plant community variation, did not appear to consistently affect plant diversity in  
345 the global experiment when considered in terms of inter-annual variation even though herbivores  
346 decreased variability in light. Thus, while herbivores can maintain plant diversity by increasing  
347 mean light availability (Borer et al., 2014b) or decreasing community biomass (McNaughton,  
348 1985; Hanke et al., 2014), their indirect effects on diversity mediated by inter-annual stability  
349 likely occur through different pathways. We suggest two alternative mechanisms by which  
350 herbivores support plant diversity by increasing inter-annual stability.

351 First, it is possible that our measures of biomass and light did not capture important determinants  
352 of community diversity. For example, community biomass may not accurately depict  
353 architectural features such as canopy height that can affect plant diversity (*e.g.*, Carson and Root,  
354 2000). Moreover, the architectural structure of the surrounding plant community can also affect  
355 light penetration throughout the day (*e.g.*, Skálová et al., 1999), an effect that would not be  
356 detected by our single measurements of light. Thus, it is possible that herbivores may stabilize  
357 light availability throughout the day or season by affecting the physical structure of a plant  
358 community without affecting total biomass.

359 Second, herbivores may prevent temporary, competitive dominance for belowground resources  
360 by preferentially consuming competitively dominant species as in the keystone (Paine, 1966) or  
361 R\*/P\* hypothesis (Holt et al., 1994). However, previous work in our global experiment indicates  
362 that herbivores do not generally prefer competitively dominant over subordinate species (Lind et  
363 al., 2013). Moreover, if availability of belowground resources is related to aboveground biomass  
364 (*e.g.*, McNaughton, 1985), and variability in biomass is not related to richness (Fig. 6b), then we  
365 may expect that variation in belowground competition will not affect richness. Finally, soil  
366 nutrient availability is not always associated with grazing (Milchunas and Lauenroth, 1993; but  
367 see Bakker et al., 2004). Thus, we find it less likely that the stabilizing effects of herbivores  
368 affected plant richness through changes in belowground resources.

### 369 *Plant richness, inter-annual variability, and potential feedbacks*

370 Herbivore reductions may prompt feedback cycles leading to the additional loss of plant species  
371 (Fig. 1b-f). Globally, herbivore reductions increased inter-annual variation in evenness, which  
372 was associated with reduced plant richness. Moreover, high pre-treatment species richness was  
373 associated with low variability in community evenness both in this study and others



374 (McNaughton, 1985; Isbell et al., 2009). Thus, losses in plant species richness following a loss  
375 or reduction in herbivores may further destabilize plant communities, leading to further losses in  
376 plant species.

### 377 *Declines in richness spatially homogenize plant communities*

378 We hypothesize that repeated pulses of dominance may be sufficient to exclude subordinate  
379 species from the larger landscape. In our restoration experiment, richness recovered following a  
380 slight decline in *C. fasciculata*; however, losses in richness had a homogenizing effect across  
381 plots leading to a loss in beta diversity that persisted into the fourth year of the experiment.  
382 Although beta diversity began to recover during the fourth year of the experiment, this recovery  
383 was not sufficient to match conditions in which herbivores remained at ambient densities.

384 Reductions in beta diversity decrease the number of patches from which novel colonizers may  
385 emigrate to replace species lost at the plot scale. Therefore, low diversity states may become  
386 more persistent following repeated pulses of dominance and reductions in beta diversity in the  
387 absence of herbivores, provided these pulses occur frequently enough to prevent recovery. In the  
388 case of the annual *C. fasciculata*, pulses of dominance must occur regularly to maintain  
389 persistent, low diversity states as suggested by the partial recovery of diversity in the final year  
390 of the experiment. However, dominance by a long-lived, perennial species may maintain low  
391 diversity states with less frequent pulses in dominance. The persistence of low diversity states  
392 may also be prolonged by the continued exclusion of herbivory after dominance has receded.  
393 For example, recovery of species richness following nutrient addition is more rapid when  
394 biomass is regularly removed (Storkey et al., 2015) than when it is relatively undisturbed (Isbell  
395 et al., 2013; Tilman and Isbell, 2015). By analogy, the effects of herbivore loss on plant species  
396 richness may strengthen with time.

### 397 *Conclusions*

398 Complementing previous studies showing that herbivores may increase plant richness by  
399 affecting mean community values of light and biomass (Gibson, 1988; Stevens and Carson,  
400 2002; Hautier et al., 2009; Borer et al., 2014b), our results show that herbivores may also prevent  
401 losses in plant richness by stabilizing evenness over time. While other studies have explicitly  
402 considered the effects of inter-annual variability in plant biomass (*e.g.*, McNaughton, 1985;

403 Polley et al., 2007; Isbell et al., 2009; Grman et al., 2010; Eisenhauer et al., 2011) as well as  
404 evenness (Hanke et al., 2014) on richness, we add to this body of knowledge that variability in  
405 biomass or light may not be universal mechanisms for maintaining diversity. In fact, another  
406 form of variability, inter-annual variation in evenness, which increases with the loss of  
407 herbivores, is significantly related to changes in plant richness. Thus, previous work focusing on  
408 the effects of herbivores on mean biomass and light as a measure of community stability may not  
409 fully capture the long-term effects of herbivores on plant evenness and diversity.

#### 410 **Authors' contributions**

411 BM developed and framed the research questions; all authors contributed to data collection; BM,  
412 BD, and WSH analyzed the data; BM led writing of the manuscript; all authors contributed to  
413 drafts and gave approval for publication. A full list of authors contributions is available in Table  
414 S8 of the Supporting Information.

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#### 429 **Data Accessibility**

430 Data deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.dd30d> (Mortensen et al.  
431 2017).

## 432 **References**

- 433 Aguiar, M. R. & Sala, O. E. (1998) Interactions among grasses, shrubs, and herbivores in  
434 Patagonian grass-shrub steppes. *Ecologia Austral*, **8**, 201-210.
- 435 Anderson, M. J., Ellingsen, K. E. & McArdle, B. H. (2006) Multivariate dispersion as a measure  
436 of beta diversity. *Ecology Letters*, **9**, 683-693.
- 437 Bach, C. E. (1980) Effects of Plant Density and Diversity on the Population Dynamics of a  
438 Specialist Herbivore, the Striped Cucumber Beetle, *Acalymma Vittata* (Fab). *Ecology*,  
439 **61**, 1515-1530.
- 440 Bakker, E. S., Olf, H., Boekhoff, M., Gleichman, J. M. & Berendse, F. (2004) Impact of  
441 herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia*,  
442 **138**, 91-101.
- 443 Bakker, E. S., Ritchie, M. E., Olf, H., Milchunas, D. G. & Knops, J. M. H. (2006) Herbivore  
444 impact on grassland plant diversity depends on habitat productivity and herbivore size.  
445 *Ecology Letters*, **9**, 780-788.
- 446 Balke, T., P. M. J. Herman, and T. J. Bouma. 2014. Critical transitions in disturbance-driven  
447 ecosystems: identifying Windows of Opportunity for recovery. *Journal of Ecology*  
448 102:700-708.
- 449 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting Linear Mixed-Effects Models  
450 Using lme4. *Journal of Statistical Software*, **67**, 1-48.
- 451 Bertiller, M. B. & Bisigato, A. (1998) Vegetation dynamics under grazing disturbance. The state-  
452 and-transition model for the Patagonian steppes. *Ecologia Austral*, **8**, 191-199.
- 453 Borer, E. T., Harpole, W. S., Adler, P. B., Lind, E. M., Orrock, J. L., Seabloom, E. W. & Smith,  
454 M. D. (2014a) Finding generality in ecology: a model for globally distributed  
455 experiments. *Methods in Ecology and Evolution*, **5**, 65-73.
- 456 Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., Adler,  
457 P. B., Alberti, J., Anderson, T. M., Bakker, J. D., Biederman, L., Blumenthal, D., Brown,  
458 C. S., Brudvig, L. A., Buckley, Y. M., Cadotte, M., Chu, C., Cleland, E. E., Crawley, M.  
459 J., Daleo, P., Damschen, E. I., Davies, K. F., DeCrappeo, N. M., Du, G., Firn, J., Hautier,

- 460 Y., Heckman, R. W., Hector, A., HilleRisLambers, J., Iribarne, O., Klein, J. A., Knops, J.  
461 M. H., La Pierre, K. J., Leakey, A. D. B., Li, W., MacDougall, A. S., McCulley, R. L.,  
462 Melbourne, B. A., Mitchell, C. E., Moore, J. L., Mortensen, B., O'Halloran, L. R.,  
463 Orrock, J. L., Pascual, J., Prober, S. M., Pyke, D. A., Risch, A. C., Schuetz, M., Smith,  
464 M. D., Stevens, C. J., Sullivan, L. L., Williams, R. J., Wragg, P. D., Wright, J. P. &  
465 Yang, L. H. (2014b) Herbivores and nutrients control grassland plant diversity via light  
466 limitation. *Nature*, **508**, 517-520.
- 467 Cadotte, Marc W. (2006) Dispersal and Species Diversity: A Meta-Analysis. *The American*  
468 *Naturalist*, **167**, 913-924.
- 469 Caldeira, M. C., Hector, A., Loreau, M. & Pereira, J. S. (2005) Species richness, temporal  
470 variability and resistance of biomass production in a Mediterranean grassland. *Oikos*,  
471 **110**, 115-123.
- 472 Carson, W. P. & Root, R. B. (2000) Herbivory and plant species coexistence: community  
473 regulation by an outbreaking phytophagous insect. *Ecological Monographs*, **70**, 73-99.
- 474 Creissen, H. E., Jorgensen, T. H. & Brown, J. K. M. (2016) Impact of disease on diversity and  
475 productivity of plant populations. *Functional Ecology*, **30**, 649-657.
- 476 Daubenmire, R. (1959) A canopy-coverage method of vegetational analysis. *Northwest Science*,  
477 **33**, 43-64.
- 478 Duffy, J. E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**,  
479 201-219.
- 480 Eisenhauer, N., Milcu, A., Allan, E., Nitschke, N., Scherber, C., Temperton, V., Weigelt, A.,  
481 Weisser, W. W. & Scheu, S. (2011) Impact of above- and below-ground invertebrates on  
482 temporal and spatial stability of grassland of different diversity. *Journal of Ecology*, **99**,  
483 572-582.
- 484 Fukami, T. (2015) Historical Contingency in Community Assembly: Integrating Niches, Species  
485 Pools, and Priority Effects. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 1-  
486 23.
- 487 Gibson, D. J. (1988) The Maintenance of Plant and Soil Heterogeneity in Dune Grassland.  
488 *Journal of Ecology*, **76**, 497-508.

- 489 Grman, E., Lau, J. A., Schoolmaster, D. R., Jr. & Gross, K. L. (2010) Mechanisms contributing  
490 to stability in ecosystem function depend on the environmental context. *Ecology Letters*,  
491 **13**, 1400-1410.
- 492 Hanke, W., Boehner, J., Dreber, N., Juergens, N., Schmiedel, U., Wesuls, D. & Dengler, J.  
493 (2014) The impact of livestock grazing on plant diversity: an analysis across dryland  
494 ecosystems and scales in southern Africa. *Ecological Applications*, **24**, 1188-1203.
- 495 Hautier, Y., Niklaus, P. A. & Hector, A. (2009) Competition for Light Causes Plant Biodiversity  
496 Loss After Eutrophication. *Science*, **324**, 636-638.
- 497 Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T. & Reich, P. B. (2015)  
498 Anthropogenic environmental changes affect ecosystem stability via biodiversity.  
499 *Science*, **348**, 336-340.
- 500 Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J.,  
501 Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B. & Smith, J. E. (2007)  
502 Consumer versus resource control of producer diversity depends on ecosystem type and  
503 producer community structure. *Proceedings of the National Academy of Sciences of the*  
504 *United States of America*, **104**, 10904-10909.
- 505 Holt, R. D., Grover, J. & Tilman, D. (1994) Simple Rules for Interspecific Dominance in  
506 Systems with Exploitative and Apparent Competition. *The American Naturalist*, **144**,  
507 741-771.
- 508 Huston, A. M. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem  
509 function of biodiversity. *Oecologia*, **110**, 449-460.
- 510 Hygnstrom, S. E., Timm, R. M. & Larson, G. E. (1994) *Prevention and Control of Wildlife*  
511 *Damage*. University of Nebraska-Lincoln.
- 512 Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M.,  
513 Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J. N., Guo, Q., Hautier, Y.,  
514 Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S. T., Mori, A. S.,  
515 Naeem, S., Niklaus, P. A., Polley, H. W., Reich, P. B., Roscher, C., Seabloom, E. W.,  
516 Smith, M. D., Thakur, M. P., Tilman, D., Tracy, B. F., van der Putten, W. H., van  
517 Ruijven, J., Weigelt, A., Weisser, W. W., Wilsey, B. & Eisenhauer, N. (2015)  
518 Biodiversity increases the resistance of ecosystem productivity to climate extremes.  
519 *Nature*, **526**, 574-577.

- 520 Isbell, F., Tilman, D., Polasky, S., Binder, S. & Hawthorne, P. (2013) Low biodiversity state  
521 persists two decades after cessation of nutrient enrichment. *Ecology Letters*, **16**, 454-460.
- 522 Isbell, F. I., Polley, H. W. & Wilsey, B. J. (2009) Biodiversity, productivity and the temporal  
523 stability of productivity: patterns and processes. *Ecology Letters*, **12**, 443-451.
- 524 Kaarlejärvi, E., Eskelinen, A. & Olofsson, J. (2013) Herbivory prevents positive responses of  
525 lowland plants to warmer and more fertile conditions at high altitudes. *Functional  
526 Ecology*, **27**, 1244-1253.
- 527 Kuznetsova, A., Brockhoff, P. B. & Bojesen, C. R. H. (2016) lmerTest: Tests in Linear Mixed  
528 Effects Models. *R package version 2.0-30*.
- 529 Lefcheck, J. S. (2016) piecewiseSEM: Piecewise structural equation modelling in R for ecology,  
530 evolution, and systematics. *Methods in Ecology and Evolution*, **7**, 573-579.
- 531 Lind, E. M., Borer, E., Seabloom, E., Adler, P., Bakker, J. D., Blumenthal, D. M., Crawley, M.,  
532 Davies, K., Firn, J., Gruner, D. S., Stanley Harpole, W., Hautier, Y., Hillebrand, H.,  
533 Knops, J., Melbourne, B., Mortensen, B., Risch, A. C., Schuetz, M., Stevens, C. &  
534 Wragg, P. D. (2013) Life-history constraints in grassland plant species: a growth-defence  
535 trade-off is the norm. *Ecology Letters*, **16**, 513-521.
- 536 Martin, L. M., Moloney, K. A. & Wilsey, B. J. (2005) An assessment of grassland restoration  
537 success using species diversity components. *Journal of Applied Ecology*, **42**, 327-336.
- 538 Martin, L. M. & Wilsey, B. J. (2006) Assessing grassland restoration success: relative roles of  
539 seed additions and native ungulate activities. *Journal of Applied Ecology*, **43**, 1098-1109.
- 540 McNaughton, S. J. (1985) Ecology of a Grazing Ecosystem: The Serengeti. *Ecological  
541 Monographs*, **55**, 260-294.
- 542 Milchunas, D. G. & Lauenroth, W. K. (1993) Quantitative Effects of Grazing on Vegetation and  
543 Soils Over a Global Range of Environments. *Ecological Monographs*, **63**, 328-366.
- 544 Morris, W. F., Hufbauer, R. A., Agrawal, A. A., Bever, J. D., Borowicz, V. A., Gilbert, G. S.,  
545 Maron, J. L., Mitchell, C. E., Parker, I. M., Power, A. G., Torchin, M. E. & Vázquez, D.  
546 P. (2007) Direct and interactive effects of enemies and mutualists on plant performance: a  
547 meta-analysis. *Ecology*, **88**, 1021-1029.
- 548 Mortensen B., Danielson B., Harpole S., Alberti J., Arnillas C., Biederman L., Borer E., Cadotte  
549 M., Dwyer J., Hagenah N., Hautier Y., Peri P., Seabloom E., Sullivan L. (2017) Data

- 550 from: Herbivores safeguard plant diversity by reducing variability in dominance. *Journal*  
551 *of Ecology* doi: 10.5061/dryad.dd30d
- 552 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., R. Minchin, P., O'Hara, R. B., Simpson, G.  
553 L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2016) *Vegan: Community Ecology*  
554 *Package. R package version 2.3-5.*
- 555 Olf, H. & Ritchie, M. E. (1998) Effects of herbivores on grassland plant diversity. *Trends in*  
556 *Ecology & Evolution*, **13**, 261-265.
- 557 Otway, S. J., Hector, A. & Lawton, J. H. (2005) Resource dilution effects on specialist insect  
558 herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology*, **74**, 234-  
559 240.
- 560 Paine, R. T. (1966) Food Web Complexity and Species Diversity. *The American Naturalist*, **100**,  
561 65-75.
- 562 Pardo, I., Doak, D. F., García-González, R., Gómez, D. & García, M. B. (2015) Long-term  
563 response of plant communities to herbivore exclusion at high elevation grasslands.  
564 *Biodiversity and Conservation*, **24**, 3033-3047.
- 565 Pinheiro, J. & Bates, D. (2000) *Mixed-Effects Models in S and S-PLUS*. Springer, New York.
- 566 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2016) nlme: Linear and  
567 Nonlinear Mixed Effects Models. R package version 3.1-128, [http://CRAN.R-](http://CRAN.R-project.org/package=nlme)  
568 [project.org/package=nlme](http://CRAN.R-project.org/package=nlme).
- 569 Polley, H. W., Wilsey, B. J. & Derner, J. D. (2007) Dominant species constrain effects of species  
570 diversity on temporal variability in biomass production of tallgrass prairie. *Oikos*, **116**,  
571 2044-2052.
- 572 Post, E. (2013) Erosion of community diversity and stability by herbivore removal under  
573 warming. *Proceedings of the Royal Society of London B: Biological Sciences*, **280**.
- 574 Post, E. & Pedersen, C. (2008) Opposing plant community responses to warming with and  
575 without herbivores. *Proceedings of the National Academy of Sciences*, **105**, 12353-12358.
- 576 R Core Team (2015) R: A language and environment for statistical computing. R Foundation for  
577 Statistical Computing, Vienna, Austria.
- 578 Sandom, C. J., Terborgh, J. & Van Valkenburgh, B. (2015) Collapse of the world's largest  
579 herbivores. *Science Advances*, **1**.

- 580 Satterthwaite, F. E. (1946) An Approximate Distribution of Estimates of Variance Components.  
581 *Biometrics Bulletin*, **2**, 110-114.
- 582 Schmitz, O. J. (2006) Predators Have Large Effects on Ecosystem Properties by Changing Plant  
583 Diversity, Not Plant Biomass. *Ecology*, **87**, 1432-1437.
- 584 Sholes, O. D. V. (2008) Effects of associational resistance and host density on woodland insect  
585 herbivores. *Journal of Animal Ecology*, **77**, 16-23.
- 586 Skálová, H., Krahulec, F., Doring, H. J., Hadincová, V., Pecháčková, S. & Herben, T. (1999)  
587 Grassland canopy composition and spatial heterogeneity in the light quality. *Plant*  
588 *Ecology*, **143**, 129-139.
- 589 Stevens, M. H. H. & Carson, W. P. (2002) Resource quantity, not resource heterogeneity,  
590 maintains plant diversity. *Ecology Letters*, **5**, 420-426.
- 591 Storkey, J., Macdonald, A. J., Poulton, P. R., Scott, T., Köhler, I. H., Schnyder, H., Goulding, K.  
592 W. T. & Crawley, M. J. (2015) Grassland biodiversity bounces back from long-term  
593 nitrogen addition. *Nature*, **528**, 401-404.
- 594 Sullivan, M. J. P., A.Thomsen, M. & Suttle, K. B. (2016) Grassland responses to increased  
595 rainfall depend on the timescale of forcing. *Global Change Biology*, **22**, 1655-1665.
- 596 Tilman, D. & Isbell, F. (2015) Biodiversity: Recovery as nitrogen declines. *Nature*, **528**, 336-  
597 337.
- 598 Tilman, D., Reich, P. B. & Knops, J. M. H. (2006) Biodiversity and ecosystem stability in a  
599 decade-long grassland experiment. *Nature*, **441**, 629-632.
- 600 Valiente-Banuet, A. & Verdú, M. (2013) Plant Facilitation and Phylogenetics. *Annual Review of*  
601 *Ecology, Evolution, and Systematics*, **44**, 347-366.
- 602 Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner,  
603 U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-  
604 analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**,  
605 702-708.
- 606 Wilsey, B. J., Chalcraft, D. R., Bowles, C. M. & Willig, M. R. (2005) Relationships among  
607 indices suggest that richness is an incomplete surrogate for grassland biodiversity.  
608 *Ecology*, **86**, 1178-1184.
- 609 Wilsey, B. J. & Polley, H. W. (2002) Reductions in grassland species evenness increase dicot  
610 seedling invasion and spittle bug infestation. *Ecology Letters*, **5**, 676-684.



- 611 Wilsey, B. J. & Polley, H. W. (2004) Realistically low species evenness does not alter grassland  
612 species-richness–productivity relationships. *Ecology*, **85**, 2693-2700.
- 613 Yang, L. H., Bastow, J. L., Spence, K. O. & Wright, A. N. (2008) What Can We Learn from  
614 Resource Pulses? *Ecology*, **89**, 621-634.
- 615 Yuan, Z. Y., Jiao, F., Li, Y. H. & Kallenbach, R. L. (2016) Anthropogenic disturbances are key  
616 to maintaining the biodiversity of grasslands. *Scientific Reports*, **6**.

617

## 618 **Supporting Information**

619 Additional supporting information may be found in the online version of this article:

620 **Table S1** *Species sown in the restoration experiment.*

621 **Table S2** *Number of *Microtus* spp. individuals removed from herbivore reduction treatments in*  
622 *the restoration experiment.*

623 **Table S3** *Locations and number of blocks for each site included in the global study.*

624 **Table S4** *Herbivores affected by the fence treatment at each Nutrient Network site.*

625 **Table S5** *Effects of pre-treatment plant species richness and herbivore reduction on the inter-*  
626 *annual coefficient of variation for evenness, biomass, and light penetration.*

627 **Table S6** *Effects of treatment duration and the inter-annual coefficient of variation for evenness,*  
628 *biomass, or light penetration on the log response ratio of species richness.*

629 **Table S7** *Site managers in the Nutrient Network that contributed data to this study.*

630 **Table S8** *Authorship contribution statement.*

631 **Figure S1** *Species rank abundance curves in the restoration experiment by year and treatment.*

## 632 **Tables**

633 **Table 1—Effects of herbivore reduction, species diversity, and treatment duration** on  
634 species richness, evenness, *C. fasciculata* cover, and beta diversity (measured as the Bray-Curtis  
635 dissimilarity to the median for each treatment group) in the restoration experiment. Results were

636 determined from mixed-effects ANOVA with the denominator degrees of freedom (DenDF)  
 637 estimated using the Satterthwaite approximation (Satterthwaite, 1946).

Effect	NumDF	Richness (S)			Evenness (H/ln(S))		
		DenDF	F	P	DenDF	F	P
Herbivores	1	6	0.19	0.6754	6	0.69	0.4377
Diversity	1	<b>46</b>	<b>23.94</b>	<b>&lt;0.0001</b>	46	0.03	0.8713
Year	3	<b>156</b>	<b>55.16</b>	<b>&lt;0.0001</b>	<b>156</b>	<b>3.42</b>	<b>0.0189</b>
Herb. x Diversity	1	46	0.83	0.3665	46	2.69	0.1076
Herb. x Year	3	<b>156</b>	<b>3.13</b>	<b>0.0274</b>	156	2.29	0.0808
Diversity x Year	3	<b>156</b>	<b>3.98</b>	<b>0.0092</b>	<b>156</b>	<b>4.35</b>	<b>0.0056</b>
Herb x Div. x Year	3	156	1.61	0.1902	156	2.16	0.0949

638

639 **Table 1 cont.**

Effect	NumDF	<i>C. fasciculata</i> cover			Beta diversity		
		DenDF	F	P	DenDF	F	P
Herbivores	1	<b>6</b>	<b>10.46</b>	<b>0.0178</b>	6	2.33	0.2935
Diversity	1	<b>46</b>	<b>165.39</b>	<b>&lt;0.0001</b>	<b>46</b>	<b>5.76</b>	<b>0.0205</b>
Year	3	<b>156</b>	<b>57.03</b>	<b>&lt;0.0001</b>	<b>156</b>	<b>4.35</b>	<b>0.0057</b>
Herb. x Diversity	1	<b>46</b>	<b>19.12</b>	<b>0.0001</b>	<b>46</b>	<b>7.59</b>	<b>0.0084</b>
Herb. x Year	3	<b>156</b>	<b>5.67</b>	<b>0.0010</b>	156	1.35	0.2599
Diversity x Year	3	<b>156</b>	<b>75.46</b>	<b>&lt;0.0001</b>	156	0.83	0.4806
Herb. x Div. x Year	3	<b>156</b>	<b>6.60</b>	<b>0.0003</b>	<b>156</b>	<b>4.83</b>	<b>0.0030</b>

640

641 **Table 2—Herbivore and treatment duration effects on mean evenness, biomass, and light**  
 642 **penetration in the global experiment.** Results were determined from mixed-effects ANCOVA  
 643 with the denominator degrees of freedom (DenDF) estimated using the Satterthwaite  
 644 approximation (Satterthwaite 1946).

Effect	NumDF	Evenness			Biomass		
		DenDF	F	P	DenDF	F	P

Herbivores	1	179.30	1.39	0.2407	<b>264.98</b>	<b>13.31</b>	<b>0.0003</b>
Treatment duration	7	1141.30	1.92	0.0634	<b>1092.78</b>	<b>2.49</b>	<b>0.0153</b>
Herb. x Trt. duration	7	1183.70	1.19	0.3064	1158.45	1.31	0.2403

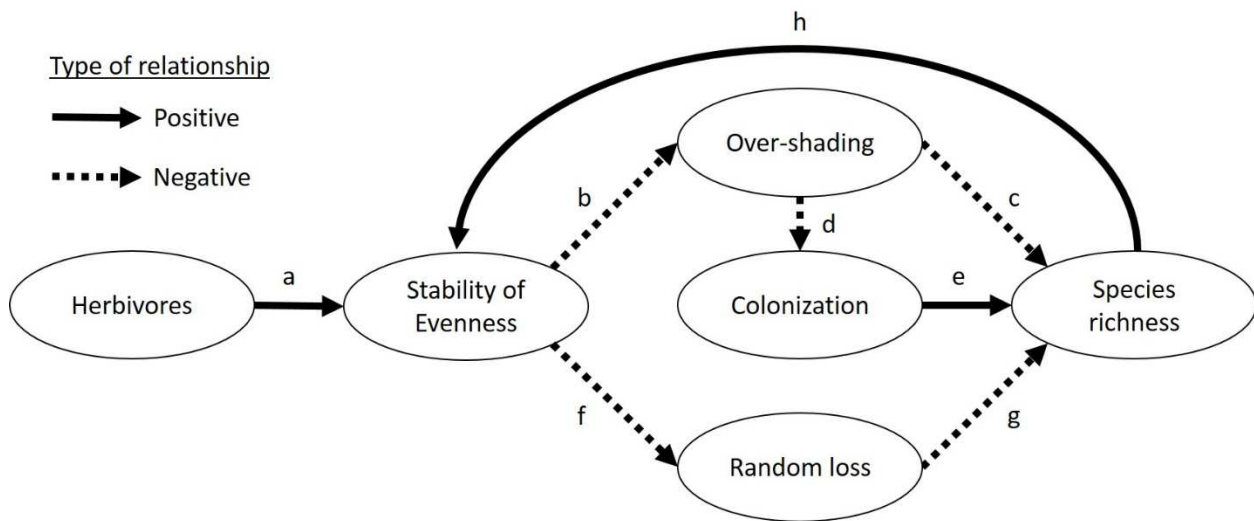
645

646 **Table 2 cont.**

Effect	NumDF	Light penetration		
		DenDF	F	P
Herbivores	1	<b>968.73</b>	<b>17.73</b>	<b>&lt;0.0001</b>
Treatment duration	7	<b>962.47</b>	<b>4.68</b>	<b>&lt;0.0001</b>
Herb. x Trt. duration	7	960.23	1.26	0.2681

647

648 **Figures**



649

650 **Fig. 1—Predicted relationship between herbivores, plant evenness, and plant richness.**

651 Overall, this models shows that herbivore loss may destabilize plant communities, resulting in a  
 652 positive feedback cycle producing species poor communities. Specifically, herbivores may  
 653 increase stability in plant community evenness, preventing temporary “pulses” of dominance (a)  
 654 that could otherwise over-shade subordinate species (b), leading to their eventual loss (c). Over-  
 655 shading can also decrease colonization (d), further limiting species richness (e). Moreover, as  
 656 the relative abundance of subordinate species declines with evenness, their probability of

657 extinction through random events increases (f), thus increasing losses to species richness (g).  
 658 Assuming species richness increases community resistance to and resilience following  
 659 disturbance as indicated in previous studies, loss of plant species could increase the likelihood of  
 660 future pulses of dominance (h).

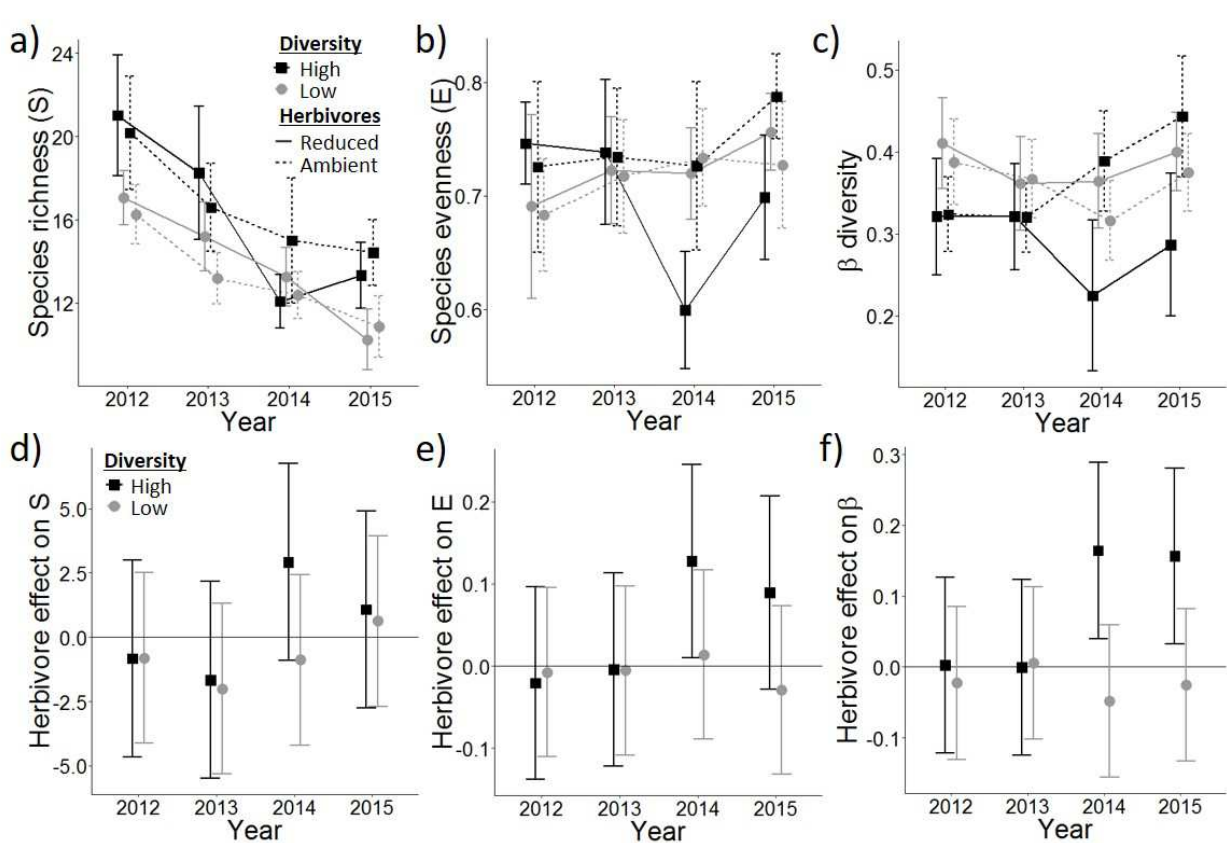


661

662 **Fig. 2—Location, richness, and evenness of all 40 sites included in the global study.** (a)

663 Coordinates for all sites, the number of blocks per site, and the number of years that experiments  
 664 have been maintained at each site are available in Table S3. (b) Plot richness and evenness are  
 665 shown for all control plots across all years included in the current study.

666



667

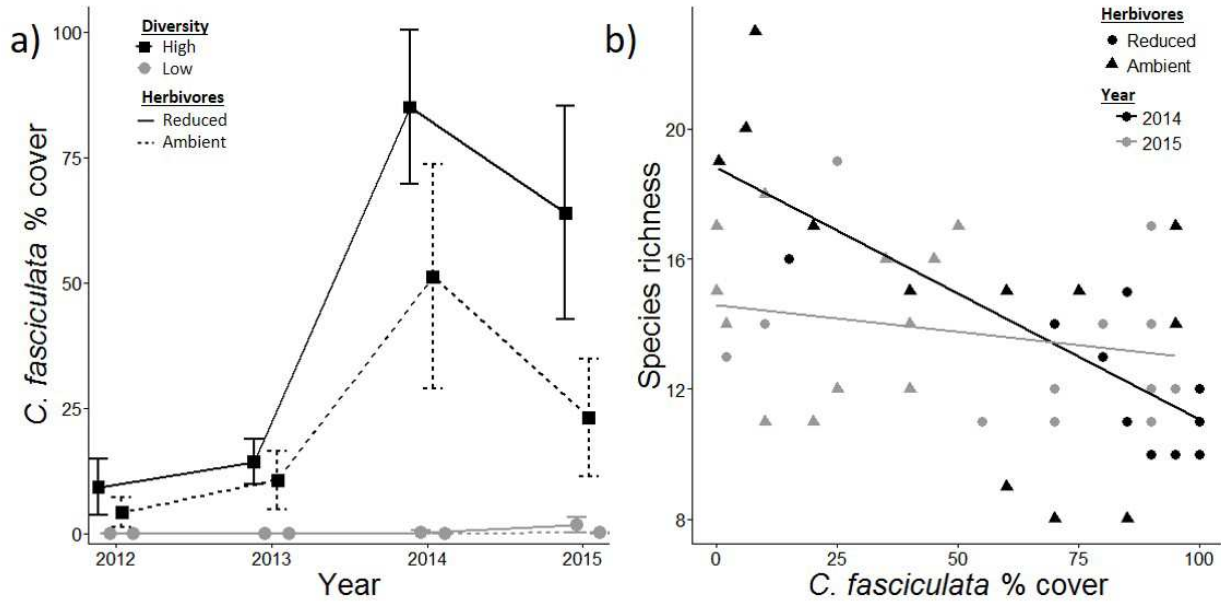
668 **Fig. 3—Herbivore and diversity effects on plant diversity in the restoration experiment.**

669 Mean diversity indices were calculated within subplots from the raw data for a) species richness  
 670 (S) and b) evenness ( $H/\ln(S)$ ), and c) beta diversity (among plots). The difference between  
 671 herbivore treatments (control - fenced) is shown for d) species richness, e) evenness, and f) beta  
 672 diversity based on the least squared means from the respective models reported in Table 1. Error  
 673 bars represent 95% confidence intervals in panels a-c and 97.5% confidence intervals at  $\alpha = 0.05$   
 674 following Bonferroni correction in panels d-f.

675

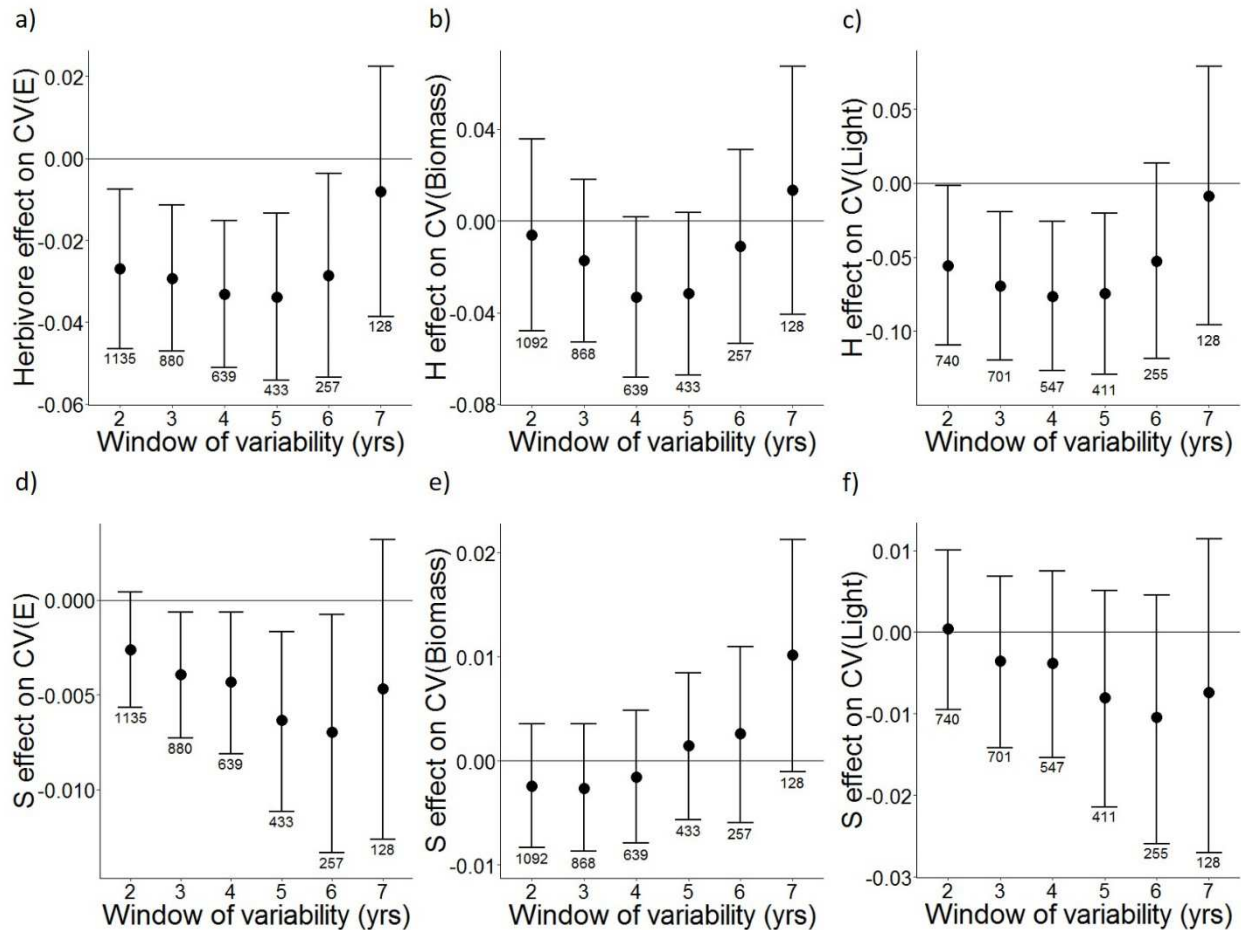
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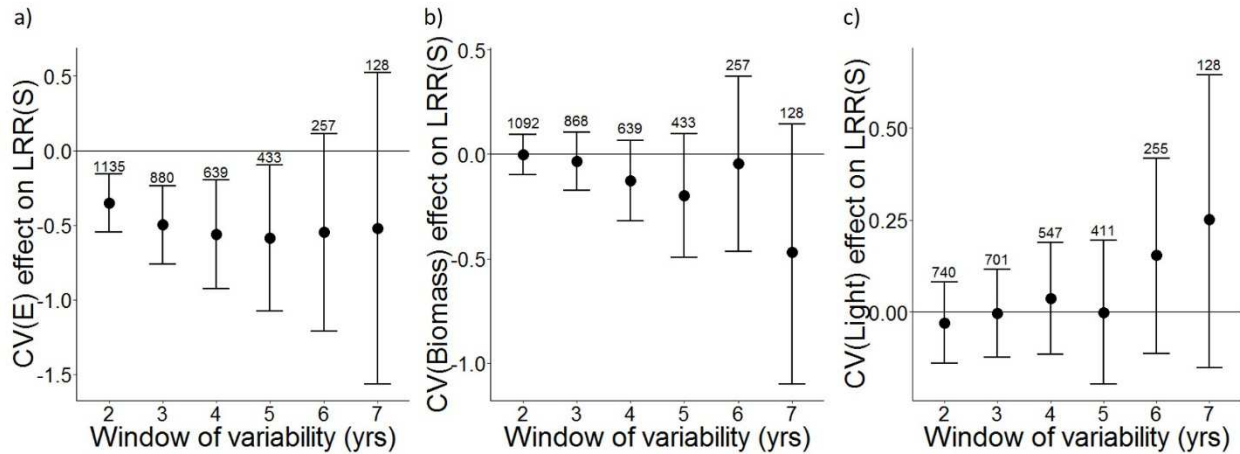
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679 **Fig. 4—*Chamaecrista fasciculata* effects on species diversity in restoration experiment.** (a)  
 680 Mean cover of *C. fasciculata* in high and low diversity communities and in relation to ambient  
 681 and reduced herbivore populations. Points were calculated as means from the raw data and error  
 682 bars represent 95% confidence intervals. (b) *C. fasciculata* cover in relation to species richness  
 683 during 2014-15 in ambient or reduced herbivore conditions in high diversity treatments where it  
 684 was sown.



685

686 **Fig. 5—Herbivore and species richness effects on inter-annual variability (coefficient of**  
 687 **variation; CV) in grasslands across the globe.** The window of variability indicates the  
 688 timeframes used to calculate the CV. The effect of herbivores (*i.e.*, control – fenced) on the CV  
 689 are shown for a) plant community evenness, b) plant biomass and c) light penetration. The slope  
 690 between the CV and pre-experimental species richness (*i.e.*,  $\Delta CV/\Delta S$ ) are shown for d) plant  
 691 community evenness, e) plant biomass, and f) light penetration. Points represent planned  
 692 contrasts for panels a-c and slopes for d-f derived from mixed-effects models (the full ANOVA  
 693 table for each model is available in Table S5). Error bars represent 99.17% confidence intervals  
 694 following Bonferroni corrections for  $\alpha = 0.05$ . Numbers below each point indicate the number of  
 695 plot/year combinations in each sample.



696

697 **Fig. 6—Slope between inter-annual variability (coefficient of variation; CV) and changes in**  
 698 **species richness (S) at different time scales in grasslands across the globe.** The slope  
 699 between CV and the log response ratio of species richness (*i.e.*,  $\Delta\text{LRR}(S)/\Delta\text{CV}$ ) was calculated  
 700 when measuring the CV over the previous 2-7 years for a) community evenness, b) plant  
 701 biomass, and c) light penetration. Points represent slopes derived from mixed-effects models  
 702 (the full ANOVA table for each model is available in Table S6). Error bars represent 99.17%  
 703 confidence intervals following Bonferroni corrections for  $\alpha = 0.05$ . Numbers above each point  
 704 indicate the number of plot/year combinations in each sample.