





RESEARCH ARTICLE

Herbivores safeguard plant diversity by reducing variability in dominance

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Funding information

Iowa Living Roadway Trust Fund, Grant/Award Number: 90-00-LRTF-211, 90-00-LRTF-306 and 90-00-LRTF-307; TogetherGreen; ISU Department of EEOB; National Science Foundation, Grant/Award Number: NSF-DEB-1042132, NSF-DEB-1234162 and DG-0001-13; Institute on the Environment

Handling Editor: Matthew Heard

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 favour 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 to 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

biomass, *Chamaecrista fasciculata*, determinants of plant community diversity and structure, light, nutrient network, plant–herbivore interactions, plant–plant interactions

1 | INTRODUCTION

Changes in relative abundance within plant communities may occur in response to factors such as disturbance (Yuan, Jiao, Li, & Kallenbach, 2016), climate (Kaarlejärvi, Eskelinen, & Olofsson, 2013; Pardo, Doak, García-González, Gómez, & García, 2015; Post, 2013; Post & Pedersen, 2008; Sullivan, Thomsen, & Suttle, 2016), disease (Creissen, Jorgensen, & Brown, 2016), the loss or appearance of mutualists or enemies (Morris et al., 2007), or a sudden resource pulse (Hillebrand et al., 2007; Kaarlejärvi et al., 2013; Yang, Bastow, Spence, & Wright, 2008) as well as interactions among these or other factors. Such environmental factors may allow temporary periods of increased dominance by one or a few species (hereafter referred to as “pulses” of dominance).

Sufficiently strong pulses of dominance can lead to losses of subordinate species (Hautier, Niklaus, & Hector, 2009; Wilsey & Polley, 2004) that can persist for multiple growing seasons depending on the colonization rates of extirpated species (Cadotte, 2006) and the priority effects imposed by remaining species (Fukami, 2015). Moreover, decreased plant diversity can further destabilize communities by reducing resistance and/or resilience to disturbance (e.g. Caldeira, Hector, Loreau, & Pereira, 2005; Duffy, 2002; Isbell et al., 2015; McNaughton, 1985), potentially increasing the probability of future pulses of dominance. Losses in plant diversity are also associated with decreased stability of plant community biomass (Caldeira et al., 2005; Eisenhauer et al., 2011; Hautier et al., 2015; Isbell, Polley, & Wilsey, 2009; McNaughton, 1985; Tilman, Reich, & Knops, 2006), suggesting increased variability in competition for light (e.g. Borer, Seabloom, et al., 2014). This potential feedback of decreased stability leading to species loss, which in turn further reduces stability, could contribute

to an “extinction cascade” (sensu Valiente-Banuet & Verdú, 2013; Figure 1).

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

We propose that herbivores maintain plant diversity, in part, by limiting strong, yet temporary, pulses of dominance that would otherwise exclude subordinate species. We tested this hypothesis by experimentally reducing herbivore abundances in communities of high and low diversity within a developing grassland in the U.S. Midwest, further assessing the generality and potential mechanisms influencing the relationships between herbivory, stability and diversity in a global herbivore reduction experiment. We predict that:

1. Reduced herbivore abundance allows pulses of increased dominance by one or a few species (Figure 1a), manifested as increased inter-annual variability (the inverse of stability) of community evenness that is associated with a loss of species (Figure 1c,d).

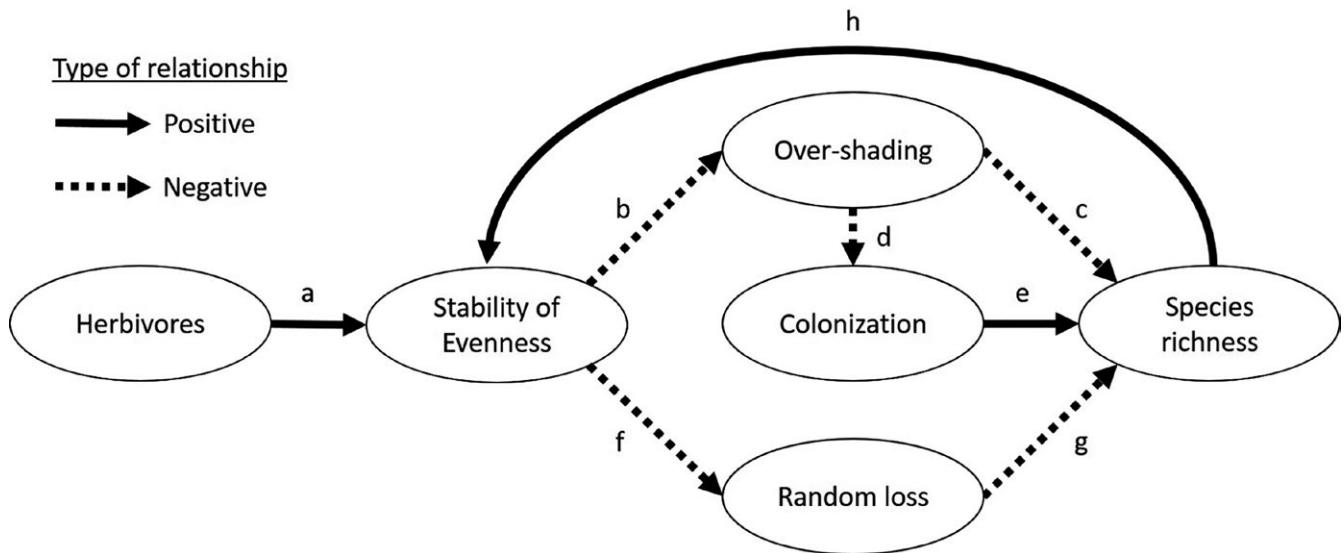


FIGURE 1 Predicted relationship between herbivores, plant evenness and plant richness. Overall, this model shows that herbivore loss may destabilize plant communities, resulting in a positive feedback cycle producing species-poor communities. Specifically, herbivores may increase stability in plant community evenness, preventing temporary “pulses” of dominance (a) that could otherwise over-shade subordinate species (b), leading to their eventual loss (c). Over-shading can also decrease colonization (d), further limiting species richness (e). Moreover, as the relative abundance of subordinate species declines with evenness, their probability of extinction through random events increases (f), thus increasing losses to species richness (g). Assuming species richness increases community resistance to and resilience following disturbance as indicated in previous studies, loss of plant species could increase the likelihood of future pulses of dominance (h)

- Losses in species diversity following herbivore reductions are associated with increased variability in biomass and light (Figure 1b–e).
- If species richness moderates temporal variability (Eisenhauer et al., 2011; Isbell et al., 2009; McNaughton, 1985), then initial plant richness is negatively associated with inter-annual variability, potentially leading to a positive feedback (Figure 1b–h).
- Herbivore loss drives spatial homogenization through lower species richness across plots (i.e. beta diversity). Such declines in richness across plots could limit potential colonizers from the species pool, further limiting plant richness following pulses of dominance. Alternatively, it is possible herbivore loss may increase beta diversity if different species increase in dominance in different locations.

2 | MATERIALS AND METHODS

2.1 | Restoration experiment

The Oakridge Research and Education Prairie is a 1.6-ha tallgrass prairie restoration in Ames, Iowa, U.S.A. (42.035°, -93.664°) that was managed for row crops for at least 100 years before its planting in March of 2012. Prior to planting, we established eight 32 × 32 m blocks, fencing off four blocks to reduce the abundance of mammalian herbivores including white-tailed deer (*Odocoileus virginianus*), prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*). Fences consist of two strands of electric fencing running ~0.4 and 1 m above ground level that are both set 1 m outside a third

strand running 0.75 m above ground level following the design by Hygnstrom, Timm, and Larson (1994). The inner fence also consists of 1.3 cm (0.5 in) mesh hardware cloth extending 0.5 m above and 0.4 m below ground level to discourage burrowing.

We trapped and removed voles from fenced areas at least three times from May to October each year with trapping periods spaced at least 1 month apart. The only exception to this trapping pattern was in the first year of the experiment (2012) when we only trapped twice. We placed 7.6 × 8.9 × 22.9 cm Sherman Live Traps (H.B. Sherman Traps, Tallahassee, FL, USA) in an even, 4 × 4 grid within each fenced block, spacing traps ~9 m apart and ~2 m from the fence. We baited traps with oats, locking them open for at least 2 days before setting to allow habituation. Trapping continued for at least three consecutive nights during each period, extending longer when needed to reduce numbers. All voles trapped inside fenced blocks were relocated >4 km away to minimize reentry, and breaches in the fences were patched whenever detected. The number of voles removed from fenced treatments is available in Table S2. Trapping and handling of animals was conducted in accordance with ethical standards approved by a local IACUC committee.

We sowed both high- and low-diversity plant communities within each of the eight experimental blocks. High-diversity treatments include 51 species in a circular area (19.2 m diameter) in the centre of each block. One species in each of the high-diversity communities was unique to that block to monitor long-distance dispersal (not reported here). We sowed the remainder of the field with a subset of 14 species from the high-diversity treatment. The number of species used in the low- and high-diversity communities approximate diversities in most prairie restorations and remnants, respectively (e.g. Martin, Moloney,

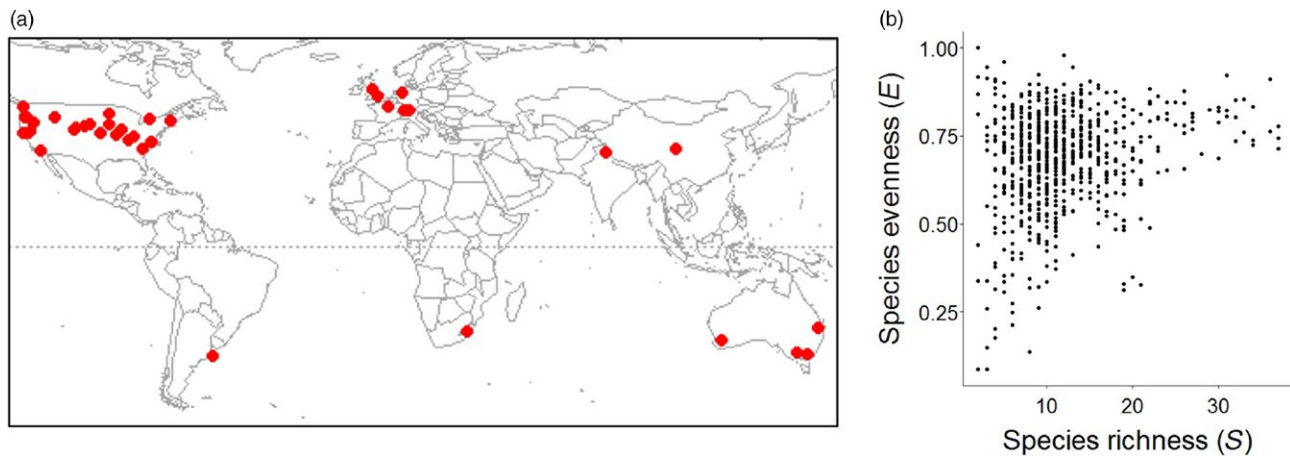


FIGURE 2 Location, richness and evenness of all 40 sites included in the global study. (a) Coordinates for all sites, the number of blocks per site and the number of years that experiments have been maintained at each site are available in Table S3. (b) Plot richness and evenness are shown for all control plots across all years included in the current study [Colour figure can be viewed at wileyonlinelibrary.com]

& Wilsey, 2005). Species in the low-diversity treatment were selected to represent all major functional groups (forb, legume, C3/C4 grass; see Table S1 for full species list).

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

We tested the effects of the herbivore reduction and the diversity treatments on all measures of diversity, inter-annual variability of community evenness and cover of a single dominant species, *Chamaecrista fasciculata* (Michx.) that was only sown in high-diversity treatments. We selected *C. fasciculata* as this was the only species in any treatment or year to achieve a mean cover of $>50\%$ per plot (Figure S1). Additionally, we compared *C. fasciculata* abundance to species richness in the high-diversity treatments. For all tests, we treated our analysis as a repeated measure, split-plot design by applying mixed-effects ANOVA, or ANCOVA when comparing *C. fasciculata* abundance to species richness, with year as a fixed effect and plot nested within block as random effects. We controlled for temporal autocorrelation among plots with an autoregressive correlation of order 1 following Pinheiro and Bates (2000). We made a priori contrasts showing the effect of herbivore reductions in each diversity treatment by year using Bonferroni corrections for multiple comparisons. Repeated measures

models were run in R using the `NLME` package (Pinheiro, Bates, DebRoy, & Sarkar, 2016) and all other models were run using the `lmerTest` (Kuznetsova, Brockhoff, & Bojesen, 2016) and `LME4` packages (Bates, Maechler, Bolker, & Walker, 2015). Denominator degrees of freedom were estimated using the Satterthwaite approximation (Satterthwaite, 1946).

2.2 | Global grasslands experiment

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

Sites are divided into two to six blocks with one 5×5 m control and herbivore reduction plot per block. Herbivore reduction plots are surrounded by 1-m tall wire mesh with four strands of wire spaced in 0.3-m increments above the mesh. Wire mesh extends 0.3 m outward from the base of the fence to discourage burrowing. Herbivores excluded at each site were reported by site managers and are listed in the supporting information (Table S4). Plant cover, biomass and light penetration measurements were collected annually at peak biomass for 2–8 years at each site, depending on site age (Table S4). Plant cover was estimated as in the restoration experiment in one permanent 1×1 m subplot per plot. Total biomass was measured by collecting living above-ground biomass rooted and plant litter lying within two 0.1×1 m strips located outside the cover subplot, drying at 60°C for 48 hr, and weighing. Photosynthetically active radiation (PAR) was measured above the plant canopy and at ground level from opposite

corners of the cover subplots within 2 hr of solar noon using a linear quantum light sensor (MQ-301; Apogee Instruments, Logan, UT, USA). Light penetration was calculated as the proportion of PAR reaching the soil surface.

We calculated plant diversity using the same metrics as in the restoration experiment. Changes in richness were calculated as the log response ratio (LRR) compared to pre-treatment values. We calculated inter-annual variability of evenness, biomass and light penetration as the coefficient of variation across years for each plot. We also calculated variability as the standard deviation across years for a plot, but results using this approach were not qualitatively different from using the coefficient of variation and so are not reported here. We calculated variability across a variable, moving window of 2–7 years depending on treatment duration at each site. Consequently, a single plot may have multiple measures of variability for each window of duration beginning with 2-year increments, building to a single measure of variability for the duration of the treatment with a single exception. We did not calculate variability across the longest possible timeframe of 8 years in the oldest sites as this would have eliminated variation in treatment duration, a covariate in our models. Including this longest window of variability in a simplified model without treatment duration did not qualitatively affect our results and so is not reported here.

We made all comparisons using mixed-effects models as in the restoration experiment with block nested within site as a random effect. We tested the indirect effect of herbivores on changes in plant diversity with two sets of models. In the first, we tested the effects of herbivores on inter-annual variability for evenness, plant biomass and light penetration with pre-treatment plant richness and treatment duration as a covariate. Second, we examined the relationship between inter-annual variability of evenness (which may vary independently of richness; Wilsey, Chalcraft, Bowles, & Willig, 2005), biomass or light penetration and the LRR of plant richness at the end of the window of variability considered with herbivore treatment as a fixed effect and treatment duration as a covariate. As variation in evenness was positively correlated with variation in both light penetration ($F_{1,85.5} = 5.92, p = .017$) and biomass ($F_{1,90.6} = 10.38, p = .001$), we tested the relationship between these factors and the LRR of plant richness separately.

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

3 | RESULTS

3.1 | Restoration experiment

The diversity treatment increased plant richness, but not evenness, across herbivore treatments in the restoration experiment (Table 1, Figure 3). By comparison, herbivores that were affected by our fencing treatment (hereafter “herbivores”) did not affect species richness or evenness when considered in the aggregate

TABLE 1 Effects of herbivore reduction, species diversity and treatment duration on species richness, evenness, *Chamaecrista fasciculata* cover and beta diversity (measured as the Bray–Curtis dissimilarity to the median for each treatment group) in the restoration experiment. Results were determined from mixed-effects ANOVA with the denominator degrees of freedom (DenDF) estimated using the Satterthwaite approximation (Satterthwaite, 1946)

Effect	Richness (S)			Evenness (H/ln(S))			<i>C. fasciculata</i> cover			Beta diversity			
	NumDF	DenDF	F	F	DenDF	F	DenDF	F	DenDF	F	DenDF	F	p
Herbivores	1	6	0.19	0.69	6	0.4377	6	10.46	6	0.178	6	2.33	.2935
Diversity	1	46	23.94	<.0001	46	.8713	46	165.39	46	<.0001	46	5.76	.0205
Year	3	156	55.16	<.0001	156	.0189	156	57.03	156	<.0001	156	4.35	.0057
Herb. × Diversity	1	46	0.83	.3665	46	.1076	46	19.12	46	.0001	46	7.59	.0084
Herb. × Year	3	156	3.13	.0274	156	.0808	156	5.67	156	.0010	156	1.35	.2599
Diversity × Year	3	156	3.98	.0092	156	.0056	156	75.46	156	<.0001	156	0.83	.4806
Herb. × Div. × Year	3	156	1.61	.1902	156	.0949	156	6.60	156	.0003	156	4.83	.0030

Significant effects ($\alpha < 0.05$) are shown in bold.

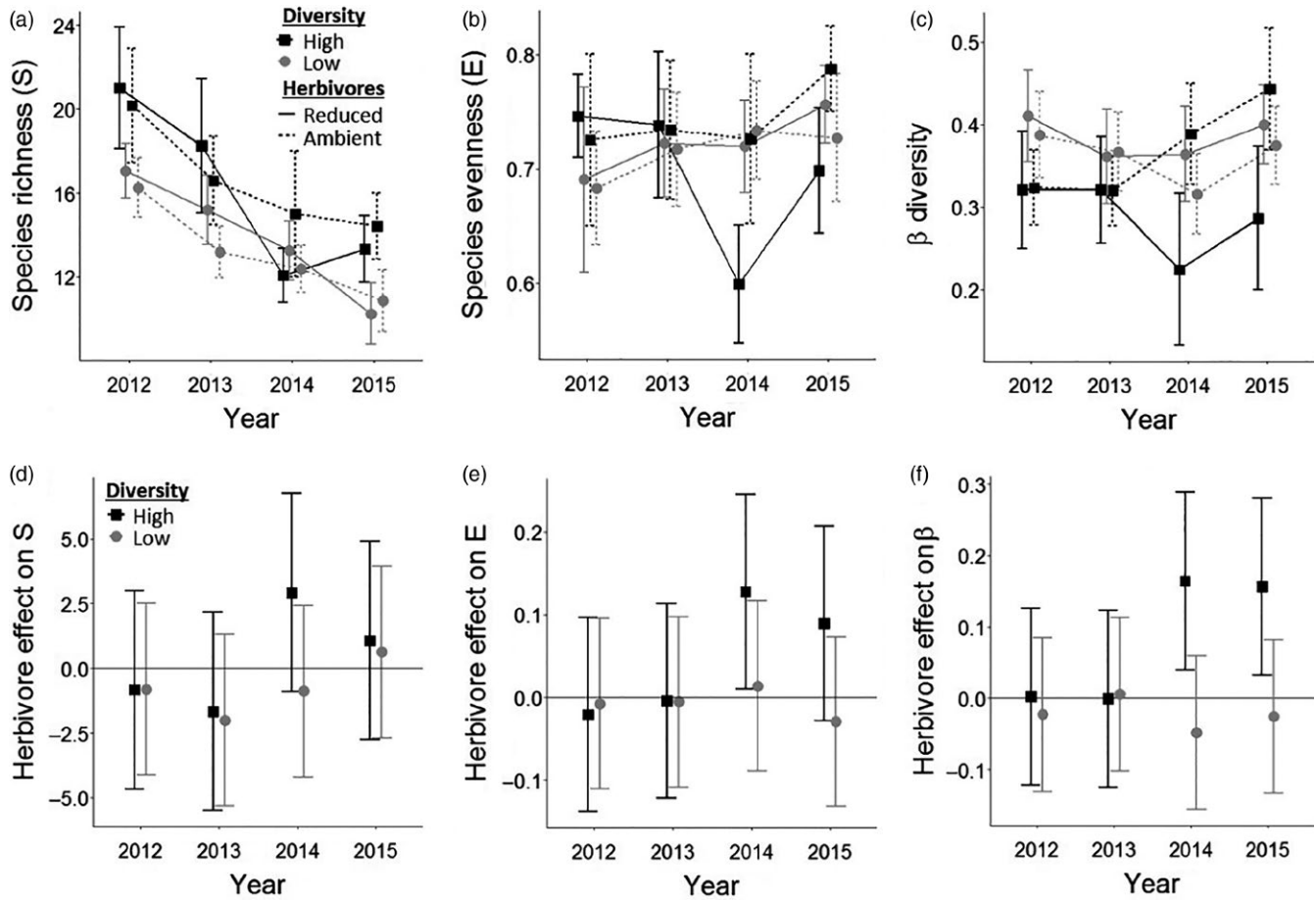


FIGURE 3 Herbivore and diversity effects on plant diversity in the restoration experiment. Mean diversity indices were calculated within subplots from the raw data for (a) species richness (S) and (b) evenness ($H/\ln(S)$), and (c) beta diversity (among plots). The difference between herbivore treatments (control–fenced) is shown for (d) species richness, (e) evenness and (f) beta diversity based on the least squared means from the respective models reported in Table 1. Error bars represent 95% confidence intervals in a–c and 97.5% confidence intervals at $\alpha = 0.05$ following Bonferroni correction in d–f

(Table 1). However, the effects of herbivores on plant richness differed significantly by year (herbivore \times year, Table 1). Pre-planned contrasts between herbivore treatments indicate that in the third year of the experiment, herbivores prevented a significant decrease in evenness within plots (Figure 3b,e) and beta diversity among plots (Figure 3c,f) while marginally increasing richness (Figure 3a,d). These effects occurred even though vole populations were lower during this year of the experiment than other years (Table S2), suggesting that herbivores can have significant effects at low abundance. The positive effect of herbivores on beta diversity persisted into the fourth year while other effects were marginal or absent. Reductions in diversity were paralleled by increased dominance of a single species.

Herbivores prevented a strong pulse of dominance by a single species in the third year of the experiment. *Chamaecrista fasciculata* (Michx.), an annual sown only in the high-diversity treatment, increased in abundance significantly in the third year of the experiment, with the greatest increase coinciding with herbivore reductions (Table 1, Figures 4a and S1), and was associated with reduced richness during this period of dominance (cover: $F_{1,85,75} = 5.23$, $p = .025$;

cover \times year: $F_{3,78,20} = 6.71$, $p = .004$; Figure 4b). The absence of species capable of achieving the same level of dominance as *C. fasciculata* during this experiment (Figure S1) precluded similar effects in the low-diversity treatment.

Neither herbivores nor the diversity treatment significantly affected inter-annual variability, measured as the coefficient of variation, in evenness in the restoration experiment (herbivores: $F_{1,52} = 1.13$, $p = .2925$; diversity: $F_{1,52} = 3.90$, $p = .0536$; herbivores \times diversity: $F_{1,52} = 0.13$, $p = .7226$), although variability was marginally greater in the high- than the low-diversity treatment (high diversity: 0.131 ± 0.014 , least squares mean \pm SE; low diversity: 0.094 ± 0.012). However, our relatively small sample size at this site ($n = 56$ plots) limited our power to detect an effect of herbivores on inter-annual variations in evenness as seen at the global scale of the Nutrient Network (power = 0.278).

3.2 | Global grasslands experiment

Herbivores indirectly support plant diversity in grasslands across the globe by reducing inter-annual variability in evenness. Herbivores

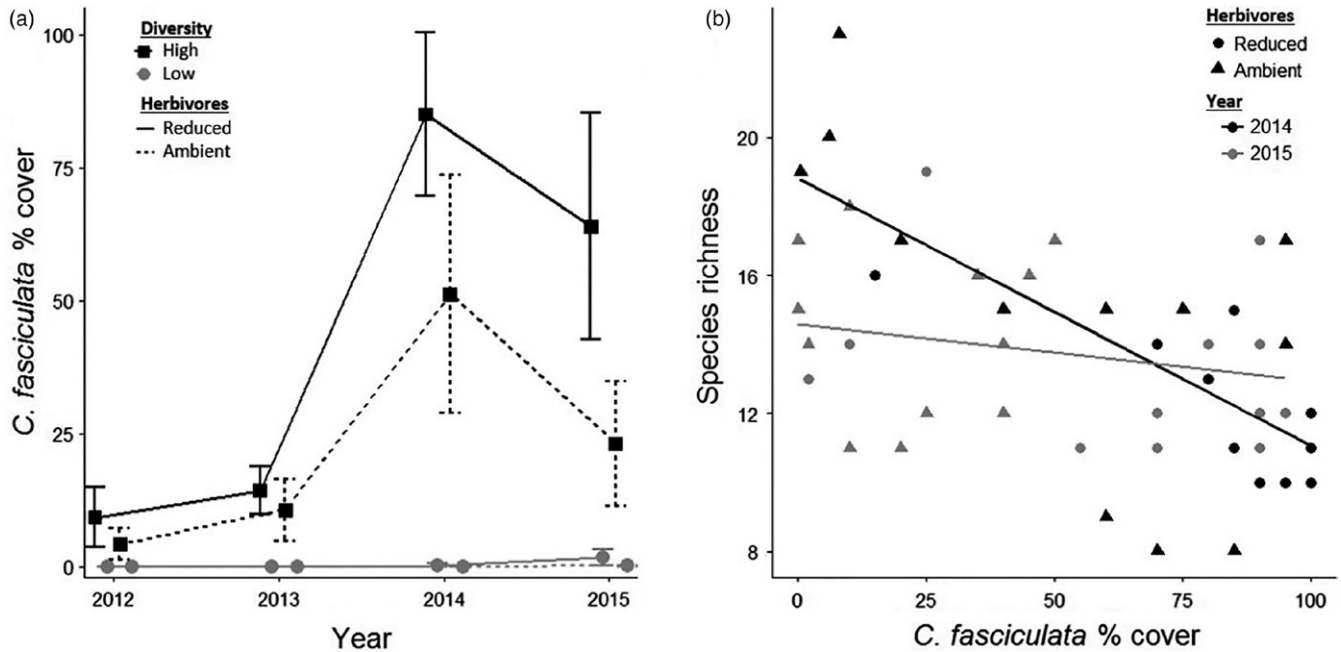


FIGURE 4 *Chamaecrista fasciculata* effects on species diversity in restoration experiment. (a) Mean cover of *C. fasciculata* in high- and low-diversity communities and in relation to ambient and reduced herbivore populations. Points were calculated as means from the raw data and error bars represent 95% confidence intervals. (b) *C. fasciculata* cover in relation to species richness during 2014–2015 in ambient or reduced herbivore conditions in high-diversity treatments where it was sown

significantly reduced inter-annual variability in plant community evenness and light penetration when variability was calculated over windows ranging in duration from 2 to 6 years (Figure 5a) and 2 to 5 years (Figure 5c), respectively. In contrast, herbivores did not affect the inter-annual variability of community biomass at any temporal scale measured here (Figure 5b). Herbivore effects on variability were not due to persistent, directional changes as herbivores did not significantly affect mean evenness, although they did increase mean light penetration (Table 2); however, this latter effect did not vary with treatment duration (i.e. herbivores \times treatment duration interaction, Table 2). Inter-annual variability in evenness was negatively associated with initial richness when variability was calculated over windows ranging in duration from 3 to 5 years (Figure 5d). Despite this relationship, inter-annual variability of light penetration and community biomass were not significantly related to initial richness (Figure 5e,f).

Inter-annual variability in evenness was associated with losses in plant richness. The LRR of richness declined significantly as inter-annual variability of evenness increased over the preceding 2–5 years of the experiment (Figure 6a). By comparison, changes in richness were not significantly associated with inter-annual variability in community biomass (Figure 6b) or light penetration (Figure 6c). The direct effect of herbivores was positively, although only occasionally significantly, associated with the LRR of richness, depending on the timeframe used to calculate variability and the other factor (evenness, biomass or light) included in the model (Table S6). However, by reducing inter-annual variability in community evenness, herbivores had a positive, indirect effect on richness.

4 | DISCUSSION

4.1 | Herbivores maintain diversity by limiting pulses of dominance

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

The mediating effect of dominance between herbivores and plant richness suggests that plant species may not be lost immediately following reductions in herbivory. Pulses of dominance, as observed in our experiments, may occur as annual climates, disturbance or other conditions change to favour one or a few species in a plant community. Consequently, the full effect of herbivores on plant richness may

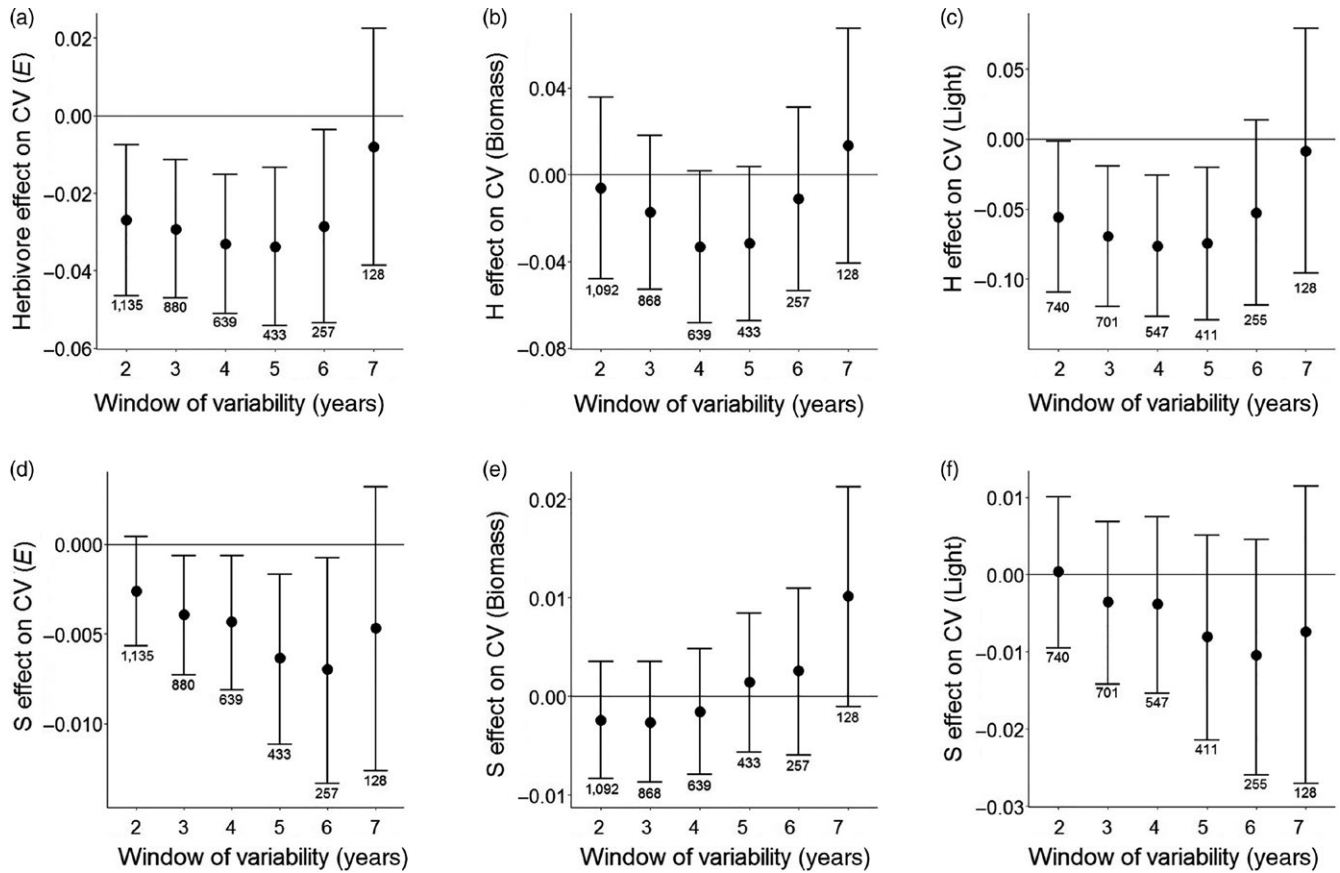


FIGURE 5 Herbivore and species richness effects on inter-annual variability (coefficient of variation; CV) in grasslands across the globe. The window of variability indicates the timeframes used to calculate the CV. The effect of herbivores (i.e. control-fenced) on the CV are shown for (a) plant community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

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

Effect	NumDF	Evenness			Biomass			Light penetration		
		DenDF	F	p	DenDF	F	p	DenDF	F	p
Herbivores	1	179.30	1.39	.2407	264.98	13.31	.0003	968.73	17.73	<.0001
Treatment duration	7	1,141.30	1.92	.0634	1,092.78	2.49	.0153	962.47	4.68	<.0001
Herb. × Trt. duration	7	1,183.70	1.19	.3064	1,158.45	1.31	.2403	960.23	1.26	.2681

Significant effects ($\alpha < 0.05$) are shown in bold.

not be observed until environmental conditions provide a “window of opportunity” (Balke, Herman, & Bouma, 2014) for a potentially dominant species to increase in relative abundance. For example, caribou (*Rangifer tarandus*) and muskox (*Ovibos moschatus*) grazing appeared to have no effect on a grassland community in Greenland prior to experimental increases in temperature, but after warming, grazing increased stability and prevented losses in forb richness (Post, 2013; Post & Pedersen, 2008). In a Spanish grassland, livestock grazing did

not strongly affect community structure until an unusually dry period when herbivores prevented shifts in dominance among grass species (Pardo et al., 2015). The effects of herbivores on limiting dominance also extend to species that are potentially invasive under certain conditions (Kaarlejärvi et al., 2013; Post & Pedersen, 2008). These delayed effects of herbivore loss on plant richness may lead to an “extinction debt” that will not be fully realized until environmental conditions shift to favour a potentially dominant species.

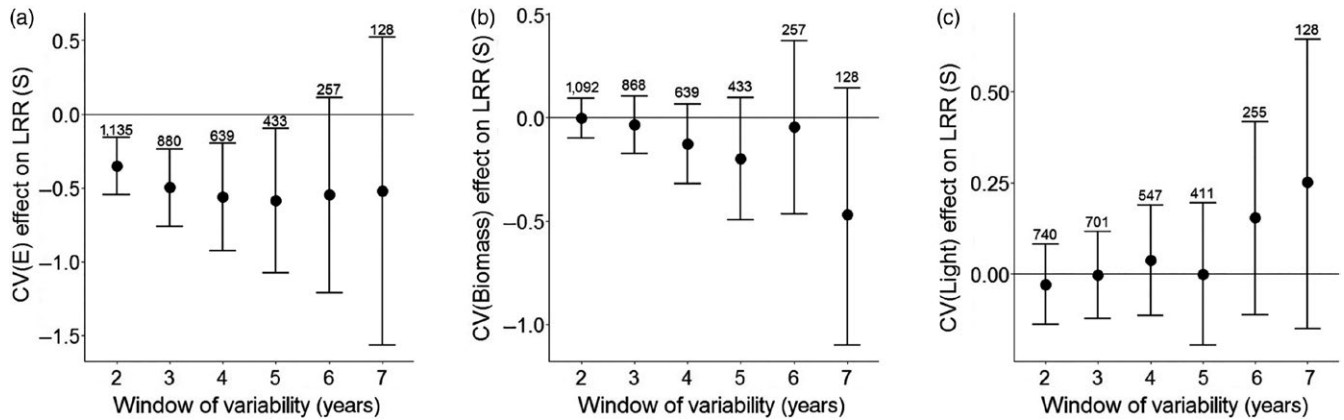


FIGURE 6 Slope between inter-annual variability (coefficient of variation; CV) and changes in species richness (S) at different time-scales in grasslands across the globe. The slope between CV and the log response ratio (LRR) of species richness (i.e. $\Delta\text{LRR}(S)/\Delta\text{CV}$) was calculated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

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

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

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

4.2 | Mechanisms of diversity in stable communities

The exact mechanisms by which herbivores indirectly maintain plant diversity via increased community stability are unclear. Light

availability (e.g. Bakker, Ritchie, Olf, Milchunas, & Knops, 2006; Borer, Seabloom, et al., 2014; Olf & Ritchie, 1998; Schmitz, 2006) and community biomass (e.g. Bakker et al., 2006; Duffy, 2002; Eisenhauer et al., 2011; McNaughton, 1985), the most commonly studied effects of herbivores on plant community variation, did not appear to consistently affect plant diversity in the global experiment when considered in terms of inter-annual variation even though herbivores decreased variability in light. Thus, while herbivores can maintain plant diversity by increasing mean light availability (Borer, Seabloom, et al., 2014) or decreasing community biomass (Hanke et al., 2014; McNaughton, 1985), their indirect effects on diversity mediated by inter-annual stability likely occur through different pathways. We suggest two alternative mechanisms by which herbivores support plant diversity by increasing inter-annual stability.

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

Second, herbivores may prevent temporary, competitive dominance for below-ground resources by preferentially consuming competitively dominant species as in the keystone (Paine, 1966) or R^*/P^* hypothesis (Holt, Grover, & Tilman, 1994). However, previous work in our global experiment indicates that herbivores do not generally prefer competitively dominant over subordinate species (Lind et al., 2013). Moreover, if availability of below-ground resources is related to above-ground biomass (e.g. McNaughton, 1985), and variability in biomass is not related to richness (Figure 6b), then we may expect that variation in below-ground competition will not affect richness. Finally, soil nutrient availability is

not always associated with grazing (Milchunas & Lauenroth, 1993; but see Bakker, Olf, Boekhoff, Gleichman, & Berendse, 2004). Thus, we find it less likely that the stabilizing effects of herbivores affected plant richness through changes in below-ground resources.

4.3 | Plant richness, inter-annual variability and potential feedbacks

Herbivore reductions may prompt feedback cycles leading to the additional loss of plant species (Figure 1b–f). Globally, herbivore reductions increased inter-annual variation in evenness, which was associated with reduced plant richness. Moreover, high pre-treatment species richness was associated with low variability in community evenness both in this study and others (Isbell et al., 2009; McNaughton, 1985). Thus, losses in plant species richness following a loss or reduction in herbivores may further destabilize plant communities, leading to further losses in plant species.

4.4 | Declines in richness spatially homogenize plant communities

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

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

5 | CONCLUSIONS

Complementing previous studies showing that herbivores may increase plant richness by affecting mean community values of light and biomass (Borer, Seabloom, et al., 2014; Gibson, 1988; Hautier et al.,

2009; Stevens & Carson, 2002), our results show that herbivores may also prevent losses in plant richness by stabilizing evenness over time. While other studies have explicitly considered the effects of inter-annual variability in plant biomass (e.g. Eisenhauer et al., 2011; Grman, Lau, Schoolmaster, & Gross, 2010; Isbell et al., 2009; McNaughton, 1985; Polley, Wilsey, & Derner, 2007) as well as evenness (Hanke et al., 2014) on richness, we add to this body of knowledge that variability in biomass or light may not be universal mechanisms for maintaining diversity. In fact, another form of variability, inter-annual variation in evenness, which increases with the loss of herbivores, is significantly related to changes in plant richness. Thus, previous work focusing on the effects of herbivores on mean biomass and light as a measure of community stability may not fully capture the long-term effects of herbivores on plant evenness and diversity.

ACKNOWLEDGEMENTS

Funding for the restoration experiment was provided by the Iowa Living Roadway Trust Fund project numbers: 90-00-LRTF-211, 90-00-LRTF-306, 90-00-LRTF-307; TogetherGreen; and the ISU Department of EEOB. A. Zhang, J. Bickley, T. Luesink and L. Sullivan assisted in data collection; and E. Bach, L. Biederman, J. Doudna, C. Duthie, T. Flick, H. Frater, P. Frater, J. Gallagher, M. Karnatz, L. Martin, L. Sullivan and R. Williams assisted with the restoration. The Nutrient Network (<http://www.nutnet.org>) experiment is funded at the site-scale by individual researchers too numerous to thank here, but not in the supporting information (see Table S7). Coordination and data management have been supported by funding to E. Borer and E. Seabloom from the National Science Foundation Research Coordination Network (NSF-DEB-1042132) and Long Term Ecological Research (NSF-DEB-1234162 to Cedar Creek LTER) programs, and the Institute on the Environment (DG-0001-13). We also thank the Minnesota Supercomputer Institute for hosting project data and the Institute on the Environment for hosting Network meetings. The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

B.M. developed and framed the research questions; all authors contributed to data collection; B.M., B.D. and W.S.H. analysed the data; B.M. led writing of the manuscript. All authors contributed to drafts and gave approval for publication. A full list of authors' contributions is available in Table S8.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.dd30d> (Mortensen et al., 2017).

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How to cite this article: Mortensen B, Danielson B, Harpole WS, et al. Herbivores safeguard plant diversity by reducing variability in dominance. *J Ecol*. 2018;106:101–112. <https://doi.org/10.1111/1365-2745.12821>