

Change in dominance determines herbivore effects on plant biodiversity

By: [Sally E. Koerner](#), Melinda D. Smith, Deron E. Burkepile, Niall P. Hanan, Meghan L. Avolio, Scott L. Collins, Alan K. Knapp, Nathan P. Lemoine, Elisabeth J. Forrestel, Stephanie Eby, Dave I. Thompson, Gerardo A. Aguado-Santacruz, John P. Anderson, T. Michael Anderson, Ayana Angassa, Sumanta Bagchi, Elisabeth S. Bakker, Gary Bastin, Lauren E. Baur, Karen H. Beard, Erik A. Beever, Patrick J. Bohlen, Elizabeth H. Boughton, Don Canestro, Ariela Cesa, Enrique Chaneton, Jimin Cheng, Carla M. D'Antonio, Claire Deleglise, Fadiala Dembélé, Josh Dorrrough, David J. Eldridge, Barbara Fernandez-Going, Silvia Fernández-Lugo, Lauchlan H. Fraser, Bill Freedman, Gonzalo García-Salgado, Jacob R. Goheen, Liang Guo, Sean Husheer, Moussa Karembé, Johannes M. H. Knops, Tineke Kraaij, Andrew Kulmatiski, Minna-Maarit Kytöviita, Felipe Lezama, Gregory Loucougaray, Alejandro Loydi, Dan G. Milchunas, Suzanne J. Milton, John W. Morgan, Claire Moxham, Kyle C. Nehring, Han Olf, Todd M. Palmer, Salvador Rebollo, Corinna Riginos, Anita C. Risch, Marta Rueda, Mahesh Sankaran, Takehiro Sasaki, Kathryn A. Schoenecker, Nick L. Schultz, Martin Schütz, Angelika Schwabe, Frances Siebert, Christian Smit, Karen A. Stahlheber, Christian Storm, Dustin J. Strong, Jishuai Su, Yadugiri V. Tiruvaimozhi, Claudia Tyler, James Val, Martijn L. Vandegehuchte, Kari E. Veblen, Lance T. Vermeire, David Ward, Jianshuang Wu, Truman P. Young, Qiang Yu, and Tamara Jane Zelikova

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Abstract:

Herbivores alter plant biodiversity (species richness) in many of the world's ecosystems, but the magnitude and the direction of herbivore effects on biodiversity vary widely within and among ecosystems. One current theory predicts that herbivores enhance plant biodiversity at high productivity but have the opposite effect at low productivity. Yet, empirical support for the

importance of site productivity as a mediator of these herbivore impacts is equivocal. Here, we synthesize data from 252 large-herbivore exclusion studies, spanning a 20-fold range in site productivity, to test an alternative hypothesis—that herbivore-induced changes in the competitive environment determine the response of plant biodiversity to herbivory irrespective of productivity. Under this hypothesis, when herbivores reduce the abundance (biomass, cover) of dominant species (for example, because the dominant plant is palatable), additional resources become available to support new species, thereby increasing biodiversity. By contrast, if herbivores promote high dominance by increasing the abundance of herbivory-resistant, unpalatable species, then resource availability for other species decreases reducing biodiversity. We show that herbivore-induced change in dominance, independent of site productivity or precipitation (a proxy for productivity), is the best predictor of herbivore effects on biodiversity in grassland and savannah sites. Given that most herbaceous ecosystems are dominated by one or a few species, altering the competitive environment via herbivores or by other means may be an effective strategy for conserving biodiversity in grasslands and savannahs globally.

Keywords: herbivores | plant biodiversity | herbaceous ecosystems | dominance

Article:

Consumers play a critical role in determining the structure and functioning of most ecosystems¹. However, human activities have greatly altered top-down control by consumers with consequences for biodiversity and other ecosystem services not yet fully understood¹. In part, this uncertainty arises because the effects of consumers on biodiversity are highly variable in both aquatic and terrestrial ecosystems^{2–7}. One theory predicts that the effects of herbivores on biodiversity (species richness, the number of species) vary with ecosystem productivity^{2,4,5,7–10}. In more productive systems, herbivory is expected to reduce the abundance of dominant species and increase biodiversity⁷. Dominant species often impact community structure¹¹, including species biodiversity, by monopolizing resources. Decreased dominance can be directly linked to increased availability of resources, including light, nutrients and water, leading to increased abundance of less common species, colonization by new species and/or a decrease in local species extinctions⁷. In contrast, at low productivity, herbivores are predicted to decrease biodiversity by either (1) increasing dominance by grazing-tolerant species, which may reduce colonization rates or enhance extinctions of other species, or (2) not affecting dominance if species are unpalatable, but instead increasing extinctions of rare palatable species via consumption⁷. Collectively, these processes may result in a positive relationship between biodiversity and productivity with herbivory. However, deviations from this pattern are common, particularly in herbaceous plant communities (for example, see Olf and Ritchie⁷, Koerner et al.¹², Milchunas and Lauenroth¹³ and Eldridge et al.¹⁴). These discrepancies call into question the generality of productivity as a mediator of herbivore effects on biodiversity via the dominance mechanism. Indeed, high levels of plant community dominance are found in both high¹⁵ and low-productivity¹⁶ systems, which suggests that changes in dominance may impact biodiversity directly and irrespective of productivity.

Here, we test how changes in dominance determine biodiversity responses to herbivory, and whether this dominance mechanism is mediated by site productivity. We synthesized data from 252 grassland and savannah sites (Fig. 1; Supplementary Table 1–3) that includes 1,212 plots

sampled inside and outside of large-herbivore exclosures. These sites encompassed a broad range of environmental conditions across six biogeographic realms¹⁷. This data set included measures of plant community composition from all sites and aboveground net primary productivity (ANPP) from half the sites, as well as a number of herbivore community and site characteristics (see Methods). To quantify herbivore-induced changes in biodiversity, we calculated the log response ratio ($\ln(G/UG)$) of plant species richness (average number of species per plot) outside (grazed, G) versus inside (ungrazed, UG) exclosures. We used two common dominance metrics—the Berger–Parker and Simpson’s Dominance Indexes¹⁸—to evaluate changes in dominance with herbivory. Change of both metrics was calculated using log response ratios. We picked these two measures of dominance because both are robust to changes in richness at levels encompassed by our data sets (> 5 ; refs.^{18,19}) and thus can vary independently of richness. The Berger–Parker Dominance Index is a measure of the relative cover of the most abundant species regardless of species identity, while Simpson’s Dominance Index is a measure of diversity that is highly sensitive to abundant species²⁰. We chose to focus on the Berger–Parker Dominance Index metric because of its simplicity and its mathematical independence from richness. However, Simpson’s Dominance Index, while more complicated, is a metric that can capture co-dominance by two or more species¹⁸. The inclusion of the Simpson’s Dominance Index metric in our analyses (see Supplementary Information) allowed us to examine the robustness of the patterns observed with the Berger–Parker Dominance Index metric.

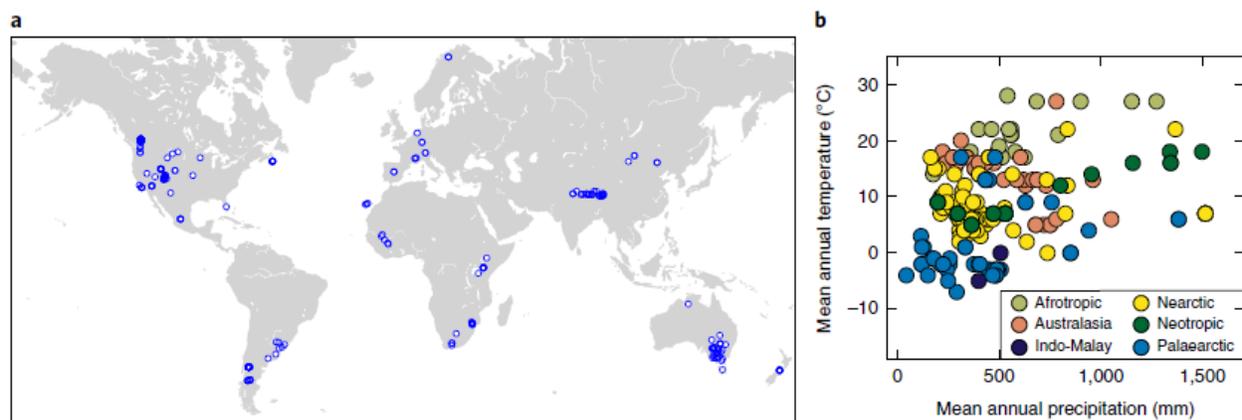


Figure 1. Location and climate of sites. **a**, Locations of the 252 grassland and savannah ecosystems where 1,212 grazed and ungrazed plots were located. All sites are represented by a single-sized open blue circle. Areas where symbols overlap appear to be darker blue. **b**, These study sites represent six biogeographic realms and encompass broad gradients of mean annual temperature and precipitation. Additional site details are provided in Supplementary Tables 1 and 2.

Results and discussion

Consistent with previous theory and several empirical studies^{2,8,9,13}, we found a positive relationship between changes in species richness in response to herbivores and ANPP, but the amount of variation explained was low (Fig. 2a). Contrary to theory, herbivory did not decrease species richness at low productivity. Instead, herbivory had, on average, either neutral or positive effects on richness across the entire 20-fold range in ANPP. Because not all studies in our data set measured ANPP, we used mean annual precipitation (MAP) as an ANPP proxy. This was possible due to the relationship between MAP and ANPP in our data set (linear regression: $R^2 = 0.21$, $P < 0.001$, $F_{106} = 27.63$) as well as in grasslands and savannahs globally^{20,21}. Even with this

expanded data set, richness responses were poorly related to MAP (Fig. 2b), consistent with the weak relationship observed for ANPP.

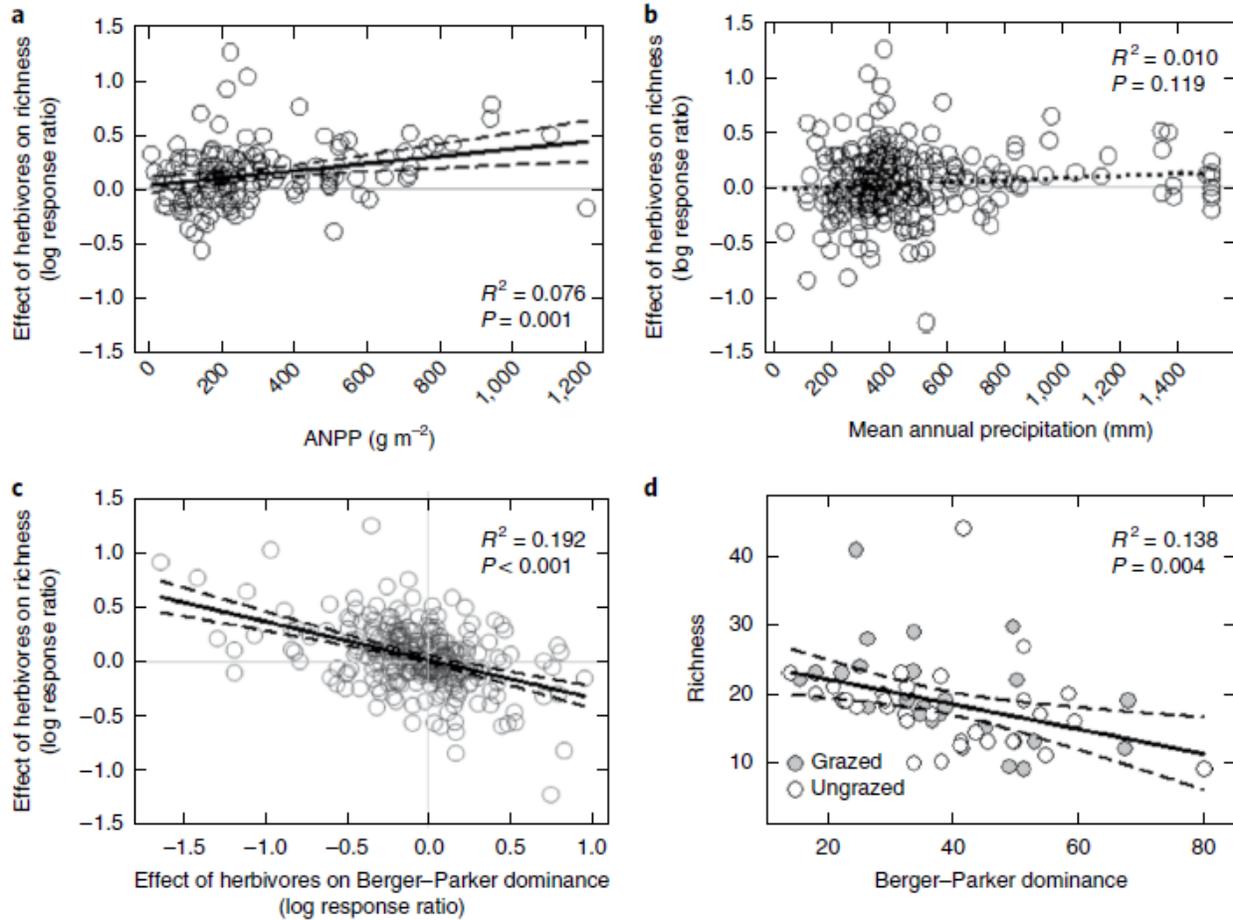


Figure 2. Herbivore effects on plant communities. **a**, Relationship between ANPP and the response of plant species richness to herbivory ($\ln(G/UG)$), where G is the average plant species richness in grazed plots and UG is the same measurement in ungrazed plots ($n = 132$; Data Subset 1 in Supplementary Table 3). **b**, Relationship between MAP and the response of plant species richness to herbivory ($n = 244$; Data Subset 2 in Supplementary Table 3). **c**, Relationship between the change in dominance (Berger-Parker dominance) and the change in species richness as a function of herbivory ($\ln(G/UG)$) ($n = 252$; all data). **d**, Relationship between dominance (Berger-Parker dominance) and species richness for grazed and ungrazed plots combined. This analysis is based only on studies with a common plot size of 25 m² ($n = 58$). The dashed lines represent 95% confidence intervals.

In contrast to the equivocal support for productivity influencing richness responses, we found a strong negative relationship between herbivore-induced changes in Berger-Parker dominance and the effect of herbivores on species richness (Fig. 2c). As predicted, when herbivores decreased dominance thereby reducing competition, species richness increased; however, when herbivores increased dominance, thereby increasing the strength of competition, richness declined. Negative relationships between species richness and dominance are common (for example, see McNaughton and Wolf¹¹, Koerner et al.¹² and Grime²²), and this relationship was also evident in both grazed and ungrazed plots in our data set (Fig. 2d). These patterns were even stronger when using Simpson's dominance (Supplementary Fig. 2; $R^2 = 0.192$ for Berger-Parker dominance and $R^2 = 0.299$ for Simpson's dominance) suggesting that changes in co-dominance may be important in many of these grazing systems. Given this relationship and because we used

measures of dominance that are mathematically independent of richness¹⁸, this suggests that changes in dominance can be causally linked to biodiversity responses to herbivory. Changes in Berger–Parker dominance in response to grazing were not significantly related to either ANPP (Supplementary Fig. 1a) or precipitation (Supplementary Fig. 1b), suggesting this pattern is independent of site productivity. Similarly, changes in Simpson’s dominance due to grazing were also not significantly related to ANPP or precipitation (Supplementary Fig. 3).

Although univariate approaches can be informative, both productivity and change in dominance could jointly influence the biodiversity response to herbivory. Therefore, we used path analysis²³ to assess whether productivity mediates the effect of change in dominance on the richness responses to herbivory. Our a priori model included additional non-mutually exclusive factors that could influence the relationship between herbivory and species richness⁷, such as characteristics of the herbivore community (estimates of herbivore pressure; herbivore species richness; if herbivores were domesticated or not; and if browsers/mixed feeders were present in addition to grazers), the plant community (size of the species pool) and the duration of herbivore exclusion. See Methods for further details. These metrics allowed us to explicitly contrast the effects of site-level productivity versus change in dominance on the richness response to herbivory and include other factors that may affect both dominance and richness responses. We examined six alternative models (Fig. 3 and Supplementary Fig. 4) to explicitly contrast the effects of changes in ANPP versus dominance on the biodiversity response to grazing.

Our first model examined the widely hypothesized relationship between precipitation, site productivity and change in species richness (Fig. 3a, Model 1). This model also included characteristics of the herbivore and plant communities (site-level richness), as well as accounted for correlations between input variables (Supplementary Table 4). Because productivity was not available from all sites, this initial model was limited to data from the 122 sites where ANPP was measured directly (see Methods; Data Subset 1 in Supplementary Table 3). As expected, precipitation was strongly related to productivity in this data set (Fig. 3a, Model 1); consistent with our univariate analysis, we found a significant positive effect of site productivity on change in species richness. Grazing had neutral to mildly positive effects on richness at low productivity and a stronger positive effect at higher productivity. In addition, we found that grazing pressure negatively influenced the richness response, but to a lesser extent than productivity. Thus, at high grazing pressure, herbivores decreased richness irrespective of site productivity. Site-level species richness also affected how richness responded to herbivory. As site richness increased, herbivores had less of an effect on changes in species richness regardless of site productivity. Overall, this model explained 13% of variation in the richness response to herbivory.

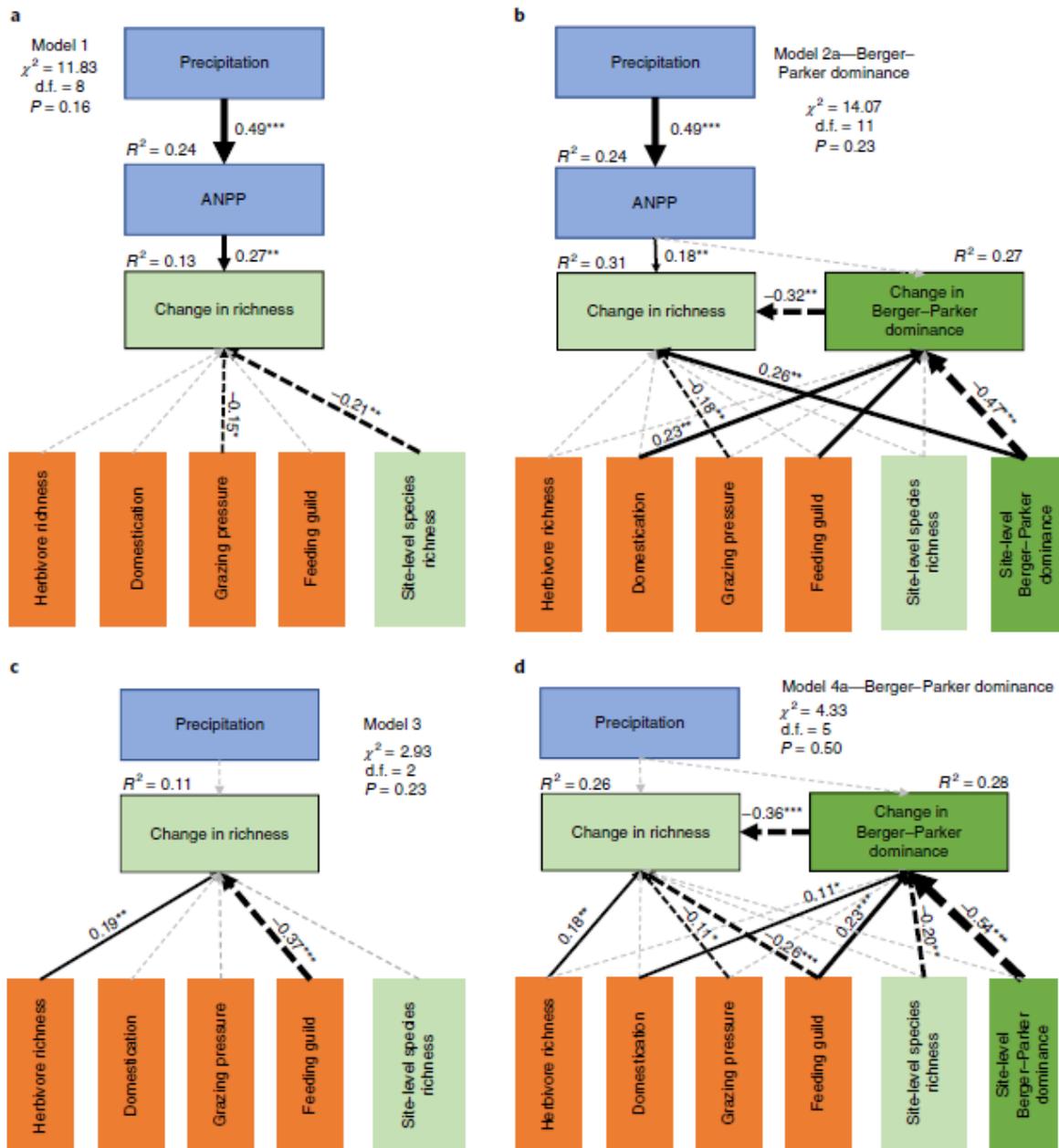


Figure 3. Drivers of plant richness response to herbivory. **a,b**, Path analyses testing the importance of ANPP (Model 1) and Berger–Parker dominance (Model 2a) on the change in species richness in response to herbivory. These models are restricted to sites where both ANPP and precipitation data were available ($n = 122$; Data Subset 3 in Supplementary Table 3). See Supplementary Tables 4 and 5 for bivariate correlations between input variables that were included in these models to improve model fit. **c,d**, Path analyses testing the importance of productivity using precipitation as a proxy (Model 3) for productivity and Berger–Parker dominance (Model 4a) on the change in species richness in response to herbivory. These models use precipitation as a surrogate for ANPP allowing the use of more data ($n = 244$; Data Subset 2 in Supplementary Table 3). See Supplementary Tables 7 and 8 for bivariate correlations between the input variables that were included in these models to improve model fit. All models also test for the effects of site and herbivore characteristics (see Methods). $***P < 0.001$, $**P < 0.05$, $*P < 0.10$. Non-significant relationships are shown in light grey dashed arrows; solid black arrows represent positive relationships and dashed black arrows represent negative relationships. The standardized effect sizes are shown, with arrow thickness proportional to the strength of the relationship. All models were a good fit to the data based on the chi-squared statistic ($P > 0.05$ goodness of fit). See Supplementary Table 10 for additional model fit parameters for all four models.

In a second model (Fig. 3b, Model 2a) we added an estimate of site-level Berger–Parker dominance in the absence of grazing (averaged across all ungrazed plots at a site (U_{dom})), as well as the change in dominance in response to grazing ($\ln(G_{\text{dom}}/U_{\text{dom}})$) to assess the relative effects of productivity versus dominance on the richness response to herbivory. (The correlations between all input variables can be found in Supplementary Table 5.) While site productivity was weakly correlated with changes in richness (Fig. 3b, Model 2a), both site-level dominance and change in dominance were significantly and more strongly correlated with the richness response to grazing. That is, as site dominance increased, grazing had a stronger positive effect on species richness. Consistent with this relationship, the change in dominance due to herbivores was strongly related to changes in species richness. Thus, when grazing reduced dominance there was a strong increase in species richness. Similar to the previous model, grazing pressure remained significantly correlated with the change in species richness. In this model, other factors related to the herbivore community were also significant (that is, domestication and feeding guild), but their effects on change in richness were indirect via change in dominance. Also, site-level total species richness no longer directly or indirectly influenced change in species richness. Overall, inclusion of Berger–Parker dominance doubled the explanatory power of the change in species richness when compared to the model that only included productivity ($R^2 = 0.31$ versus 0.13). When this second model included Simpson’s instead of Berger–Parker dominance (Supplementary Fig. 4a, Model 2b; Supplementary Table 6), the explanatory power of the change in species richness increased ($R^2 = 0.39$), providing robust support for change in dominance as key to explaining changes in richness with herbivory. Additionally, ANPP no longer has a significant effect on change in richness from herbivory when Simpson’s dominance was included in the model.

Models 1, 2a and 2b (Supplementary Information) were limited to the 122 sites that had productivity measurements. Because productivity is strongly correlated with MAP in our data set (Fig. 3a,b, Models 1 and 2a) as well as more broadly²⁰, we used precipitation as a proxy for productivity in Models 3, 4a and 4b (Supplementary Information). This allowed us to include 244 sites in the analysis (Data Subset 3 in Supplementary Table 3). In Model 3, we examined the relationship between precipitation and change in species richness without dominance (similar to Model 1 but using a larger data set) as well as accounted for correlations between input variables (Supplementary Table 7). As with the ANPP data set, Model 3 could only explain 11% of the variation in change in richness, and there was no effect of precipitation in this model. When Berger–Parker dominance was included in the model (Model 4a; Supplementary Table 8), our explanatory power of change in richness more than doubled ($R^2 = 0.11$ versus 0.26); when Simpson’s dominance was included (Supplementary Fig. 4b: Model 4b; Supplementary Table 9) our explanatory power of change in richness more than tripled ($R^2 = 0.11$ versus 0.36). Similar to Model 2, we again found that site-level Berger–Parker dominance and change in Berger–Parker dominance with herbivores were the main drivers of herbivory-induced changes in species richness ($R^2 = 0.26$). However, precipitation, as a surrogate for productivity, had no significant effect in the model. Importantly, incorporating the larger data set in Models 4a and 4b demonstrated that herbivore-driven changes in dominance exert stronger effects on richness change than site-level dominance per se (standardized partial effect sizes of -0.35 versus not significant, respectively). These models also identified a strong, negative relationship between site-level dominance and change in dominance (standardized partial effect size of -0.54 and

-0.58). This occurred because change in dominance is expressed as a ratio of grazed to ungrazed dominance and indicates that grazers reduce dominance more in sites with higher dominance. With this more comprehensive data set, we identified additional factors with direct and indirect effects on richness response to herbivory. For example, grazers alone had a stronger impact on changes in species richness than when grazers and browsers were both present (standardized partial effect size for herbivore guild of -0.26 and -0.23). This pattern suggests that grazers target dominant grasses that then outcompete subordinate species when released from herbivory. However, grazers and browsers may have less of a net effect on species richness due to compensatory feeding, supporting the theory⁷ and patterns from previous studies^{12,24,25}. Overall, the more data-rich models confirm the role of dominance in controlling the richness response to herbivory rather than productivity.

To further explore the relationship between community dominance and herbivory, we focused on the palatability of the dominant species. Palatability strongly influences how a plant species responds to herbivory. Previous research has shown that herbivores reduce the dominance of palatable tall grasses in the productive mesic grasslands of North America, resulting in increased biodiversity^{12,26}. Alternatively, large herbivores in a mesic South African savannah dominated by an unpalatable grass had only minor impacts on dominance and diversity¹². Dominant species can also be palatable but grazing-tolerant so that dominance increases with herbivory. This is the case in East African mesic grasslands where large herbivores generate extensive grazing lawns in which a few grazing-tolerant grasses withstand high densities of large herbivores and high rates of consumption^{27,28}. Such grazing lawns exhibit both high dominance and low biodiversity²⁷. Finally, high dominance and low biodiversity also could occur if there is another species in the community capable of compensating for reduced abundance of the dominant species. Thus, including traits that confer palatability of dominant species into analyses may be key to a more detailed mechanistic understanding of herbivore effects on biodiversity.

Assessing the role of palatability in determining dominance responses to herbivory was not possible with our empirical analysis due to a lack of trait data for the whole suite of plant species. However, we incorporated palatability into a stochastic community assembly model to simulate the effect of herbivory on Berger–Parker dominance and richness independent of productivity. This model considered community assembly, as well as dominance and richness responses following grazing, as random processes (see Methods for details). Change in dominance was calculated using the relative cover of the dominant species. In the model, changes in dominance and species richness can occur via competitor release, local extinction and new species arrivals. We assessed three scenarios with the model: (1) all dominant species are palatable, that is, grazed (Fig. 4a); (2) all dominant species are unpalatable (Fig. 4b); and (3) communities have a random chance of being dominated by either a palatable or unpalatable species (Fig. 4c). We found that when all simulated communities were dominated by palatable species (Fig. 4a) or when communities were dominated by either a palatable or unpalatable species (Fig. 4c), the resulting ensembles of 1,000 simulations generated richness and dominance responses to herbivory that were remarkably similar to empirical observations (Fig. 2c). In contrast, if the dominant species was unpalatable (leaving only less common species to be grazed), there were few instances where richness increased while dominance decreased (that is, few points in the upper left-hand quadrant of Fig. 4b). These simulations are consistent with the

biodiversity response to herbivory depending primarily on the palatability and subsequent response of the dominant species, irrespective of productivity.

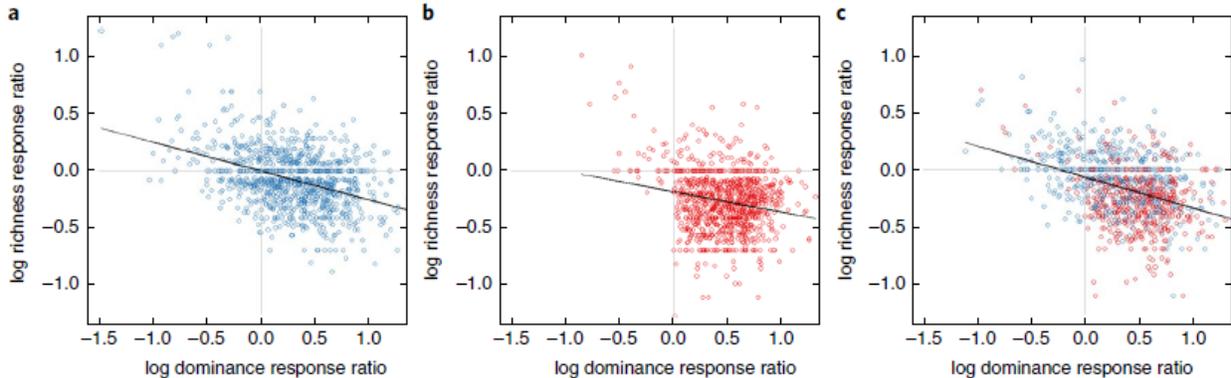


Figure 4. Simulation of plant community assembly in response to herbivory with three scenarios of palatability of the dominant species. **a**, In the first scenario, each assembled community has a dominant species that is grazed (blue) and all subordinate species have a 50% probability of being a grazed species. **b**, In the second scenario, each assembled community has a dominant species that is not grazed (red) and all subordinate species have a 50% probability of being a grazed species. **c**, In the third scenario, in each assembled community all plant species have a 50% probability of being a grazed species including the dominant species. The blue dots represent communities that have a dominant species that is grazed. The red dots represent assembled communities in which the dominant species was ungrazed. All scenarios treat community assembly and dominance, and richness responses following grazing, as random processes (see details in Methods).

Conclusion

Our findings extend theory^{2,5,7,22,29} by identifying change in community dominance, and thus the competitive landscape, as the primary and generalizable mechanism underlying biodiversity response to herbivory. Change in dominance explains herbivore impacts on biodiversity—both positive and negative—globally across grasslands and savannahs with 20-fold differences in productivity and vastly different biogeographic and evolutionary histories. This dominance mechanism is consistent with the light availability mechanism identified by Borer et al.⁵ because increases in dominance can increase light limitation³⁰. But dominance also changes with herbivory in sites where light is not limiting²⁷. Thus, the dominance mechanism applies to a wider range of ecosystems, reflecting competitive interactions for the availability of either above- or below-ground resources⁷. This dominance mechanism is also consistent with the evolutionary history mechanism identified by Milchunas and colleagues^{13,31} as dominance and the traits of the dominant species, particularly those related to palatability, are determined by a site's evolutionary history. Strong community dominance by just a few species is a nearly universal feature of ecosystems^{15,22,29}, and dominant species are known to control most ecosystem processes^{22,32}. As a consequence, our results point to 'dominance management' as an effective strategy for conserving species biodiversity and ecosystem functioning in grasslands and savannahs globally.

Methods

Data. We compiled a database, the Grazing Exclusion Database, consisting of plant community composition data from 252 large vertebrate herbivore exclusion sites (Supplementary Tables 1 and 2). To be included in the Grazing Exclusion Database, sites had to meet five criteria: (1)

exclosures had to be located in herbaceous-dominated communities—sites ranged from tallgrass prairie to alpine meadows to desert, but all are dominated or co-dominated by herbaceous species; (2) large vertebrate herbivores (adult body mass > 45 kg) had to be excluded from plots using fencing with adjacent plots exposed to herbivores; herbivore type and number varies among the sites, including domesticated cattle, sheep, goats, burros and horses, as well as native wildlife such as caribou, kangaroo and the full complement of large African herbivores, and the inside of the exclosure could not be manipulated or managed other than the removal of herbivores (that is, no mowing or burning that did not also occur outside the exclosure); (3) data had to be collected after at least three years of exclusion of large herbivores; this was to ensure sufficient time for the plant community to respond to the absence of herbivores; (4) paired plots inside and outside the exclosure had to be sampled at the same time and sampling intensity; (5) community data had to be available at the species level; data types include cover, line intercept, biomass and pin hits (but not frequency or density), all of which were converted to relative abundance values.

Explanatory variables. Several covariates were used in the analyses that described plant, experiment and herbivore community characteristics. Site primary productivity was based on ungrazed vegetation, as reported by individual investigators for a subset of the sites ($n = 132$). Individual investigators supplied precipitation data, while mean annual temperature was based on WorldClim³³. Site-level richness and dominance were calculated using the species composition data. Site richness was calculated as the total number of plant species found across all plots. Site dominance was calculated as the mean dominance across all ungrazed plots using the Berger–Parker Dominance Index, which is the relative abundance of the most abundant species in the plot. Four variables were used to describe the herbivore community. Investigators provided an assessment of herbivory pressure (low, moderate, high) and species of large herbivores excluded. We converted herbivore species information into three variables: herbivore richness; feeding guild; and domestication. Herbivore richness is the number of large-herbivore species excluded by the fences. Predominantly, these exclosures excluded grazers (feeding guild = 0); when browsers or mixed feeders were present either in combination with grazers or alone (feeding guild = 1), we hypothesized this would have different effects on the herbaceous community. Domestication refers to human involvement with herbivore species presence and abundance. Native herbivores (wildlife) were coded as domestication = 0, while domesticated herbivores (for example, cattle) or the combination of the two were coded as domestication = 1 since they were hypothesized to have different effects than native herbivores alone. Experiment length was the number of years post exclosure construction; this variable was included in many exploratory analyses but was never significant and often led to poor model fit to the data. Exclosure age was not significantly correlated with either change in richness or change in dominance. Therefore, exclosure age was dropped from all path analyses.

Although many sites provided multiple years of data, here we present only the most recent year of data collected from each site. For analyses involving ANPP, a subset of sites was used ($n = 132$; Data Subset 1 in Supplementary Table 3), while nearly all sites were included in analyses using only precipitation ($n = 244$; 8 sites were strategically placed in topographic locations that were either wetter or drier than expected based on precipitation and were, therefore, only used in the ANPP analysis but not the precipitation analyses; Data Subset 2 in Supplementary Table 3). Likewise, when models included both ANPP and precipitation, a subset was used ($n = 122$; Data

Subset 3 in Supplementary Table 3). When models did not include either ANPP or precipitation as predictors, we used all sites in the database ($n = 252$).

Response variables. The majority of sites had a single enclosure ($n = 132$). When more than one enclosure was built in the same year, each enclosure and corresponding paired plot was considered a block. When multiple subplots were sampled within each enclosure or paired plot, species abundance was summed for each species across the subplots to obtain species data at the plot level (that is, one plot per block). Plant community richness and dominance were calculated at the plot level for inside and outside the enclosure. Plant community richness was calculated as the number of species in the plot in that year. Dominance was quantified in two ways. The Berger–Parker Dominance Index was calculated as the maximum relative abundance of the most abundant species in each plot. The Simpson’s Dominance Index was calculated as

$$D_{\text{Simp}} = \sum_{s=1}^S p_s^2$$

where S is the number of species in the sample and p_s is the proportional abundance of the s th species. To quantify herbivore-induced changes in biodiversity, we calculated the log response ratio ($\ln(G/UG)$) of plant species richness outside (grazed, G) versus inside (ungrazed, UG) each enclosure. Change in community dominance with herbivory (both Berger–Parker and Simpson’s) was also estimated by using this log response ratio. The log response ratios were then averaged across blocks to obtain a single value for each site.

Analyses. We developed linear models using R version 3.1 (R Foundation for Statistical Computing). We used the `lm()` R function to analyse the relationships between the effect of herbivores on richness (log response ratio) and ANPP (Fig. 2a), MAP (Fig. 2b), and the effect of herbivores on dominance (log response ratio; Fig. 2c), and for the relationship between dominance and richness (Fig. 2d).

To determine the relative importance of various proposed explanatory variables on the richness response to herbivory (log response ratio), we used path analysis conducted in AMOS version 7 (SPSS). We contrasted the effects of site-level productivity versus dominance on species richness response to herbivory using two alternative models. All models also included hypothesized influential covariates, such as the characteristics of the herbivore community, the plant community and experimental duration. Data were screened for distributional properties and nonlinear relations. Site-level plant richness and herbivore richness were log-transformed as a result of these evaluations. While site-level dominance and richness theoretically could be driven by precipitation, the correlations between site-level richness and precipitation (Pearson’s correlation coefficient = 0.357; linear regression $R^2 = 0.126$) and between site-level Berger–Parker dominance and precipitation (Pearson’s correlation coefficient = -0.246 ; linear regression $R^2 = 0.06$) within our data set were low. Therefore, these relationships were dropped from the path analysis due to replication constraints. Model 1 examined the widely hypothesized relationship between precipitation, ANPP and change in species richness (Fig. 3a). Because ANPP was not available from all sites, this model used data from 122 of the 252 sites where ANPP was measured and precipitation was a good proxy for ANPP. Model 2a (Fig. 3b) used the same data as Model 1 but included an estimate of site-level Berger–Parker dominance in the

absence of grazing (U_{dom}), as well as the change in Berger–Parker dominance in response to grazing ($\ln(G_{\text{dom}}/U_{\text{dom}})$) to assess the relative effects of ANPP versus Berger–Parker dominance on richness response to herbivory. Model 2b—Simpson’s dominance (Supplementary Fig. 4a)—was the same as Model 2a but included an estimate of site-level Simpson’s dominance in the absence of grazing (U_{SimpDom}), as well as the change in Simpson’s dominance in response to grazing ($\ln(G_{\text{SimpDom}}/U_{\text{SimpDom}})$) to assess the relative effects of ANPP versus Simpson’s dominance on richness response to herbivory. Because ANPP is strongly correlated with MAP, in our data set (Fig. 3a,b) and more broadly²⁰, we used precipitation as a proxy for ANPP, allowing us to run similar models again but including 244 sites in the analysis (Model 3 and Models 4a and 4b). Several input variables were correlated (based on AMOS recommendations for correlated variables that improve model fit); therefore, they were included as such in the models (Supplementary Tables 4–9). All models were a good fit to the data, according the chi-squared statistic with $P > 0.05$ as well as other measures of goodness of fit (see Supplementary Table 10).

Null model simulation. To explore possible mechanisms for observed herbaceous community responses to herbivory, we created a simple community assembly and grazing response model in which idealized plant communities first assemble stochastically, with each new species assigned a canopy cover drawn from a negative binomial distribution (mean cover, $\mu = 15\%$; dispersion = 1.0) until the collective canopy cover = 100% of available space, after which time no further species can be added. The grazing process is then simulated with (1) species in the community assigned as ‘palatable’ or ‘unpalatable’ using a random binomial process ($P = 0.5$), and (2) reduction in cover of palatable species simulated as a random uniform process where ~50% of palatable species are excluded by grazing (that is, cover is reduced to 0%), and the cover of the remaining palatable species is reduced by 50–99% of their original extent. The community response to the resources made available through grazing-induced loss in plant cover is then simulated via the effect of two mechanisms: (1) competitive release of ungrazed species (‘growth response’); and (2) establishment of novel species (that is, species assumed to have been absent in the ungrazed community, but available in the regional species pool; ‘immigration response’). The growth and immigration responses are simulated alternately until the resulting community again occupies all available space, with each ungrazed species increasing its cover in proportion to the grazing-induced loss in total cover in the plot, and new immigrants arriving via the negative binomial stochastic process used in the original community assembly.

Reporting summary. Further information on experimental research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

While not all raw species abundances are publicly available because of lack of permission from data owners (contact individual data set owners listed in Supplementary Table 1), all data generated and analysed during the current study (site-level richness response to herbivory, site-level Berger–Parker and Simpson’s dominance response to herbivory, site ANPP, and site MAP) are provided in Supplementary Table 2.

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Author contributions

S.E.K. managed the project including conceptualizing the questions, collecting and analysing the data, developing the figures and writing the manuscript. M.D.S. conceptualized the questions and wrote the manuscript. D.E.B. conceptualized the questions, collected the data and wrote the manuscript. N.P.H. performed simulations and wrote the manuscript. M.L.A. and N.P.L. executed the path analyses and developed the figures. S.L.C. and A.K.K. wrote the manuscript. S.E., E.J.F. and D.I.T. contributed to data collection and management. S.E.K., M.D.S., D.E.B., N.P.H., M.L.A., S.L.C., A.K.K., N.P.L., E.J.F., S.E. and D.I.T. attended multiple working groups to complete this manuscript while all other co-authors contributed data to the synthesis; all authors (both members of the working group and not) edited the manuscript. See the author contribution table (Supplementary Table 11) for a complete list of contributions.

Competing interests

The authors declare no competing interests.

Supplementary information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-018-0696-y>.

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