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1 **Change in dominance determines herbivore effects on plant biodiversity**

2

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157



158 **Herbivores alter plant biodiversity (species richness) in many of the world's ecosystems,**  
159 **but the magnitude and the direction of herbivore effects on biodiversity vary widely within**  
160 **and among ecosystems. One current theory predicts that herbivores enhance plant**  
161 **biodiversity at high productivity but have the opposite effect at low productivity. Yet,**  
162 **empirical support for the importance of site productivity as a mediator of these herbivore**  
163 **impacts is equivocal. Here, we synthesize data from 252 large-herbivore exclusion studies,**  
164 **spanning a 20-fold range in site productivity, to test an alternative hypothesis - that**  
165 **herbivore-induced changes in the competitive environment determine the response of plant**  
166 **biodiversity to herbivory irrespective of productivity. Under this hypothesis, when**  
167 **herbivores reduce the abundance (biomass, cover) of dominant species (e.g., because the**  
168 **dominant plant is palatable), additional resources become available to support new species,**  
169 **thereby increasing biodiversity. By contrast, if herbivores promote high dominance by**  
170 **increasing the abundance of herbivory-resistant, unpalatable species, then resource**  
171 **availability for other species decreases reducing biodiversity. We show that herbivore-**  
172 **induced change in dominance, independent of site productivity or precipitation (a proxy**  
173 **for productivity), is the best predictor of herbivore effects on biodiversity in grassland and**  
174 **savanna sites. Given that most herbaceous ecosystems are dominated by one or a few**  
175 **species, altering the competitive environment via herbivores or by other means may be an**  
176 **effective strategy for conserving biodiversity in grasslands and savannas globally.**

177

178 Consumers play a critical role in determining the structure and functioning of most ecosystems<sup>1</sup>.  
179 However, human activities have greatly altered top-down control by consumers with  
180 consequences for biodiversity and other ecosystem services not yet fully understood<sup>1</sup>. In part,

181 this uncertainty arises because effects of consumers on biodiversity are highly variable in both  
182 aquatic and terrestrial ecosystems<sup>2-7</sup>. One theory predicts that the effects of herbivores on  
183 biodiversity (species richness, the number of species) vary with ecosystem productivity<sup>2,4,5,7-10</sup>.  
184 In more productive systems, herbivory is expected to reduce the abundance of dominant species  
185 and increase biodiversity<sup>7</sup>. Dominant species often impact community structure<sup>11</sup>, including  
186 species biodiversity, by monopolizing resources. Decreased dominance can be directly linked to  
187 increased availability of resources, including light, nutrients and water, leading to increased  
188 abundance of less common species, colonization by new species, and/or a decrease in local  
189 species extinctions<sup>7</sup>. In contrast, at low productivity, herbivores are predicted to decrease  
190 biodiversity by either 1) increasing dominance by grazing-tolerant species, which may reduce  
191 colonization rates or enhance extinctions of other species, or 2) not affecting dominance if  
192 species are unpalatable, but instead increasing extinctions of rare palatable species via  
193 consumption<sup>7</sup>. Collectively, these processes may result in a positive relationship between  
194 biodiversity and productivity with herbivory. However, deviations from this pattern are common,  
195 particularly in herbaceous plant communities (e.g.,<sup>7,12-14</sup>). These discrepancies call into question  
196 the generality of productivity as a mediator of herbivore effects on biodiversity via the  
197 dominance mechanism. Indeed, high levels of plant community dominance are found in both  
198 high<sup>15</sup> and low<sup>16</sup> productivity systems, which suggests that changes in dominance may impact  
199 biodiversity directly and *irrespective* of productivity.

200

201 Here, we test for how changes in dominance determine biodiversity responses to herbivory, and  
202 whether this dominance mechanism is mediated by site productivity. We synthesized data from  
203 252 grassland and savanna sites (Fig. 1; Supplementary Table 1-3) that includes 1,212 plots

204 sampled inside and outside of large-herbivore exclosures. These sites encompassed a broad range  
205 of environmental conditions across six biogeographic realms<sup>17</sup>. This dataset included measures  
206 of plant community composition from all sites and aboveground net primary productivity  
207 (ANPP) from half the sites, as well as a number of herbivore community and site characteristics  
208 (see Methods). To quantify herbivore-induced changes in biodiversity, we calculated the log  
209 response ratio ( $\ln(G/UG)$ ) of plant species richness (average number of species per plot) outside  
210 (grazed, G) vs. inside (ungrazed, UG) exclosures. We used two common dominance metrics –  
211 Berger-Parker Dominance and Simpson’s Dominance<sup>18</sup> – to evaluate changes in dominance with  
212 herbivory. Change of both metrics was calculated using log response ratios. We picked these two  
213 measures of dominance as both are robust to changes in richness at levels encompassed by our  
214 datasets ( $>5$ ; <sup>18,19</sup>), and thus can vary independently of richness. Berger-Parker Dominance is a  
215 measure of the relative cover of the most abundant species agnostic of species identity, while  
216 Simpson’s Dominance is a measure of diversity that is highly sensitive to abundant species<sup>20</sup>. We  
217 chose to focus on the Berger-Parker metric due to its simplicity and its mathematical  
218 independence from richness. However, Simpson’s Dominance, while more complicated, is a  
219 metric that can capture co-dominance by two or more species<sup>18</sup>. The inclusion of the Simpson’s  
220 Dominance metric in our analyses (see Supplementary Information) allowed us to examine the  
221 robustness of the patterns observed with the Berger-Parker dominance metric.

222

## 223 **Results**

224 Consistent with previous theory and several empirical studies<sup>2,8,9,13</sup>, we found a positive  
225 relationship between changes in species richness in response to herbivores and ANPP, but the  
226 amount of variation explained was low (Fig. 2a). Contrary to theory, herbivory did not decrease

227 species richness at low productivity. Instead, herbivory had, on average, either neutral or positive  
228 effects on richness across the entire 20-fold range in ANPP. Because not all studies in our dataset  
229 measured ANPP, we used mean annual precipitation (MAP) as an ANPP proxy. This was  
230 possible due to the relationship between MAP and ANPP in our dataset (linear regression:  
231  $R^2=0.21$ ,  $p < 0.001$ ,  $F\text{-stat}_{106} = 27.63$ ) as well as in grasslands and savannas globally<sup>20,21</sup>. Even  
232 with this expanded dataset, richness responses were poorly related to MAP (Fig. 2b), consistent  
233 with the weak relationship observed for ANPP.

234

235 In contrast to the equivocal support for productivity influencing richness responses, we found a  
236 strong negative relationship between herbivore-induced changes in Berger-Parker dominance  
237 and the effect of herbivores on species richness (Fig. 2c). As predicted, when herbivores  
238 decreased dominance thereby reducing competition, species richness increased, but when  
239 herbivores increased dominance, thereby increasing the strength of competition, richness  
240 declined. Negative relationships between species richness and dominance are common (e.g.,  
241 <sup>11,12,22</sup>), and this relationship was evident in both grazed and ungrazed plots in our data set as well  
242 (Fig. 2d). These patterns were even stronger when using Simpson's Dominance (Supplementary  
243 Figure 2;  $r^2=0.192$  for BP Dominance and  $r^2=0.299$  for S Dominance) suggesting that changes in  
244 co-dominance may be important in many of these grazing systems. Given this relationship and  
245 because we used measures of dominance that are mathematically independent of richness<sup>18</sup>, this  
246 suggests that changes in dominance can be causally linked to biodiversity responses to herbivory.  
247 Changes in Berger-Parker Dominance in response to grazing were not significantly related to  
248 either ANPP (Supplementary Figure 1a) or precipitation (Supplementary Figure 1b), suggesting

249 this pattern is independent of site productivity. Similarly, changes in Simpson's Dominance due  
250 to grazing were also not significantly related to ANPP or precipitation (Supplementary Figure 3).

251  
252 Although univariate approaches can be informative, both productivity and change in dominance  
253 could jointly influence the biodiversity response to herbivory. Therefore, we utilized path  
254 analysis<sup>23</sup> to assess whether productivity mediates the effect of change in dominance on the  
255 richness responses to herbivory. Our *a priori* model included additional non-mutually exclusive  
256 factors that could influence the relationship between herbivory and species richness<sup>7</sup>, such as  
257 characteristics of the herbivore community (estimates of herbivore pressure, herbivore species  
258 richness, if herbivores were domesticated or not, and if browsers/mixed feeders were present in  
259 addition to grazers), the plant community (size of the species pool), and the duration of herbivore  
260 exclusion. See Methods for further detail. These metrics allowed us to explicitly contrast the  
261 effects of site-level productivity vs. change in dominance on the richness response to herbivory  
262 and include other factors that may affect both dominance and richness responses. We examined  
263 six alternative models (Fig. 3 & Supplementary Figure 4) to explicitly contrast the effects of  
264 changes in ANPP vs. dominance on the biodiversity response to grazing.

265  
266 Our first model examined the widely-hypothesized relationship between precipitation, site  
267 productivity, and change in species richness (Fig. 3 – Model 1). This model also included  
268 characteristics of the herbivore community and the plant community (site-level richness) as well  
269 as accounted for correlations between input variables (Supplementary Table 4). Because  
270 productivity was not available from all sites, this initial model was limited to data from the 122  
271 sites where ANPP was measured directly (see Methods; Data Subset 1 in Supplementary Table

272 3). As expected, precipitation was strongly related to productivity in this data set (Fig. 3 – Model  
273 1), and consistent with our univariate analysis, we found a significant positive effect of site  
274 productivity on change in species richness. Grazing had neutral to mildly positive effects on  
275 richness at low productivity and a stronger positive effect at higher productivity. In addition, we  
276 found that grazing pressure negatively influenced the richness response, but to a lesser extent  
277 than productivity. Thus, at high grazing pressure, herbivores decreased richness irrespective of  
278 site productivity. Site-level species richness also affected how richness responded to herbivory.  
279 As site richness increased, herbivores had less of an effect on changes in species richness  
280 regardless of site productivity. Overall, this model explained 13% of variation in the richness  
281 response to herbivory.

282

283 In a second model (Fig. 3 – Model 2a) we added an estimate of site-level Berger-Parker  
284 dominance in the absence of grazing (averaged across all ungrazed plots at a site [ $U_{dom}$ ]), as well  
285 as the change in dominance in response to grazing ( $\ln(G_{dom}/U_{dom})$ ) to assess the relative effects of  
286 productivity vs. dominance on the richness response to herbivory (correlations between all input  
287 variables can be found in Supplementary Table 5). While site productivity was weakly correlated  
288 with changes in richness (Fig. 3 – Model 2a), both site-level dominance and the change in  
289 dominance were significantly and more strongly correlated with the richness response to grazing.  
290 That is, as site dominance increased, grazing had a stronger positive effect on species richness.  
291 Consistent with this relationship, the change in dominance due to herbivores was strongly related  
292 to changes in species richness. Thus, when grazing reduced dominance there was a strong  
293 increase in species richness. Similar to the previous model, grazing pressure remained  
294 significantly correlated with the change in species richness. In this model, other factors related to

295 the herbivore community were also significant (i.e., domestication and feeding guild), but their  
296 effects on change in richness were indirect via change in dominance. Also, site-level total species  
297 richness no longer directly or indirectly influenced change in species richness. Overall, inclusion  
298 of Berger-Parker dominance doubled the explanatory power of the change in species richness  
299 when compared to the model that only included productivity ( $R^2=0.31$  vs.  $0.13$ ). When this  
300 second model included Simpson's Dominance instead of Berger Parker Dominance  
301 (Supplementary Figure 4a – Model 2b; Supplementary Table 6) explanatory power of the change  
302 in species richness increased ( $R^2=0.39$ ), providing robust support for change in dominance as  
303 key to explaining changes in richness with herbivory. Additionally, ANPP no longer has any  
304 effect on change in richness from herbivory when Simpson's Dominance was included in the  
305 model.

306  
307 Models 1, 2a, and 2b (Supplementary Information) were limited to the 122 sites that had  
308 productivity measurements. Because productivity is strongly correlated with MAP both in our  
309 data set (Fig. 3, Model 1 & 2) as well as more broadly<sup>20</sup>, we used precipitation as a proxy for  
310 productivity in Model 3 & 4a and 4b (Supplementary Information). This allowed us to include  
311 244 sites in the analysis (Data Subset 3 in Supplementary Table 3). In Model 3, we examined the  
312 relationship between precipitation and change in species richness without dominance (similar to  
313 Model 1 but utilizing a larger dataset) as well as accounted for correlations between input  
314 variables (Supplementary Table 7). Like with the ANPP dataset, Model 3 was only able to  
315 explain 11% of the variation in change in richness and there was no effect of precipitation in this  
316 model. When Berger-Parker dominance was included in the model (Model 4a; Supplementary  
317 Table 8), our explanatory power of change in richness more than doubled ( $R^2=0.11$  vs.  $0.26$ ), and

318 when Simpson's Dominance was included (Supplementary Figure 4b: Model 4b; Supplementary  
319 Table 9) our explanatory power of change in richness more than tripled ( $R^2=0.11$  vs.  $0.36$ ).  
320 Similar to Model 2, we again found that site-level Berger-Parker dominance and change in  
321 Berger-Parker dominance with herbivores were the main drivers of herbivory-induced changes in  
322 species richness ( $R^2=0.26$ ). Precipitation, however, as a surrogate for productivity, had no  
323 significant effect in the model. Importantly, incorporating the larger dataset in Model 4a and  
324 Model 4b demonstrated that herbivore-driven changes in dominance exert stronger effects on  
325 richness change than site level dominance *per se* (standardized partial effect sizes of  $-0.35$  vs. not  
326 significant, respectively). These models also identified a strong, negative relationship between  
327 site-level dominance and change in dominance (standardized partial effect size of  $-0.54$  and -  
328  $0.58$ ). This occurred because change in dominance is expressed as a ratio of grazed to ungrazed  
329 dominance and indicates that grazers reduce dominance more in sites with higher dominance.  
330 With this more comprehensive data set, we identified additional factors with direct and indirect  
331 effects on richness response to herbivory. For example, grazers alone had a stronger impact on  
332 changes in species richness than when grazers and browsers were both present (standardized  
333 partial effect size for Herbivore Guild of  $-0.26$  and  $-0.023$ ). This pattern suggests that grazers  
334 target dominant grasses that then outcompete subordinate species when released from herbivory.  
335 But, grazers and browsers may have less of a net effect on species richness due to compensatory  
336 feeding, supporting theory<sup>7</sup> and patterns from previous experiments<sup>12,24,25</sup>. Overall, the more  
337 data-rich models confirm the role of dominance in controlling the richness response to herbivory  
338 rather than productivity.

339



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

354

355 Assessing the role of palatability in determining dominance responses to herbivory was not  
356 possible with our empirical analysis due to a lack of trait data for the whole suite of plant  
357 species. However, we incorporated palatability into a stochastic community assembly model to  
358 simulate the effect of herbivory on Berger-Parker dominance and richness independent of  
359 productivity. This model considered community assembly, as well as dominance and richness  
360 responses following grazing, as random processes (see Methods for details). Change in  
361 dominance was calculated using relative cover of the dominant species. In the model, changes in  
362 dominance and species richness can occur via competitor release, local extinction and new

363 species arrivals. We assessed three scenarios with the model: 1) all dominant species are  
364 palatable, *i.e.*, grazed (Fig. 4a), 2) all dominant species are unpalatable (Fig. 4b), and 3)  
365 communities have a random chance of being dominated by either a palatable or unpalatable  
366 species (Fig. 4c). We found that when all simulated communities were dominated by palatable  
367 species (Fig. 4a) or when communities were dominated by either a palatable or unpalatable  
368 species (Fig. 4c), the resulting ensembles of 1000 simulations generated richness and dominance  
369 responses to herbivory that were remarkably similar to empirical observations (Fig. 2c). In  
370 contrast, if the dominant species was unpalatable (leaving only less common species to be  
371 grazed), there were few instances where richness increased while dominance decreased (*i.e.*, few  
372 points in the upper left-hand quadrant of Fig 4b). These simulations are consistent with the  
373 biodiversity response to herbivory depending primarily on palatability of and subsequent  
374 response of the dominant species, irrespective of productivity.

375

## 376 **Discussion**

377 Our findings extend theory<sup>2,5,7,22,29</sup> by identifying *change in community dominance*, and thus the  
378 competitive landscape, as the primary and generalizable mechanism underlying biodiversity  
379 response to herbivory. Change in dominance explains herbivore impacts on biodiversity – both  
380 positive and negative – globally across grasslands and savannas with 20-fold differences in  
381 productivity and vastly different biogeographic and evolutionary histories. This dominance  
382 mechanism is consistent with the light availability mechanism identified by Borer *et al.* <sup>5</sup>,  
383 because increases in dominance can increase light limitation<sup>30</sup>. But dominance also changes with  
384 herbivory in sites where light is not limiting<sup>27</sup>. Thus, the dominance mechanism applies to a  
385 wider range of ecosystems, reflecting competitive interactions for the availability of either

386 above- or below-ground resources<sup>7</sup>. This dominance mechanism is also consistent with the  
387 evolutionary history mechanism identified by Milchunas and colleagues<sup>13,31</sup> as dominance and  
388 the traits of the dominant species, particularly those related to palatability, are determined by a  
389 site's evolutionary history. Strong community dominance by just a few species is a nearly  
390 universal feature of ecosystems<sup>15,22,29</sup>, and dominant species are known to control most  
391 ecosystem processes<sup>22,32</sup>. As a consequence, our results point to “dominance management” as an  
392 effective strategy for conserving species biodiversity and ecosystem functioning in grasslands  
393 and savannas globally.

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483

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485 collecting and analyzing the data, developing the figures, and writing the manuscript. MDS  
486 conceptualized the questions and wrote the manuscript. DEB conceptualized the questions,  
487 collected the data, and wrote the manuscript. NPH performed simulations and wrote the  
488 manuscript. MLA & NPL executed the path analyses and developed figures. SLC & AKK wrote  
489 the manuscript. SE, EJJ, DIT contributed to data collection and management. All authors who  
490 were not members from the Grazing Exclusion Working Group contributed data to the synthesis,  
491 and all authors (both members of the working group and not) edited the manuscript. See author  
492 contribution table (Supplementary Table 11) for complete list of contributions.

493

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497 materials should be addressed to SEK.

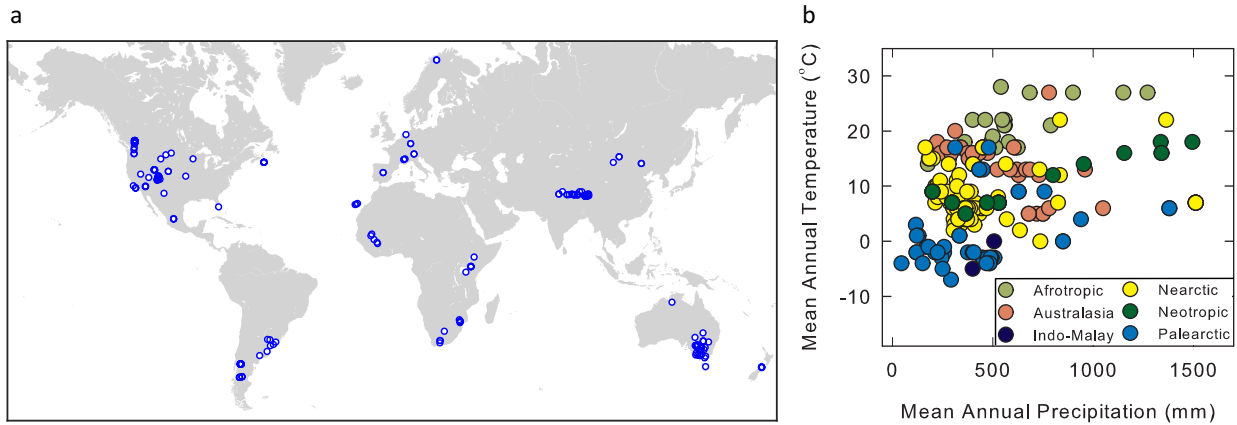
498

499 **Competing Interests** The authors declare no competing financial interests.

500

501 **Data Availability** While raw species abundances are not publicly available due to lack of  
502 permission from data owners (contact individual dataset owners listed in Supplementary Table  
503 1), all data generated and analyzed during the current study (site level richness response to  
504 herbivory, site level Berger-Parker and Simpson's dominance response to herbivory, site ANPP,  
505 and site MAP) are provided in Supplementary Table 2.  
506

507 **Figure Legends**



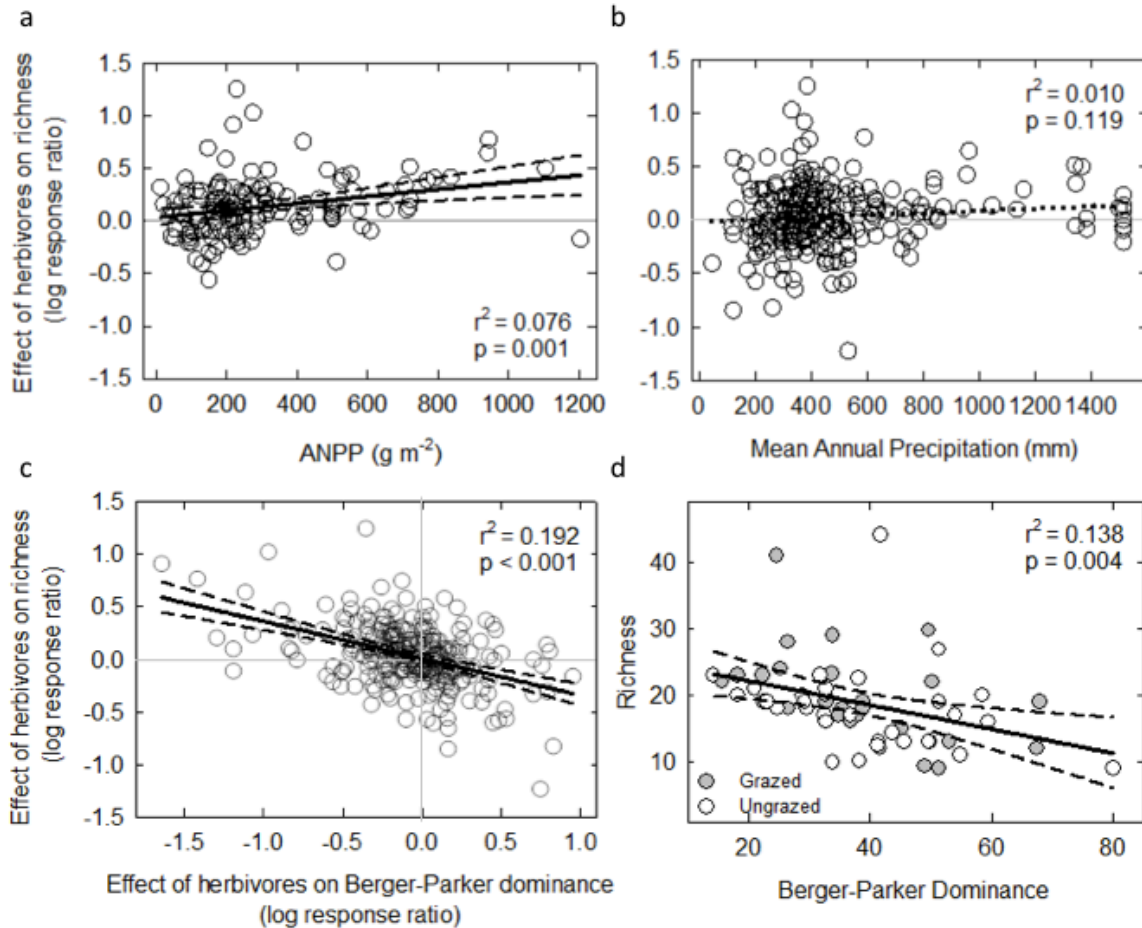
508

509 Figure 1. Location and climate of sites. **a**, Locations of the 252 grassland and savanna  
510 ecosystems where 1,212 grazed and ungrazed plots were located. All sites are represented by a  
511 single sized open blue circle. Areas where symbols overlap appear to be darker blue. **b**, These  
512 study sites represent six biogeographic realms and encompass broad gradients of mean annual  
513 temperature and precipitation. Additional site details are provided in Supplementary Tables 1 &  
514 2.

515

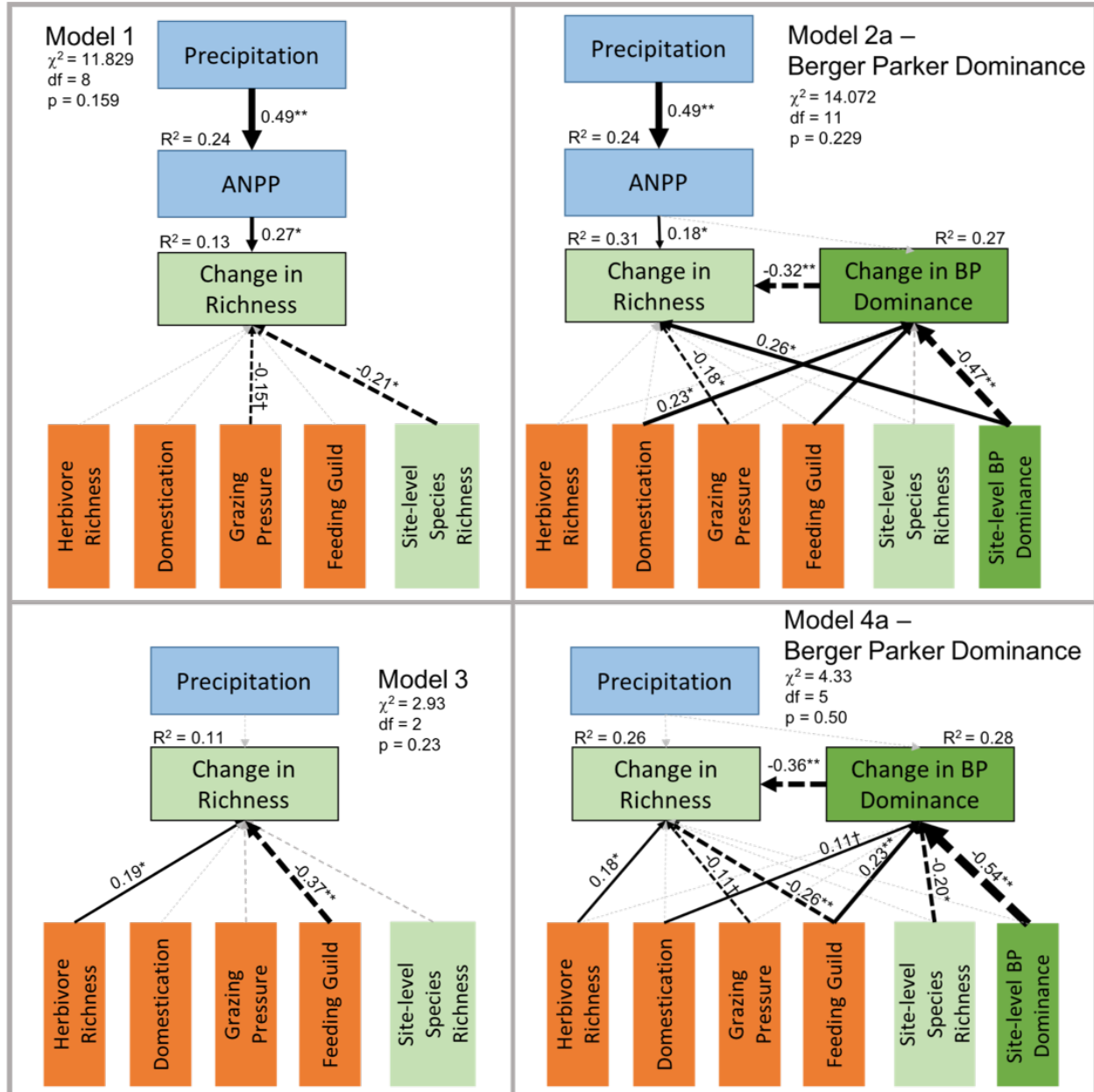
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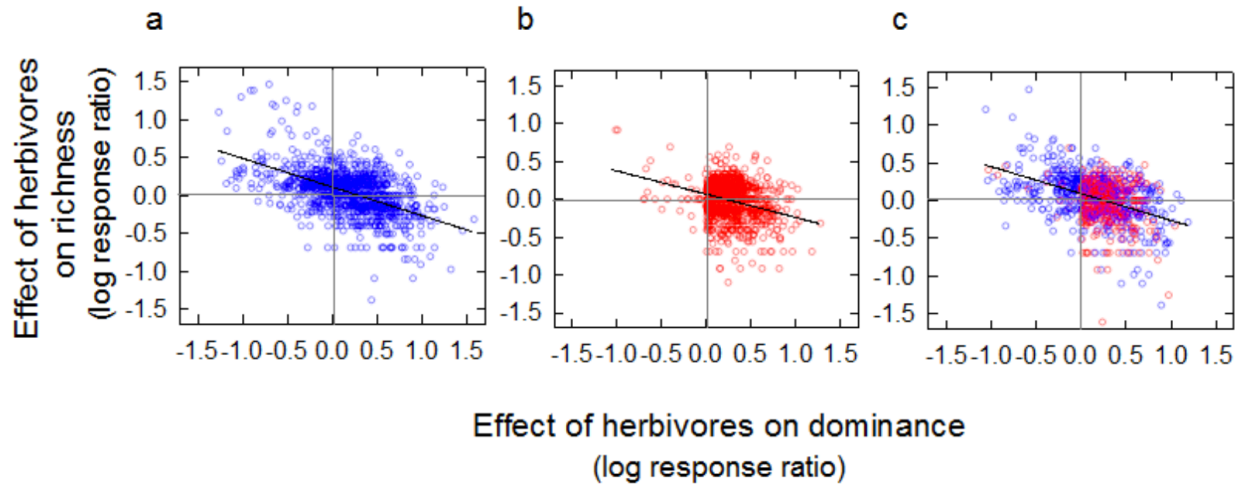
518 Figure 2. Herbivore effects on plant communities. **a**, Relationship between aboveground net  
 519 primary production (ANPP) and the response of plant species richness to herbivory ( $\ln(G/UG)$ ),  
 520 where G is the average plant species richness in grazed plots and UG is the same measurement in  
 521 ungrazed plots ( $n=132$ ; Data Subset 1 in Supplementary Table 3). **b**, Relationship between mean  
 522 annual precipitation and the response of plant species richness to herbivory ( $n=244$ ; Data Subset  
 523 2 in Supplementary Table 3). **c**, Relationship between the change in dominance (Berger-Parker  
 524 Dominance) and the change in species richness as a function of herbivory ( $\ln(G/UG)$ ) ( $n=252$ ; all  
 525 data). **d**, Relationship between dominance (Berger-Parker Dominance) and species richness for  
 526 grazed and ungrazed plots combined. This analysis is based only on studies with a common plot  
 527 size of 25 m<sup>2</sup> ( $n=58$ ). Dashed lines represent 95% confidence intervals.



529

530 Figure 3. Drivers of plant richness response to herbivory. **a, b** Path analyses testing the  
 531 importance of aboveground net primary productivity (ANPP, Model 1) and Berger-Parker  
 532 dominance (Model 2a) on the change in species richness in response to herbivory. These models  
 533 are restricted to sites where both ANPP and precipitation data were available ( $n=122$ ; Data  
 534 Subset 3 in Supplementary Table 3). See Supplementary Tables 4 & 5 for bivariate correlations

535 between input variables which were included in these models to improve model fit. **c,d** Path  
536 analyses testing the importance of productivity using precipitation as a proxy (Model 3) for  
537 productivity and Berger-Parker dominance (Model 4a) on the change in species richness in  
538 response to herbivory. These models use precipitation as a surrogate for ANPP allowing the use  
539 of more data (n=244; Data Subset 2 in Supplementary Table 3) . See Supplementary Table 7 & 8  
540 for bivariate correlations between input variables which were included in these models to  
541 improve model fit. All models also test for the effects of site and herbivore characteristics (see  
542 Methods). \*\*p<0.001, \*p<0.05, †p<0.10. Non-significant relationships are shown in light gray  
543 dashed arrows, solid black arrows represent positive relationships and dashed black arrows  
544 represent negative relationships. Shown are standardized effect sizes, with arrow thickness  
545 proportional to the strength of the relationship. All models were a good fit to the data based on  
546 the  $\chi^2$  statistic (p>0.05 is good). See Supplementary Table 10 for additional model fit parameters  
547 for all four models.  
548



549

550 Figure 4. Simulation of plant community assembly in response to herbivory with three scenarios  
 551 of palatability of the dominant species. a) In the first scenario, each assembled community has a  
 552 dominant species that is grazed (blue), and all subordinate species have a 50% probability of  
 553 being a grazed species. b) In the second scenario, each assembled community has a dominant  
 554 species that is not grazed (red), and all subordinate species have a 50% probability of being a  
 555 grazed species. c) In the third scenario, in each assembled community all plant species have 50%  
 556 probability of being a grazed species including the dominant species. Blue dots represent  
 557 communities that have a dominant species that is grazed. Red dots represent assembled  
 558 communities in which the dominant species was ungrazed. All scenarios treat community  
 559 assembly and dominance and richness responses following grazing as random processes (see  
 560 details in methods).

561

562 **METHODS**

563 **Data.** We compiled a database (Grazing Exclusion Database = GEx) consisting of plant  
564 community composition data from 252 large vertebrate herbivore exclusion sites (Supplementary  
565 Tables 1 & 2). To be included in GEx, sites had to meet five criteria. (1) Exlosures had to be  
566 located in herbaceous-dominated communities - sites ranged from tallgrass prairie to alpine  
567 meadows to desert, but all are dominated or co-dominated by herbaceous species. (2) Large  
568 vertebrate herbivores (adult body mass >45 kg) had to be excluded from plots using fencing with  
569 adjacent plots exposed to herbivores. Herbivore type and number varies among the sites,  
570 including domesticated cattle, sheep, goats, burros, and horses, as well as native wildlife such as  
571 caribou, kangaroo, and the full complement of large African herbivores. The inside of the  
572 enclosure could not be manipulated or managed other than the removal of herbivore (*i.e.*, no  
573 mowing or burning that did not also occur outside the enclosure). (3) Data had to be collected  
574 after at least three years of exclusion of large herbivores. This was to ensure sufficient time for  
575 the plant community to respond to the absence of herbivores. (4) Paired plots inside and outside  
576 the enclosure had to be sampled at the same time and sampling intensity. (5) Community data  
577 had to be available at the species level. Data types include cover, line intercept, biomass, and pin  
578 hits (but not frequency or density), all of which were converted to relative abundance values.

579

580 **Explanatory Variables.** Several covariates were used in the analyses which described plant,  
581 experiment, and herbivore community characteristics. Site primary productivity was based on  
582 ungrazed vegetation, as reported by individual investigators for a subset of the sites ( $n=132$ ).  
583 Individual investigators supplied precipitation data, while mean annual temperature (MAT) was  
584 based on WorldClim<sup>33</sup>. Site-level richness and dominance were calculated using the species

585 composition data. Site richness was calculated as the total number of plant species found across  
586 all plots. Site dominance was calculated as the mean dominance across all ungrazed plots using  
587 Berger-Parker Dominance, which is the relative abundance of the most abundant species in the  
588 plot. Four variables were used to describe the herbivore community. Investigators provided an  
589 assessment of herbivory pressure (low, moderate, high) and species of large herbivores excluded.  
590 We converted herbivore species information into three variables: herbivore richness, feeding  
591 guild, and domestication. Herbivore richness is the number of large herbivore species excluded  
592 by the fences. Predominantly, these exclosures excluded grazers (feeding guild = 0), and when  
593 browsers or mixed feeders were present either in combination with grazers or alone (feeding  
594 guild = 1), we hypothesized this would have different effects on the herbaceous community.  
595 Domestication refers to human involvement with herbivore species presence and abundance.  
596 Native herbivores (wildlife) were coded as domestication = 0, while domesticated herbivores  
597 (e.g., cattle) or the combination of the two were coded as domestication = 1 as they were  
598 hypothesized to have different effects than native herbivores alone. Experiment length was the  
599 number of years post exclosure construction; this variable was included in many exploratory  
600 analyses but was never significant and often led to poor model fit to the data. Exclosure age was  
601 not significantly correlated with either change in richness or change in dominance. Therefore,  
602 exclosure age was dropped from all path analyses.

603         Although many sites provided multiple years of data, here we present only the most recent  
604 year of data collected from each site. For analyses involving ANPP, a subset of sites was used  
605 ( $n=132$ ; Data Subset 1 in Supplementary Table 3), while nearly all sites were included in  
606 analyses using only precipitation ( $n=244$ ; 8 sites were strategically placed in topographic  
607 locations that were either wetter or drier than expected based on precipitation and were therefore

608 only used in the ANPP analysis but not the precipitation analyses; Data Subset 2 in  
609 Supplementary Table 3). Likewise, when models included both ANPP and precipitation a subset  
610 was used ( $n=122$ ; Data Subset 3 in Supplementary Table 3). When models did not include either  
611 ANPP or precipitation as predictors, we used all sites in the database ( $n=252$ ).

612

613 **Response Variables.** The majority of sites had a single exclosure ( $n=132$ ). When more than one  
614 exclosure was built in the same year, each exclosure and corresponding paired plot was  
615 considered a block. When multiple subplots were sampled within each exclosure or paired plot,  
616 species abundance was summed for each species across the subplots, to obtain species data at the  
617 plot level (i.e., 1 plot per block). Plant community richness and dominance were calculated at the  
618 plot level for inside and outside the exclosure. Plant community richness was calculated as the  
619 number of species in the plot in that year. Dominance was quantified in two ways. Berger-Parker  
620 Dominance (BP Dominance) was calculated as the maximum relative abundance of the most  
621 abundant species in each plot. Simpson's Dominance was calculated as

622 
$$D_{Simp} = \sum_{s=1}^S p_s^2$$

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

629

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

635 To determine the relative importance of various proposed explanatory variables on the  
636 richness response to herbivory (log response ratio), we used path analysis conducted in AMOS  
637 v7 (SPSS, Chicago, IL, USA). We contrasted the effects of site-level productivity vs. dominance  
638 on species-richness response to herbivory utilizing two alternative models. All models also  
639 included hypothesized influential covariates such as characteristics of the herbivore community,  
640 the plant community, and experimental duration. Data were screened for distributional properties  
641 and nonlinear relations. Site-level plant richness and herbivore richness were log-transformed as  
642 a result of these evaluations. While site level dominance and richness theoretically could be  
643 driven by precipitation, the correlations between site-level richness and precipitation (Pearson  
644 correlation coefficient = 0.357; linear regression  $R^2 = .126$ ) and between site-level Berger-Parker  
645 dominance and precipitation (Pearson Correlation Coefficient = -0.246; linear regression  $R^2 =$   
646  $.06$ ) within our dataset were low. Therefore, these relationships were dropped from the path  
647 analysis due to replication constraints. Model 1 examined the widely hypothesized relationship  
648 between precipitation, ANPP, and change in species richness (Fig. 3a). Because ANPP was not  
649 available from all sites, this model used data from 122 of the 252 sites where ANPP was  
650 measured and precipitation was a good proxy for ANPP. Model 2a (Fig. 3b) used the same data  
651 as Model 1 but included an estimate of site level Berger-Parker dominance in the absence of  
652 grazing ( $U_{dom}$ ), as well as the change in Berger-Parker dominance in response to grazing



653  $(\ln(G_{\text{dom}}/U_{\text{dom}}))$  to assess the relative effects of ANPP vs. Berger-Parker dominance on richness  
654 response to herbivory. Model 2b - Simpson's (Supplementary Figure 4a) was the same as Model  
655 2a but included an estimate of site level Simpson's dominance in the absence of grazing  
656  $(U_{\text{SimpDom}})$ , as well as the change in Simpson's dominance in response to grazing  
657  $(\ln(G_{\text{SimpDom}}/U_{\text{SimpDom}}))$  to assess the relative effects of ANPP vs. Simpson's dominance on  
658 richness response to herbivory. Because ANPP is strongly correlated with MAP both in our data  
659 set (Fig. 3A & B) as well as more broadly<sup>20</sup>, we used precipitation as a proxy for ANPP,  
660 allowing us to run similar models again but including 244 sites in the analysis (Model 3 & 4a and  
661 4b). Several input variables were correlated (based on AMOS recommendations for correlated  
662 variables that improve model fit), therefore, included as such in the models (Supplementary  
663 Table 4-9). All models were a good fit to the data, according the  $X^2$  statistic with  $P > 0.05$  as well  
664 as other measures of goodness of fit (see Supplementary Table 10).

665  
666 **Null Model Simulation.** To explore possible mechanisms for observed herbaceous community  
667 responses to herbivory, we created a simple community assembly and grazing response model in  
668 which idealized plant communities first assemble stochastically, with each new species assigned  
669 a canopy cover drawn from a negative binomial distribution (mean cover,  $\mu = 15\%$ ; dispersion  
670  $= 1.0$ ) until the collective canopy cover = 100% of available space, after which time no further  
671 species can be added. The grazing process is then simulated with (i) species in the community  
672 assigned as "palatable" or "unpalatable" using a random binomial process ( $P=0.5$ ), and (ii)  
673 reduction in cover of palatable species simulated as a random-uniform process where  $\sim 50\%$  of  
674 palatable species are excluded by grazing (i.e. cover reduced to 0%), and the cover of the  
675 remaining palatable species is reduced by 50-99% of their original extent. The community

676 response to the resources made available through grazing-induced loss in plant cover is then  
677 simulated via the effect of two mechanisms: (i) competitive release of ungrazed species (“growth  
678 response”) and (ii) establishment of novel species (i.e. species assumed to have been absent in  
679 the ungrazed community, but available in the regional species pool; “immigration response”).  
680 The growth and immigration responses are simulated alternately until the resulting community  
681 again occupies all available space, with each ungrazed species increasing its cover in proportion  
682 to the grazing-induced loss in total cover in the plot, and new immigrants arriving via the  
683 negative binomial stochastic process used in the original community assembly.