

## 1 HERBIVORES AND NUTRIENTS CONTROL GRASSLAND PLANT DIVERSITY VIA LIGHT LIMITATION

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47 biodiversity

48 **Human alterations to nutrient cycles<sup>1,2</sup> and herbivore communities<sup>3-7</sup> are dramatically altering global**  
49 **biodiversity<sup>2</sup>. Theory predicts these changes to be strongly counteractive: nutrient addition drives**  
50 **plant species loss through intensified competition for light, whereas herbivores prevent competitive**  
51 **exclusion by increasing ground-level light, especially in productive systems<sup>8,9</sup>. Using experimental**  
52 **data spanning a globally-relevant range of conditions, we test the generality of the hypothesis that**  
53 **herbaceous plant species losses caused by eutrophication may be offset by increased light availability**  
54 **due to herbivory. Our multi-year experiment replicated in 40 grasslands on six continents**  
55 **demonstrates that nutrients and herbivores can serve as counteracting forces controlling local plant**  
56 **diversity via light limitation, independent of site productivity, soils, herbivore type, and climate.**  
57 **Nutrient addition consistently reduced local diversity via light limitation, and herbivory rescued**  
58 **diversity at sites where it alleviated light limitation. Thus, species loss from anthropogenic**  
59 **eutrophication can be ameliorated where herbivory increases ground-level light.**

60

61 The astounding diversity of life on Earth underlies critical ecosystem functions and economically  
62 important services<sup>10</sup>, and the current rapid rate of biodiversity loss<sup>2</sup> lends urgency to the task of  
63 understanding the forces maintaining biodiversity. Resources required for economic growth, energy,  
64 and agriculture have all impacted natural ecosystems on a global scale. Introductions and extirpations of  
65 herbivore species, especially as land is converted for grazing<sup>3-7</sup>, and increased nutrient supply are  
66 symptoms of humanity's global footprint<sup>1,2</sup>. Such widespread alteration of herbivores and nutrient  
67 supply may jointly determine the future diversity of ecosystems. For example, in highly productive,  
68 eutrophic systems where plant species extinction is likely due to a loss of ecological niches<sup>8</sup>, ecological  
69 theory predicts that herbivores can act to maintain local-scale plant diversity if they selectively consume  
70 the superior resource competitors<sup>9</sup>. Empirical studies in many ecosystem types find highly variable

71 effects of herbivores on plant species diversity<sup>11-13</sup>, with the magnitude of herbivore mediation of  
72 diversity frequently observed to be greatest in regions of high ecosystem productivity<sup>11-17</sup>. Thus,  
73 ecosystem productivity and its regional climate drivers have been observed to mediate the local-scale  
74 effects of herbivores on plant diversity. The availability of ground-level light is the commonly postulated  
75 mechanism modulating the relationships among plant diversity, herbivory, and observed gradients of  
76 plant productivity. However, these patterns and predictions have primarily emerged from studies across  
77 observed gradients of productivity or reviews and meta-analyses based on an extremely limited number  
78 of single-site experiments that manipulate both nutrients and herbivory, often with different methods  
79<sup>11-15,17</sup>. In most of these studies, ground-level light has not been measured. Thus, the generality of  
80 these effects is only suggestive, and the mechanisms underlying the observed relationships remain  
81 elusive.

82 Local-scale plant diversity is likely maintained via an interdependent system of interactions with multiple  
83 plant species sharing herbivores and competing for light and nutrients. In particular, terrestrial plants  
84 compete for nutrients and light at the scale of interactions among individuals (~1m<sup>2</sup> neighborhood in  
85 grasslands), and one important mechanism for maintaining local coexistence is a tradeoff in competitive  
86 ability for nutrients (belowground) and for carbon via light (aboveground)<sup>18-22</sup>. Nutrient enrichment can  
87 lead to competitive exclusion of inferior competitors for light<sup>19,20</sup>, but herbivores can remove plant  
88 biomass, potentially alleviating understory light limitation. However, herbivory creates another axis of  
89 potential tradeoffs among plant species, involving investment in rapid growth and light capture vs.  
90 investment in defense against herbivory<sup>23-26</sup>. These interactions result in a dynamic local community,  
91 where composition responds quickly to changes in the strength of nutrient limitation or herbivory<sup>25,26</sup>.  
92 In eutrophied systems, where nutrient limitation is alleviated and productivity is increased, theory  
93 predicts that these tradeoffs among plant strategies will simplify the plant community to species sharing  
94 an herbivore and competing for a single resource – light<sup>9,19</sup>.

95 Using data from a multi-year experiment, replicated at 40 sites on six continents (Fig. 1), we tested the  
96 hypothesis that herbivores mediate species losses caused by nutrient addition by increasing ground-  
97 level light, especially in eutrophic and highly productive systems. To test this hypothesis, we  
98 manipulated herbivores and nutrients using a factorial experiment (nutrient addition  $\times$  exclusion of  
99 herbivores  $>50$  g, details in Methods section and Borer *et al.* <sup>27</sup>) replicated in 40 herbaceous-dominated  
100 sites spanning broad environmental gradients of productivity (114 to 1,976 g m<sup>-2</sup> yr<sup>-1</sup>), precipitation  
101 (mean annual precipitation from 224 to 1,898 mm yr<sup>-1</sup>), temperature (mean annual temperature from 0  
102 to 22.1<sup>o</sup> C), and soil nitrogen (mean soil %N from 0.018 to 1.182%)(Fig. 1, Extended Data Table 1). In  
103 each plot, we measured local-scale responses of productivity, light, and the number of plant species  
104 (diversity) using standard methods <sup>27</sup>. We also examined site-level covariates including precipitation,  
105 temperature, herbivory intensity, soil nitrogen, and atmospheric nitrogen deposition rates. Although  
106 most sites provided three years of data, a subset of sites contributed four years of post-treatment data,  
107 and a few sites, established later, provided only one or two years of data (Extended Data Table 1).  
108 Effects of the experimental treatments were broadly consistent across all years of treatments (Extended  
109 Data Figure 1); we present results from the three year duration in the main text, for a balance of spatial  
110 and temporal extent (see Extended Data Tables 2-8 for statistical models).

111 Our results support an important mechanism by which nutrients lead to diversity loss. In particular,  
112 nutrient addition caused declines in diversity (Fig. 2a, Extended Data Table 2,  $p < 0.001$ ), increased total  
113 plant biomass (Fig. 2b, Extended Data Table 3,  $p < 0.001$ ), and increased light limitation (reduced  
114 transmission of photosynthetically active radiation (PAR) to ground level, Fig. 2c, Extended Data Table 4,  
115  $p < 0.001$ ) both inside and outside of fences. Ground level light availability, a function of light  
116 interception by live, photosynthetically active biomass and by standing dead biomass, declined with  
117 increasing total biomass (Fig. 2d, Extended Data Table 5,  $p < 0.001$ ). This result is consistent with  
118 eutrophication-induced loss of niches for coexistence <sup>8,9,19,28</sup> and demonstrates the generality of

119 eutrophication as a primary force controlling the diversity of grassland communities by reducing ground-  
120 level light<sup>20</sup>.

121 Although the removal of vertebrate herbivores did not have consistent effects on diversity (Fig. 2a,  $p =$   
122 0.522) or biomass (Fig. 2b,  $p = 0.803$ ), herbivore removal increased light limitation (Fig. 2c,  $p = 0.013$ ).

123 The lack of a consistent effect of herbivore removal on diversity across these globally distributed  
124 grassland sites (Fig. 2a) reflects the broad range of positive and negative effects found in past studies  
125<sup>11,17,29</sup>. However, a critical assumption underlying the hypothesis that grassland diversity is jointly  
126 controlled by nutrient supply and consumers is that diversity should be rescued consistently by  
127 herbivory. In both ambient and eutrophied plots, herbivory should lead to greater diversity because  
128 herbivores can alleviate ground-level light limitation, thereby increasing the number of possible  
129 tradeoffs (nutrients, light) that maintain plant species diversity<sup>9,16</sup>.

130 We tested whether the inconsistent herbivore effects on plant diversity reflected variable herbivore  
131 effects on light and found that plant diversity increased quantitatively with herbivore effects on ground-  
132 level light (Fig. 3,  $p = 0.003$ ); nutrient addition did not modify this relationship (Extended Data Figure 2).  
133 Sites with the greatest effects of herbivores on light and diversity spanned four continents and were  
134 dominated by larger vertebrates including wild and domestic ungulates, macropods, and lagomorphs  
135 (Fig. 3, Table 1). Thus, our results, across experimentally imposed nutrient supply gradients at each site  
136 and greater than a 26-fold observed productivity gradient across sites, clarify that to the extent that  
137 herbivores enhanced ground-level light, they rescued plant diversity regardless of herbivore identity or  
138 nutrient supply.

139 Herbivore effects on plant diversity were not related to variation in soil nitrogen, nitrogen deposition  
140 rates, or site productivity. The change in ground-level light caused by removing herbivores was greatest  
141 at sites with high herbivory intensity (estimated as change in biomass in response to fencing;  $p=0.006$ ,

142 AIC-weighted importance = 0.98, Extended Data Table 6). Herbivory intensity, in turn, was greatest at  
143 sites with a cool dry season climate ( $p=0.01$ , importance = 1.0, Extended Data Table 7) and sites where  
144 the annual temperature is relatively warm ( $p=0.03$ , importance = 0.52) and constant ( $p=0.05$ ,  
145 importance =0.63). However, the change in diversity due to herbivores was best described by their  
146 effect on ground-level light ( $p=0.012$ , importance = 1.0, Extended Data Table 8); site-level climate,  
147 productivity, soil nitrogen, nitrogen deposition rates, and herbivory intensity were not significant  
148 descriptors of changes in site-level plant diversity ( $p>0.05$  and importance  $< 0.25$  for these factors).  
149 Thus, climate, which predicts herbivory intensity, places an ultimate constraint on the effects of  
150 herbivores on plant diversity, but local plant diversity is determined primarily via herbivore effects on  
151 ground level light. These experimental data demonstrate that across a wide range of the world's  
152 grasslands, herbivores serve as a significant force maintaining plant diversity where they increase  
153 ground-level light availability, consistent with the theoretical prediction that light limitation is a critical  
154 factor controlling grassland species diversity<sup>9,16</sup>, but counter to the interpretation of nutrient supply or  
155 ecosystem productivity as the dominant force constraining herbivore effects on local plant diversity<sup>11-17</sup>.  
156 Because of the steady conversion of the world's grasslands for livestock production<sup>3-7</sup>, a predictive  
157 understanding of the forces controlling grassland diversity is critical for informing issues of  
158 environmental and agricultural sustainability on all continents. Whereas previous work observed that  
159 herbivores have the greatest effects on diversity in high productivity ecosystems<sup>11-16</sup>, the experimental  
160 results presented here demonstrate that in grasslands where herbivores increase ground-level light,  
161 they rescue plant diversity regardless of nutrient addition or environmental productivity. This result is  
162 consistent with ecological theory<sup>9,16,20</sup>, simultaneously providing greater mechanistic understanding<sup>20</sup>  
163 and clarifying the apparent overall lack of response of plant diversity to herbivory<sup>11</sup>. Our global-scale  
164 experimental results suggest that where anthropogenic nutrient inputs to natural systems are high,

165 grassland plant diversity will decline. However, in grasslands where herbivory leads to increased  
166 ground-level light availability, we expect that these diversity losses will be ameliorated.

167

## 168 **Methods Summary**

169 All 40 herbaceous dominated ("grassland") sites in the analysis (Fig. 1) implemented a full factorial  
170 combination of nutrient addition (Control or All Nutrients) and herbivore exclusion (Control or Fenced).  
171 The experimental design, treatments, and sampling procedures to document plant diversity, biomass,  
172 light interception by the canopy, and soil chemistry were replicated at all sites, as detailed in Borer et al.  
173 2014<sup>27</sup> and described in the full Methods section. Climate data were derived for all sites using the  
174 WorldClim database (version 1.4)<sup>30</sup>. All sites contributed at least 1 year of post-treatment data. Light,  
175 biomass, and species richness were measured concurrently at 29 sites contributing 3 or more years of  
176 data (Extended Data Table 1); we focus on these in our main analyses.

177 We developed mixed effects models with site and block within site as random effects using R (version  
178 3.1; R Foundation for Statistical Computing, Vienna, Austria). Analyses in Figs 2a and 2b were performed  
179 using the *nlme* library; where proportion of light (binomial error structure) was the response variable  
180 (Figs 2c and 2d), we used the *lme4* library. We used the *glm* library to analyze changes in each factor  
181 estimated as  $\log(S_{f+}/S_f)$ , where  $S_{f+}$  is species richness or proportion PAR reaching the ground in fenced  
182 plots and  $S_f$  represents the comparable control plot measurement (Fig. 3). Finally, we used the dredge  
183 function in the *MuMIn* library to assess the relative importance of potentially covarying site-level  
184 factors. Using this function, we fit all possible models, estimated parameter values, errors, and AIC-  
185 weighted importance (the relativized sum of the Akaike weights summed across all models in which the  
186 parameter appears that are within 4 AIC units of the model with the lowest AIC value) using the  
187 `model.avg` function for all models within 4 AIC<sub>C</sub> units of the top model.

188

189 **Full Methods** and any associated references are available in the online version of the paper at  
190 [www.nature.com/nature](http://www.nature.com/nature).

191 **References and Notes**

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256 **Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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273 addressed to E.T. Borer ([borer@umn.edu](mailto:borer@umn.edu)).

274

## FIGURE LEGENDS

275 **Fig. 1** | Geographic and climatic distribution of experimental sites. **(A)** Locations of the 40 Nutrient  
276 Network sites replicating the full factorial experiment manipulating herbivores and nutrient supply and  
277 contributing 1-4 years of plot-scale PAR, plant species richness, and total plant biomass data. **(B)** Study  
278 sites represent a wide range of mean annual temperature and precipitation (n=40). Additional site  
279 details are provided in Extended Data Table 1.

280 **Fig. 2** | Mixed-effects model parameters showing average response of plots (N=360) to three years of  
281 nutrient addition (Nut) and herbivore exclusion via fencing (Fnc). Nut and Fnc represent the difference  
282 from control plots; Nut\*Fnc is the additional effect of combining nutrients and fences (i.e. interaction).  
283 Error bars represent 95% CI. (a) Plot-scale diversity declines with nutrients, but is not consistently  
284 altered with fencing. (b) Total biomass increases with nutrients, but is not consistently affected by  
285 fencing. (c) Exclusion of herbivores and addition of nutrients independently reduce ground-level light.  
286 (d) The proportion of light reaching the ground declines with increasing aboveground biomass.

287 **Fig. 3** | Effects of herbivore exclusion via fencing on mean grassland species richness and the mean  
288 proportion of PAR reaching ground-level at 29 sites after three treatment years. Values represent the  
289 log ratio comparing light and richness inside and outside fences, and the gray region indicates 95% CI for  
290 regression slope fitted through site means ( $p=0.003$ ). Extended Data Table 1 shows site number codes.  
291 Herbivore exclusion generally leads to reduced ground-level light ( $<0$  on x-axis) coupled with reduced  
292 grassland species richness ( $<0$  on y-axis). Herbivore effects are consistent across fertilized and  
293 unfertilized plots (Extended Data Figure 2).

294

295

## METHODS

296 **Site selection.** The Nutrient Network (NutNet) is a network of researchers working at herbaceous-  
297 dominated ("grassland") sites in countries spread across six continents performing coordinated, globally-  
298 distributed observations and experiments. The full experimental design is detailed here and in <sup>27</sup>. All  
299 NutNet sites are located in areas dominated by herbaceous vegetation representing the regional species  
300 composition (e.g., shortgrass steppe, tallgrass prairie), referred to as "grassland" here. The NutNet  
301 experimental design analyzed here is a completely randomized block design with four 5 x 5 m plots per  
302 block and three replicate blocks at most sites (with blocks ranging from 1 [n=1 site] to 5 [n=3 sites]).  
303 Within-site replication is used to determine relative strength of responses, but the main experimental  
304 replication comes from the number of sites.

305 **Experimental treatments.** All 40 sites included in the current analysis (Fig. 1) implemented a full  
306 factorial combination of nutrient addition (Control or All Nutrients) and consumer density (Control or  
307 Fenced) for a total of 4 treatments in randomized, complete blocks. Standard nutrient addition and  
308 sampling protocols were carefully replicated among sites <sup>27</sup>. All sites collected data prior to application  
309 of treatments (year 0); most sites began sampling in 2007, but a subset began sampling in subsequent  
310 years. Nutrient and fencing treatments <sup>27</sup> were implemented the following year (year 1) and have been  
311 maintained continuously since then. All sites contributed at least 1 year of post-treatment data; 39 of  
312 these sites contributed 3 or more years of post-treatment data. Light, biomass, and species richness  
313 measurements (see below) were conducted concurrently at 29 sites contributing 3 or more years of  
314 data; we focus on these in our main analyses.

315 Fences designed to exclude aboveground mammalian herbivores (>50 g) were erected around two plots  
316 in each block, one receiving a nutrient combination (described next) and one ambient nutrient control  
317 plot. Fences were 230 cm tall with the lower 90 cm surrounded by 1 cm woven wire mesh. An

318 additional 30 cm outward-facing flange was stapled to the ground to exclude digging animals (e.g.,  
319 rabbits, voles), though not fully subterranean ones (e.g., gophers, moles). Four strands of barbless wire  
320 were strung at equal vertical distances above the wire mesh. Enclosures were built at all sites before the  
321 second year of plant growth. While most (33) sites built fences exactly to these specifications, a few  
322 sites (8) faced challenges (e.g. snowpack, materials availability, elephant activity) that required minor  
323 modifications. Modifications are described in Appendix Table S1.

324 Nitrogen, phosphorus, and potassium were applied annually to experimental plots; micronutrients were  
325 applied once at the start of the experiment to avoid toxic levels from over-application. Nutrient  
326 addition rates and sources were: 10 g N m<sup>-2</sup> yr<sup>-1</sup> as timed-release urea [(NH<sub>2</sub>)<sub>2</sub>CO], 10 g P m<sup>-2</sup> yr<sup>-1</sup> as  
327 triple-super phosphate, [Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub>], 10 g K m<sup>-2</sup> yr<sup>-1</sup> as potassium sulfate [K<sub>2</sub>SO<sub>4</sub>] and 100 g m<sup>-2</sup> yr<sup>-1</sup> of a  
328 micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%), and Mo  
329 (0.05%).

330 Each sampling area was separated by at least 1.5 meters from neighboring plots (1 m walkway and 0.5  
331 m within-plot buffer), which served to minimize indirect effects of treatments in one plot on adjacent  
332 plots (e.g. nutrient leaching, shading, or mycelial networks). Note that the nutrient and fence treatments  
333 had strong measurable effects on plant responses (e.g. biomass, richness) indicating that plots and  
334 measurements were sufficiently sized and spaced.

335 **Species diversity.** All NutNet sites followed standard sampling protocols. A randomly designated 1 x 1 m  
336 subplot within each 5 x 5 m plot was permanently marked and sampled annually at peak biomass. In the  
337 1 x 1 m permanently marked subplot, cover was estimated visually to the nearest 1% for every species  
338 overhanging the subplot; cover estimates also included woody over-story, litter, bare soil, and rock.

339 **Productivity.** Adjacent to the permanent 1 x 1 m cover subplot, standing crop was estimated  
340 destructively by clipping at ground level all aboveground biomass of individual plants rooted within two

341 0.1 m<sup>2</sup> strips (for a total of 0.2 m<sup>2</sup>). All biomass was dried at 60°C to constant mass prior to weighing to  
342 the nearest 0.01 g. Weights were multiplied by 5 to estimate grams per square meter. Pre-treatment  
343 data (Y0) from each site in this study demonstrate high correlation 0.976 (95% CI: 0.955 – 0.987)  
344 between Y0 mean plant biomass in the control plots (n=3 for most sites) and Y0 mean plant biomass for  
345 the site as characterized by all plots (n=30 for most sites).

346 **Light interception.** At the time of biomass clipping, photosynthetically active radiation (PAR,  $\mu\text{mol}$   
347 photons m<sup>-2</sup> s<sup>-1</sup>) was determined at approximately solar noon (between 11am – 2pm). Two  
348 measurements, integrated across a 1 m light ceptometer, were made at ground level from opposite  
349 corners of each 1 m<sup>2</sup> plant diversity plot, diagonal to each other, and one measurement was made  
350 above the canopy of each plot. We calculated the proportion of PAR available at ground level as the  
351 ratio of the average of the ground level to the ambient measurements.

352 **Climate.** We used the WorldClim database to derive comparable climate data for all sites (version 1.4;  
353 <http://www.worldclim.org/bioclim>). This database provides high-resolution interpolated global climate  
354 data for stations with 10-30 years of data <sup>30</sup>. To examine climate covariates with site-level fencing effects  
355 on net consumption (biomass inside minus outside of fences), light, and richness, we used climate  
356 variables that summarized the mean and seasonality of site-level temperature and precipitation. These  
357 were (BIO designator indicates the variable code in the WorldClim database): mean annual temperature  
358 (°C; BIO1), mean maximum temperature of the warmest month (BIO5), mean minimum temperature of  
359 the warmest month (BIO5), mean annual precipitation (mm per year; BIO12), precipitation variability  
360 (coefficient of variation in precipitation among months; BIO15), rainfall-potential evapotranspiration  
361 (mm per month), temperature variability (standard deviation of temperature among months; BIO4),  
362 mean temperature in the wettest quarter (°C; BIO8), and mean temperature in the driest quarter (°C;  
363 BIO9).

364 **Nitrogen deposition.** We used nitrogen deposition modeled by Dentener<sup>31</sup> to determine the annual  
365 atmospheric N deposition ( $\text{kg N ha}^{-1} \text{y}^{-1}$ ) for each experimental site (associated with model output based  
366 on latitude and longitude). N-deposition was modeled based on existing measurements and future  
367 projections using a global three-dimensional chemistry-transport model (TM3)<sup>31</sup>. The spatial resolution  
368 of the model, 5 degrees longitude by 3.75 degrees latitude, and the resolution of the output grid (50 km  
369 x 50 km sub-grids), provide sufficient resolution to distinguish site-level variation in annual N-deposition  
370 among our experimental sites.

371 **Statistical analysis.** To explore the independent and interactive effects of vertebrate herbivory and  
372 nutrient supply on species diversity, total biomass, and photosynthetically active radiation, we  
373 developed mixed effects models with site and block within site as random effects. Analyses in Figs 2a  
374 and 2b were performed using the *nlme* library in R (R version 3.1; R Foundation for Statistical  
375 Computing, Vienna, Austria); for Figs 2c and 2d, we used the *lme4* R library to fit models in which  
376 proportion of light was the response variable (binomial error structure and a proportion bounded  
377 between 0 and 1). Although not presented here, models using logit and arcsin square root  
378 transformations of the data generated qualitatively identical results. Site and block nested within sites  
379 were included in all regressions. We also estimated the effects of herbivores on richness and light at  
380 each site as the change in these factors resulting from fencing in both fertilized and unfertilized plots.  
381 Change in each factor was estimated as the log ratio of the treatment divided by the control,  $\log(S_{f+}/S_f)$ ,  
382 where  $S_{f+}$  is the species richness or proportion PAR reaching the ground in fenced plots and  $S_f$  is the  
383 species richness or proportion PAR reaching the ground in control plots. We examined residuals to  
384 ensure homogeneity of variance. Because of missing PAR data for a few sites, this analysis included 29  
385 sites. The relationships were independent of whether plots had been fertilized (see Extended Data  
386 Figure 2 for more details), so we present a final model of site means including both fertilized and  
387 unfertilized plots in the main text. The log ratio analyses were performed using the *glm* library in R (R



388 version 3.1; R Foundation for Statistical Computing, Vienna, Austria). We generated models separately  
389 for each experimental year (N(Y1)=40, N(Y2) = 38, N(Y3)=34, N(Y4)=30). The results were broadly  
390 consistent (Extended Data Figure 1), so we present results from 3 years of manipulations in the main  
391 text and results comparing 1-4 years of manipulations, greater spatial (Y1 and Y2) or temporal (Y4)  
392 extent, in Extended Data Figure 1.

393 Finally, to examine the effects of climate and site productivity as predictors for site-level mean herbivore  
394 effects on biomass, ground-level light, and plant richness, we analyzed site-level mean values using  
395 model averaging following Grueber *et al.*<sup>32</sup>. The model averaging approach allowed us to assess the  
396 relative importance of a range of covarying factors, and to explicitly recognize that there could be a suite  
397 of similar models. Prior to fitting the models, all of the independent variables were standardized using  
398 the standardize function in the *arm* R library. "Importance" in this modeling approach is a term  
399 representing the relativized sum of the Akaike weights summed across all of the models in which the  
400 parameter appears that are within 4 AIC units of the model with the lowest AIC. We used the dredge  
401 function in the *MuMIn* R library to fit all possible models. We estimated parameter values, errors, and  
402 AIC-weighted importance using the model.avg function in the *MuMIn* R library and using the subset of  
403 all models that were within 4 AIC<sub>c</sub> units of the top model.

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414 **EXTENDED DATA TABLE TITLES AND FIGURE LEGENDS**

415

416 **Extended Data Table 1 | Sites Table.** Nutrient Network sites with 1-4 years of experimental  
417 manipulations of both nutrients and herbivores. Site codes with a \* are the sites used in the main text  
418 analyses (richness, biomass, and PAR measurements in Y3). “Exp’t years” indicates the number of years  
419 of experimental data collected at each site for the current analyses. “Mean soil %N” is the average site  
420 value across all plots measured prior to establishment of experimental treatments. “Control plot mass”  
421 and “Control plot richness” indicate the mean total biomass and mean number of species per square  
422 meter in unmanipulated plots across all sample years.

423 **Extended Data Tables 2-8 | Statistical models after three years of treatments.** The statistical models in  
424 the following tables underlie the panels of Figure 2. All models describe responses in data collected 3  
425 years after initiation of the experimental treatments. Results of 1-4 years of manipulations are broadly  
426 consistent with these and are presented in Extended Data Figure 1. N represents the number of sites  
427 from which each data type was available. The intercept in each model is the estimated mean value of  
428 the control plots (no fence, no nutrients).

429 **Extended Data Table 2 | Fig. 2a STATISTICAL MODEL: Treatment effects on Richness after 3 years of**  
430 **treatment (N=29) as a function of NPK fertilization, fence, and their interaction.** Linear mixed-effects  
431 model was fit by maximum likelihood. Random effects in model were site (SD=5.60) and block within  
432 site (SD=1.22).

433 **Extended Data Table 3 | Fig. 2b STATISTICAL MODEL: Treatment effects on Biomass after 3 years of**  
434 **treatment (N=29) as a function of NPK fertilization, fence, and their interaction.** Linear mixed-effects  
435 model was fit by maximum likelihood. Random effects in model were site (SD=0.73) and block within  
436 site (SD=0.20).

437 **Extended Data Table 4 | Fig. 2c STATISTICAL MODEL: Treatment effects on proportion of PAR reaching**  
438 **ground-level after three treatment years (N=29) as a function of NPK fertilization, fence, and their**  
439 **interaction.** Linear mixed-effects model was fit by maximum likelihood. Random effects in model were  
440 site (SD=0.23) and block within site (SD= $6.24 \times 10^{-6}$ ).

441 **Extended Data Table 5 | Fig. 2d STATISTICAL MODEL: Biomass effects on ground-level proportion of**  
442 **PAR after 3 years of treatment (N=29) as a function of total plot-scale biomass.** Generalized linear  
443 mixed-effects model with logit link and binomial errors was fit by maximum likelihood. Random effects  
444 in model were site (SD=1.68) and block within site (SD= $1.06 \times 10^{-5}$ ).

445 **Extended Data Table 6 | Effects of climate, nitrogen deposition, soil nitrogen, and site productivity on**  
446 **change in ground-level light across experimental fencing treatments after three years of treatments.**  
447 Summary results of change in site-level means of ground-level light after model averaging; all factors are  
448 normalized. Soil nitrogen was included in the original models, but was never significant so was dropped  
449 from final models because of missing values.

450 **Extended Data Table 7 | Effects of climate, nitrogen deposition, soil nitrogen, and site productivity on**  
451 **site-level mean biomass change across experimental fencing treatments after three years of**  
452 **treatments.** Summary results of site-level means of biomass off-take after model averaging; all factors  
453 are normalized. Soil nitrogen was included in the original models, but was never significant so was  
454 dropped from final models because of missing values.

455 **Extended Data Table 8 | Effects of climate, nitrogen deposition, soil nitrogen, site productivity, and**  
456 **change in light on change in site-level mean plant species richness across experimental fencing**  
457 **treatments after three years of treatments.** Summary results of change in site-level means of plant  
458 richness after model averaging; all factors are normalized. Soil nitrogen was included in the original  
459 models, but was never significant so was dropped from final models because of missing values.

## EXTENDED DATA FIGURE LEGENDS

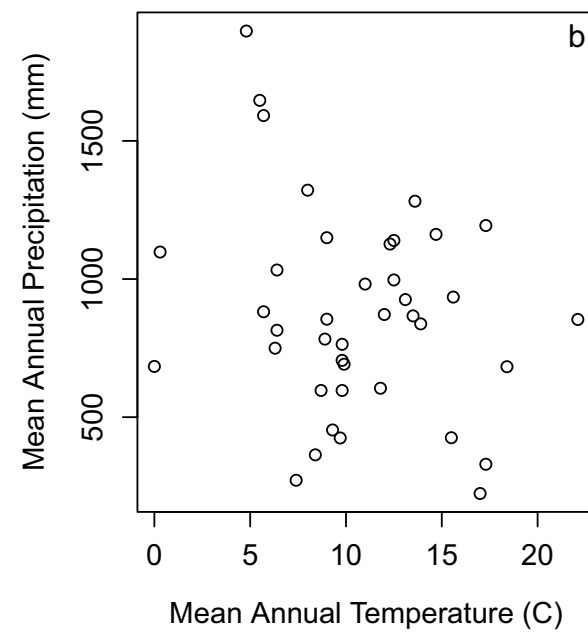
460

461

462 **Extended Data Figure 1 | Regression parameters for multi-year treatment effects.** All available data are  
463 shown for (a) richness, (b) total biomass, and (c) ambient light reaching ground level. Error bars  
464 represent  $\pm 2$  SE. Treatment years and their associated sample sizes are shown in each panel. One and  
465 two year models represent greater spatial extent and replication, but reduced temporal extent  
466 compared to Fig. 2 in the main text. Four year models represent longer temporal effects, but reduced  
467 spatial extent, particularly for light measurements. All models were fitted as in Extended Data Tables 2-  
468 4 and described in the Methods.

469

470 **Extended Data Figure 2 | Fertilization does not alter the relationship between fence effects on light**  
471 **and diversity.** The log ratio model of the effect of fences on richness and light (Y3 data) demonstrates  
472 no additional effect of nutrient addition on the relationship shown in Fig. 3. Whereas the effect of  
473 fences on ground-level light predicts changes in plot-scale species richness ( $p=0.00254$ ), fertilization is  
474 not included in the final statistical model of this relationship ( $p>0.05$ ). Thus, the magnitude of the effect  
475 of grazers on richness is dependent on the magnitude of their effect on light regardless of whether a  
476 plot has been fertilized.



Species Richness Change (spp m<sup>-2</sup>)

