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Herbivores and nutrients control grassland plant diversity via light limitation

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Human alterations to nutrient cycles^{1,2} and herbivore communities³⁻⁷ are affecting global biodiversity dramatically². Ecological theory predicts these changes should be strongly counteractive: nutrient addition drives plant species loss through intensified competition for light, whereas herbivores prevent competitive exclusion by increasing ground-level light, particularly in productive systems^{8,9}. Here we use experimental data spanning a globally relevant range of conditions to test the hypothesis that herbaceous plant species losses caused by eutrophication may be offset by increased light availability due to herbivory. This experiment, replicated in 40 grasslands on 6 continents, demonstrates that nutrients and herbivores can serve as counteracting forces to control local plant diversity through light limitation, independent of site productivity, soil nitrogen, herbivore type and climate. Nutrient addition consistently reduced local diversity through light limitation, and herbivory rescued diversity at sites where it alleviated light limitation. Thus, species loss from anthropogenic eutrophication can be ameliorated in grasslands where herbivory increases ground-level light.

The diversity of life on Earth underlies critical ecosystem functions and economically important services¹⁰, and the current rapid rate of biodiversity loss² lends urgency to the task of understanding the forces that maintain biodiversity. Resources required for economic growth, energy and agriculture have all impacted natural ecosystems on a global scale. Introductions and extirpations of herbivore species, particularly as land is converted for grazing³⁻⁷, and increased nutrient supply are symptoms of humanity's global footprint^{1,2}. Such widespread alteration of herbivores and nutrient supply may jointly determine the future diversity of ecosystems. For example, in highly productive, eutrophic

systems in which plant species extinction is likely to occur owing to a loss of ecological niches⁸, ecological theory predicts that herbivores can act to maintain local-scale plant diversity if they selectively consume the superior resource competitors⁹. Empirical studies in many ecosystem types find highly variable effects of herbivores on plant species diversity¹¹⁻¹³, with the magnitude of herbivore mediation of diversity frequently observed to be greatest in regions of high ecosystem productivity¹¹⁻¹⁷. Thus, ecosystem productivity and its regional climate drivers have been observed to mediate the local-scale effects of herbivores on plant diversity. The availability of ground-level light is the commonly postulated mechanism modulating the relationships among plant diversity, herbivory and observed gradients of plant productivity. However, these patterns and predictions have primarily emerged from studies across observed gradients of productivity or reviews and meta-analyses based on an extremely limited number of single-site experiments that manipulate both nutrients and herbivory, often with different methods^{11-15,17}. In most of these studies, ground-level light has not been measured. Thus, the generality of these effects is only suggestive, and the mechanisms underlying the observed relationships remain elusive.

Local-scale plant diversity is likely to be maintained through an interdependent system of interactions with multiple plant species that are consumed by the same herbivores and that compete for light and nutrients. In particular, terrestrial plants compete for nutrients and light at the scale of interactions among individuals (neighbourhood of ~1 m² in grasslands), and one important mechanism for maintaining local coexistence is a trade-off in competitive ability for nutrients (below-ground) and for carbon via light (above-ground)¹⁸⁻²². Nutrient enrichment can lead to competitive exclusion of inferior competitors for light^{19,20},

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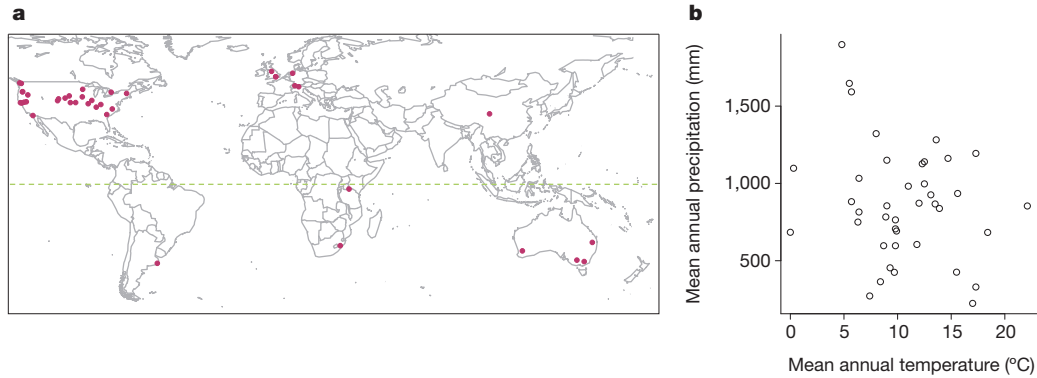


Figure 1 | Geographic and climatic distribution of experimental sites.

a, Locations of the 40 'Nutrient Network' sites at which the full factorial experiment was replicated. At each site, nutrient supply and plot access by large herbivores were manipulated. Sites contributed 1–4 years of plot-scale

but herbivores can remove plant biomass, potentially alleviating understorey light limitation. However, herbivory creates another axis of potential trade-offs among plant species, involving investment in rapid growth and light capture versus investment in defence against herbivory^{23–26}. These interactions result in a dynamic local community in which composition responds quickly to changes in the strength of nutrient limitation or herbivory^{25,26}. In eutrophied systems, where nutrient limitation is alleviated and productivity is increased, theory predicts that these tradeoffs among plant strategies will simplify the plant community to species sharing an herbivore and competing for a single resource—light^{9,19}.

We used an experiment replicated at 40 sites on 6 continents (Fig. 1) to test the hypothesis that herbivores mediate species losses caused by nutrient addition by increasing ground-level light, particularly in eutrophic and highly productive systems. We manipulated herbivores and nutrients using a factorial experiment (nutrient addition \times exclusion of herbivores $>$ about 50 g, see Methods and ref. 27 for details) replicated in 40 sites dominated by herbaceous plants, spanning broad environmental gradients of productivity (114 to 1,976 g m⁻² yr⁻¹), precipitation (mean annual precipitation from 224 to 1,898 mm yr⁻¹), temperature (mean annual temperature from 0 to 22.1 °C), and soil nitrogen (mean percentage of soil N from 0.018 to 1.182%) (Fig. 1 and Extended Data Table 1). In each plot, we measured local-scale responses of productivity, light and the number of plant species (diversity) using standard methods²⁷. We also examined site-level covariates including precipitation, temperature, herbivory intensity, soil nitrogen and atmospheric-nitrogen deposition rates. Although most sites provided 3 years of data, a subset of sites contributed 4 years of post-treatment data, and a few sites, established later, provided only 1 or 2 years of data (Extended Data Table 1). Effects of the experimental treatments were broadly consistent across all years of treatments (Extended Data Fig. 1); we present results from the three year duration in the main text, for a balance of spatial and temporal extent (see Extended Data Tables 2–8 for statistical models that describe responses in data collected 3 years after initiation of the experimental treatments).

Our results support an important mechanism by which nutrients lead to diversity loss. In particular, nutrient addition caused declines in diversity (Fig. 2a and Extended Data Table 2, $P < 0.001$), increased total plant biomass (Fig. 2b and Extended Data Table 3, $P < 0.001$), and increased light limitation (reduced transmission of photosynthetically active radiation (PAR) to ground level, Fig. 2c and Extended Data Table 4, $P < 0.001$) both inside and outside of fences. Ground-level light availability, a function of light interception by live and dead biomass, declined with increasing total biomass (Fig. 2d and Extended Data Table 5, $P < 0.001$). This result is consistent with eutrophication-induced loss of niches for coexistence^{8,9,19,28} and demonstrates the generality of eutrophication as a primary force controlling the diversity of grassland communities by reducing ground-level light²⁰.

photosynthetically active radiation (PAR), plant species richness and total plant biomass data. **b**, Study sites represent a wide range of mean annual temperature and precipitation ($n = 40$). Additional site details are provided in Extended Data Table 1.

Although the removal of vertebrate herbivores did not have consistent effects on diversity (Fig. 2a, $P = 0.522$) or biomass (Fig. 2b, $P = 0.803$), herbivore removal increased light limitation (Fig. 2c, $P = 0.013$). The lack of a consistent effect of herbivore removal on diversity across these globally distributed grassland sites (Fig. 2a) reflects the broad range of positive and negative effects found in past studies^{11,17,29}. However, a critical assumption underlying the hypothesis that grassland diversity is jointly controlled by nutrient supply and consumers is that diversity should be rescued consistently by herbivory. In both ambient and eutrophied plots, herbivory should lead to greater diversity because herbivores can alleviate ground-level light limitation, thereby increasing the number of possible tradeoffs (nutrients, light) that maintain plant species diversity^{9,16}.

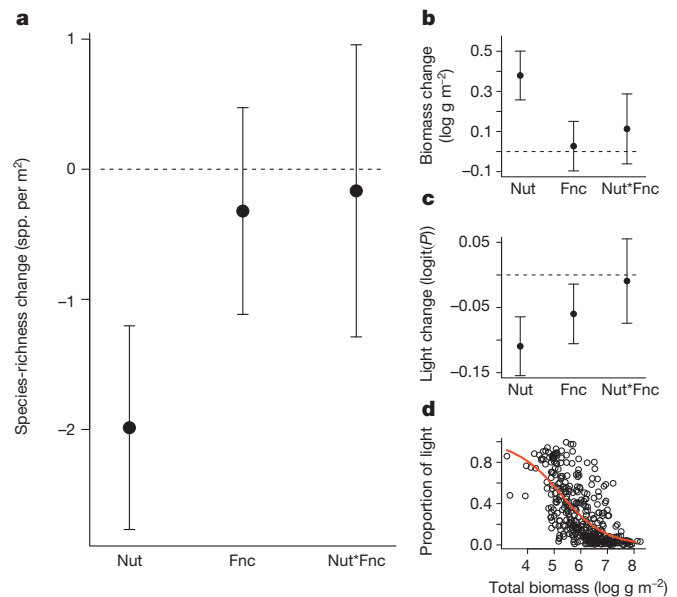


Figure 2 | Mixed-effects model parameters showing average response of plots ($n = 360$) to 3 years of nutrient addition and herbivore exclusion by fencing. a–d, Nutrient addition (Nut) and herbivore exclusion by fencing (Fnc) represent the difference from control plots; Nut*Fnc is the additional effect of combining nutrients and fences (the interaction). Error bars represent the 95% confidence interval. **a** Plot-scale diversity declines with nutrients, but is not consistently altered with fencing. **b**, Total biomass increases with nutrients, but is not consistently affected by fencing. **c**, Exclusion of herbivores and addition of nutrients independently reduce ground-level light. **d**, The proportion of light reaching the ground declines with increasing aboveground biomass.

We tested whether the inconsistent herbivore effects on plant diversity reflected variable herbivore effects on light and found that plant diversity increased quantitatively with herbivore effects on ground-level light (Fig. 3, $P = 0.003$); nutrient addition did not modify this relationship (Extended Data Fig. 2). Sites with the greatest effects of herbivores on light and diversity spanned four continents and were dominated by larger vertebrates including wild and domestic ungulates, macropods, and lagomorphs (Fig. 3 and Extended Data Table 1). Thus, we show that under conditions of experimentally imposed nutrient supply gradients and among sites spanning greater than a 26-fold observed productivity gradient, herbivores rescue plant diversity to the extent that they enhance ground-level light, regardless of herbivore identity or nutrient supply.

Herbivore effects on plant diversity were not related to variation in soil nitrogen, nitrogen deposition rates, or site productivity. The change in ground-level light caused by removing herbivores was greatest at sites with high herbivory intensity (estimated as change in biomass in response to fencing; $P = 0.006$, AIC (Akaike information criterion)-weighted importance = 0.98, Extended Data Table 6). Herbivory intensity, in turn, was greatest at sites with a cool dry-season climate ($P = 0.01$, importance = 1.0, Extended Data Table 7) and sites at which the annual temperature is relatively warm ($P = 0.03$, importance = 0.52) and constant ($P = 0.05$, importance = 0.63). However, the change in diversity due to herbivores was best described by their effect on ground-level light ($P = 0.012$, importance = 1.0, Extended Data Table 8); site-level climate, productivity, soil nitrogen, nitrogen deposition rates, and herbivory intensity were not significant descriptors of changes in site-level plant diversity ($P > 0.05$ and importance < 0.25 for these factors). Thus, climate, which predicts herbivory intensity, places an ultimate constraint on the effects of herbivores on plant diversity, but local plant diversity is determined primarily through herbivore effects on ground-level light. These experimental data demonstrate that across a wide

range of the world's grasslands, herbivores serve as an important force to maintain plant diversity in grassland ecosystems in which they increase ground-level light availability, consistent with the prediction that light limitation is a critical factor controlling grassland species diversity^{9,16}, but counter to the interpretation of nutrient supply or ecosystem productivity as the dominant force constraining herbivore effects on local plant diversity^{11–17}.

A predictive understanding of the forces controlling grassland diversity is critical for informing issues of environmental and agricultural sustainability on all continents because of the steady conversion of the world's grasslands for use in livestock production^{3–7}. Previous work observed that herbivores have the greatest effects on diversity in high productivity ecosystems^{11–16}, whereas the experimental results presented here demonstrate that in grasslands in which herbivores increase ground-level light, they rescue plant diversity regardless of nutrient addition or environmental productivity. This result is consistent with ecological theory^{9,16,20}, simultaneously providing greater mechanistic understanding²⁰ and clarifying the apparent overall lack of response of plant diversity to herbivory¹¹. The results from our global-scale experiment suggest that in cases in which anthropogenic nutrient inputs to natural systems are high, grassland plant diversity will decline. However, in grasslands in which herbivory leads to increased ground-level light availability, we expect that these diversity losses will be ameliorated.

METHODS SUMMARY

All 40 herbaceous-dominated ('grassland') sites in the analysis (Fig. 1) implemented a full factorial combination of nutrient addition ('control' or 'all nutrients') and herbivore exclusion ('control' or 'fenced'). The experimental design, treatments and sampling procedures to document plant diversity, biomass, light interception by the canopy, and soil chemistry were replicated at all sites, as detailed in ref. 27 and described in the Methods. Climate data were derived for all sites using the WorldClim database (version 1.4)³⁰. All sites contributed at least 1 year of post-treatment data. Light, biomass and species richness were measured concurrently at 29 sites contributing 3 or more years of data (Extended Data Table 1); we focus on these in our main analyses.

We developed mixed-effects models with 'site' and 'block nested within site' as random effects using R (version 3.1; R Foundation for Statistical Computing). Analyses in Fig. 2a, b were performed using the nlme R library; we used the lme4 R library when the proportion of light (binomial error structure) was the response variable (Fig. 2c, d). We used the glm R function to analyse changes in each factor estimated as $\log(S_{f+}/S_{f-})$, where S_{f+} is species richness or proportion PAR reaching the ground in fenced plots and S_{f-} represents the comparable control plot measurement (Fig. 3). Finally, we used the dredge function in the MuMIn R library to assess the relative importance of potentially covarying site-level factors. We fit all possible models, deriving parameter values with error, and kept those models not more than four AIC_C (AIC corrected for small sample size) units higher than the best model. For each parameter, we further estimated AIC-weighted 'importance', a unitless metric indicating summed Akaike information across all models in which the parameter appears. Importance ranges from 0 (parameter not given explanatory weight) to 1 (parameter in all top models).

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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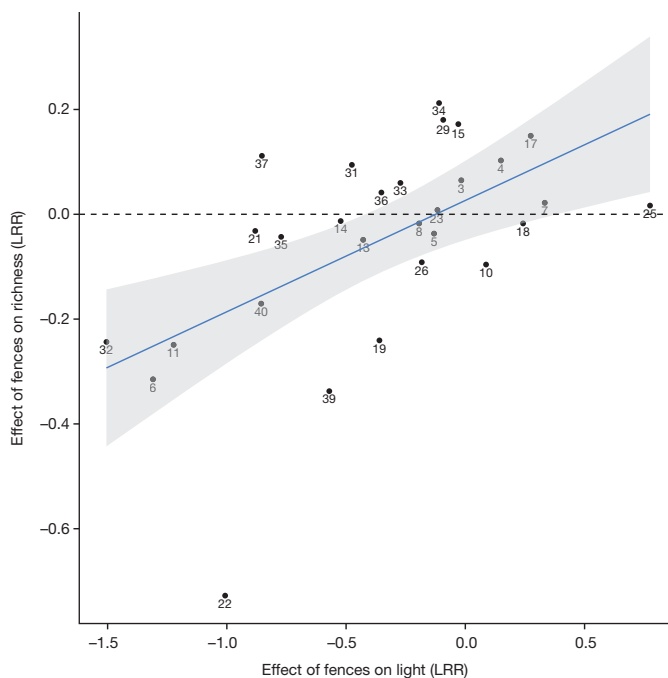


Figure 3 | Effects of herbivore exclusion by fencing on mean grassland species richness and the mean proportion of PAR reaching ground level at 29 sites after 3 years of treatment. Log response ratios (LRRs) compare light and richness inside and outside fences. The grey region indicates the 95% confidence interval around the regression ($P = 0.003$). Extended Data Table 1 shows site number codes. Herbivore exclusion generally leads to reduced ground-level light (< 0 on x axis) coupled with reduced grassland species richness (< 0 on y axis). Herbivore effects are consistent across fertilized and unfertilized plots (Extended Data Fig. 2).

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Supplementary Information is available in the online version of the paper.

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Author Contributions E.T.B., E.W.S., W.S.H. and E.M.L. are Nutrient Network coordinators. E.T.B., W.S.H., H.H. and D.S.G. developed and framed the research questions in this paper. All authors contributed data from this experiment. E.T.B. and E.W.S. analysed the data. D.S.G., W.S.H. and E.M.L. contributed to data analyses. E.T.B. wrote the paper with input from all authors. Supplementary Information Appendix S2 provides further information on author contributions.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to E.T.B. (borer@umn.edu).

METHODS

Site selection. The Nutrient Network (NutNet) is a network of researchers working at herbaceous-dominated ('grassland') sites in countries spread across six continents, who are performing coordinated, globally distributed observations and experiments. The full experimental design is detailed here and in ref. 27. All NutNet sites are located in areas dominated by herbaceous vegetation representing the regional species composition (for example, shortgrass steppe, tallgrass prairie), referred to as 'grassland' here. The NutNet experimental design analysed here is a completely randomized block design with four 5×5 m plots per block and three replicate blocks at most sites (with blocks ranging from 1 ($n = 1$ site) to 5 ($n = 3$ sites)). Within-site replication is used to determine relative strength of responses, but the main experimental replication comes from the number of sites.

Experimental treatments. All 40 sites included in the current analysis (Fig. 1) implemented a full factorial combination of nutrient addition ('control' or 'all nutrients') and consumer density ('control' or 'fenced') for a total of four treatments in randomized, complete blocks. Standard nutrient addition and sampling protocols were carefully replicated among sites²⁷. All sites collected data before application of treatments (year 0); most sites began sampling in 2007, but a subset began sampling in subsequent years. Nutrient and fencing treatments²⁷ were implemented the following year (year 1) and have been maintained continuously since then. All sites contributed at least 1 year of post-treatment data; 39 of these sites contributed 3 or more years of post-treatment data. Light, biomass and species richness measurements (see below) were conducted concurrently at 29 sites contributing 3 or more years of data; we focus on these in our main analyses.

Fences designed to exclude aboveground mammalian herbivores (> about 50 g) were erected around two plots in each block, one receiving a nutrient combination (described next) and one used as an ambient nutrient control plot. Fences were 230 cm tall with the lower 90 cm surrounded by 1-cm woven wire mesh. An additional 30-cm outward-facing flange was stapled to the ground to exclude digging animals (for example, rabbits, voles), although not fully subterranean animals (for example, gophers, moles). Four strands of barbless wire were strung at equal vertical distances above the wire mesh. Enclosures were built at all sites before the second year of plant growth. Although most (33) sites built fences exactly to these specifications, a few sites (8) faced challenges (for example, snow-pack, materials availability, elephant activity) that required minor modifications. Modifications are described in Supplementary Table 1.

Nitrogen, phosphorus and potassium were applied annually to experimental plots; micronutrients were applied once at the start of the experiment to avoid toxic levels from over-application. Nutrient addition rates and sources were: 10 g N m⁻² yr⁻¹ as timed-release urea ((NH₂)₂CO), 10 g P m⁻² yr⁻¹ as triple-super phosphate (Ca(H₂PO₄)₂), 10 g K m⁻² yr⁻¹ as potassium sulphate (K₂SO₄) and 100 g m⁻² yr⁻¹ of a micronutrient mix of Fe (15%), S (14%), Mg (1.5%), Mn (2.5%), Cu (1%), Zn (1%), B (0.2%) and Mo (0.05%).

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

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

Productivity. Adjacent to the permanent 1 × 1 m cover subplot, standing crop was estimated destructively by clipping at ground level all aboveground biomass of individual plants rooted within two 1 × 0.1 m strips (for a total of 0.2 m²). All biomass was dried at 60 °C to constant mass before weighing to the nearest 0.01 g. Weights were multiplied by five to estimate grams per square meter. Pre-treatment data (year 0) from each site in this study demonstrate high correlation (0.976 (95% confidence interval: 0.955–0.987) between year 0 mean plant biomass in the control plots ($n = 3$ for most sites) and year 0 mean plant biomass for the site as characterized by all plots ($n = 30$ for most sites)).

Light interception. At the time of biomass clipping, photosynthetically active radiation (PAR, μmol photons per m² per s) was determined at approximately solar noon (between 11:00 and 14:00). Two measurements, integrated across a 1-m light ceptometer, were made at ground level from opposite corners of each 1-m² plant-diversity plot, diagonal to each other, and one measurement was made above

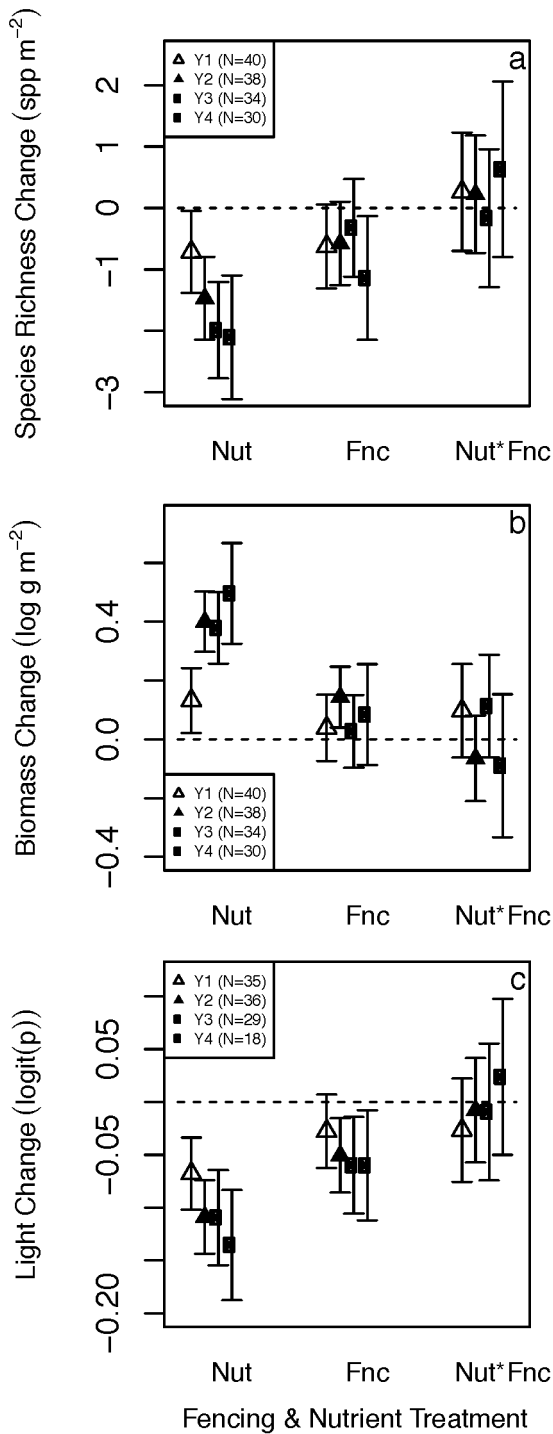
the canopy of each plot. We calculated the proportion of PAR available at ground level as the ratio of the average of the ground level to the ambient measurements. **Climate.** We used the WorldClim database to derive comparable climate data for all sites (version 1.4; <http://www.worldclim.org/bioclimate>). This database provides high-resolution interpolated global climate data for stations with 10 to 30 years of data³⁰. To examine climate covariates with site-level fencing effects on net consumption (biomass inside minus outside of fences), light and richness, we used climate variables that summarized the mean and seasonality of site-level temperature and precipitation. These were (BIO designator indicates the variable code in the WorldClim database): mean annual temperature (°C; BIO1), mean maximum temperature of the warmest month (°C; BIO5), mean minimum temperature of the warmest month (°C; BIO5), mean annual precipitation (mm per year; BIO12), precipitation variability (coefficient of variation in precipitation among months; BIO15), rainfall-potential evapotranspiration (mm per month), temperature variability (standard deviation of temperature among months; BIO4), mean temperature in the wettest quarter (°C; BIO8), and mean temperature in the driest quarter (°C; BIO9).

Nitrogen deposition. We used modelled nitrogen deposition rates³¹ to determine the annual atmospheric N deposition (kg N ha⁻¹ yr⁻¹) for each experimental site (associated with model output based on latitude and longitude). N deposition was modelled based on existing measurements and future projections using a global three-dimensional chemistry-transport model (TM3)³¹. The spatial resolution of the model, 5 degrees longitude by 3.75 degrees latitude, and the resolution of the output grid (50 × 50 km sub-grids), provide sufficient resolution to distinguish site-level variation in annual N deposition among our experimental sites.

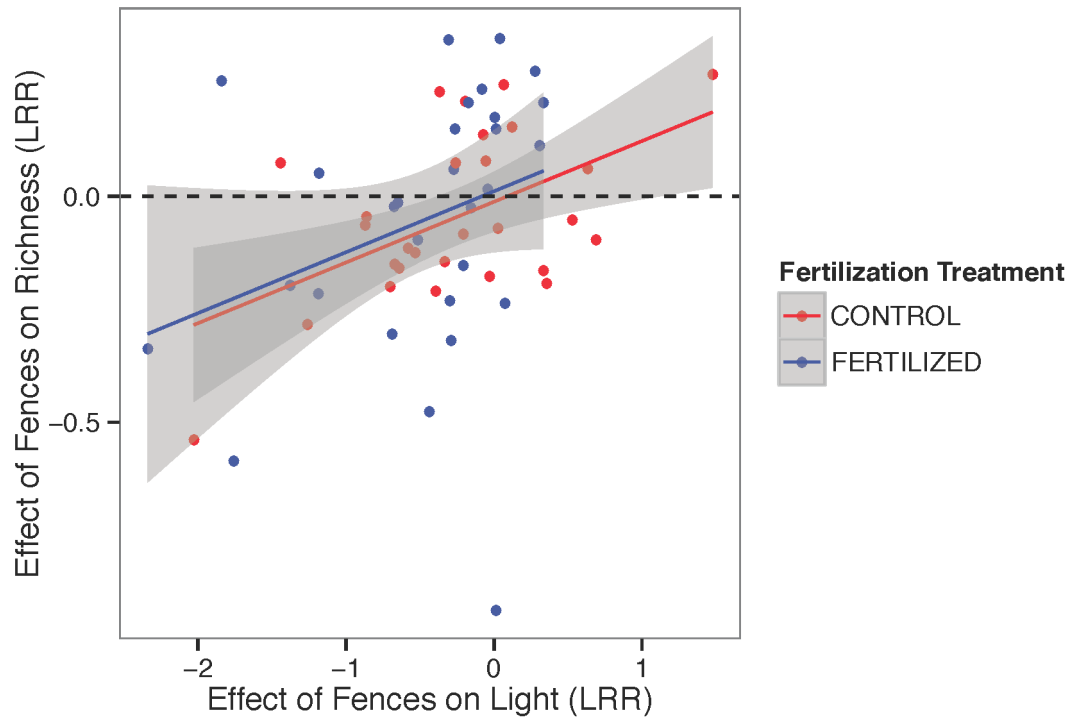
Statistical analysis. To explore the independent and interactive effects of vertebrate herbivory and nutrient supply on species diversity, total biomass and photosynthetically active radiation, we developed mixed effects models with site and block within site as random effects. Analyses in Fig. 2a, b were performed using the nlme library in R (R version 3.1; R Foundation for Statistical Computing); for Fig. 2c, d, we used the lme4 R library to fit models in which proportion of light was the response variable (binomial error structure and a proportion bounded between 0 and 1). Although not presented here, models using logit and arcsin square root transformations of the data generated qualitatively identical results. Site and block nested within sites were included in all regressions. We also estimated the effects of herbivores on richness and light at each site as the change in these factors resulting from fencing in both fertilized and unfertilized plots. Change in each factor was estimated as the log ratio of the treatment divided by the control, $\log(S_{f+}/S_{f-})$, where S_{f+} is the species richness or proportion PAR reaching the ground in fenced plots and S_{f-} is the species richness or proportion PAR reaching the ground in control plots. We examined residuals to ensure homogeneity of variance. Because of missing PAR data for a few sites, this analysis included 29 sites. The relationships were independent of whether plots had been fertilized (see Extended Data Fig. 2 for more details), so we present a final model of site means including both fertilized and unfertilized plots in the main text. The log ratio analyses were performed using the glm library in R (R version 3.1; R Foundation for Statistical Computing). We generated models separately for each experimental year (year 1, $n = 40$; year 2, $n = 38$; year 3, $n = 34$; year 4, $n = 30$). The results were broadly consistent (Extended Data Fig. 1), so we present results from 3 years of manipulations in the main text and results comparing 1 to 4 years of manipulations, greater spatial (year 1 and year 2) or temporal (year 4) extent, in Extended Data Fig. 1.

Finally, to examine the effects of climate and site productivity as predictors for site-level mean herbivore effects on biomass, ground-level light and plant richness, we analysed site-level mean values using model averaging³². The model averaging approach allowed us to assess the relative importance of a range of covarying factors, and to recognize explicitly that there could be a suite of similar models. Prior to fitting the models, all of the independent variables were standardized using the standardize function in the arm R library. 'Importance' in this modelling approach is a term representing the relativized sum of the Akaike weights summed across all of the models in which the parameter appears that are within four AIC_C (AIC corrected for small sample size) units of the model with the lowest AIC. Importance ranges from 0 (parameter not given explanatory weight) to 1 (parameter in all top models). We used the dredge function in the MuMIn R library to fit all possible models. We estimated parameter values, errors, and AIC-weighted importance using the model.avg function in the MuMIn R library.

31. The Oak Ridge National Laboratory Distributed Active Archive Center. <http://daac.ornl.gov/> (accessed 25 August 2011).
32. Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711 (2011).



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



Extended Data Figure 2 | Fertilization does not alter the relationship between 'fence' effects on light and diversity. The log response ratio (LRR) model of the effect of fences (herbivore exclusion) on richness and light (year 3 data) demonstrates no additional effect of nutrient addition on the relationship shown in Fig. 3. The grey region indicates the 95% confidence interval around

the regression. The effect of fences on ground-level light predicts changes in plot-scale species richness ($P = 0.00254$), whereas fertilization is not included in the final statistical model of this relationship ($P > 0.05$). Thus, the magnitude of the effect of grazers on richness is dependent on the magnitude of their effect on light regardless of whether a plot has been fertilized.

Extended Data Table 1 | Sites contributing experimental data

Site #	Site code*	Country	Continent	Lat.	Long.	Exp't years	MAT (°C)	MAP (mm)	Mean soil %N	Control plot mass (g m ⁻²)	Control plot richness (m ⁻²)
1	azi.cn	China	Asia	33.670	101.870	4	0.0	684	0.556	411.40	33.17
2	bart.us	USA	N Amer.	42.245	-99.652	4	8.7	597	0.057	442.90	13.75
3	bldr.us*	USA	N Amer.	39.972	-105.234	4	9.7	425	0.089	283.45	8.10
4	bnch.us*	USA	N Amer.	44.277	-121.968	4	5.5	1647	0.537	281.87	9.43
5	bogong.au*	Australia	Australia	-36.874	147.254	4	5.7	1592	0.722	554.27	18.93
6	burrawan.au*	Australia	Australia	-27.735	151.140	4	18.4	683	0.087	251.18	10.33
7	cbgb.us*	USA	N Amer.	41.785	-93.385	3	9.0	855	0.063	870.38	8.08
8	cdcr.us*	USA	N Amer.	45.401	-93.201	4	6.3	750	0.039	270.40	10.55
9	cdpt.us	USA	N Amer.	41.200	-101.630	4	9.3	454	0.097	233.59	11.72
10	cowi.ca*	Canada	N Amer.	48.460	-123.380	4	9.8	764	0.374	1018.63	4.80
11	elliott.us*	USA	N Amer.	32.875	-117.052	4	17.0	224	0.165	463.98	11.25
12	frue.ch	Switz.	Europe	47.113	8.542	3	9.0	1150	0.364	1046.54	13.58
13	gilb.za*	S Africa	Africa	-29.284	30.292	3	13.1	926	1.182	223.23	27.08
14	hall.us*	USA	N Amer.	36.872	-86.702	4	13.6	1282	0.139	948.55	6.13
15	hart.us*	USA	N Amer.	42.724	-119.498	4	7.4	272	0.109	113.82	10.33
16	hero.uk	UK	Europe	51.411	-0.639	4	9.9	692	NA	740.88	16.00
17	hnvr.us*	USA	N Amer.	43.419	-72.138	3	6.4	1033	0.395	524.58	9.50
18	hopl.us*	USA	N Amer.	39.013	-123.060	4	12.3	1127	NA	347.28	18.43
19	kiny.au*	AUS	Australia	-36.200	143.750	4	15.5	426	0.120	490.11	11.20
20	koffler.ca	Canada	N Amer.	44.024	-79.536	1	6.4	815	NA	964.47	9.39
21	konz.us*	USA	N Amer.	39.071	-96.583	4	12.0	872	NA	433.15	15.07
22	lancaster.uk*	UK	Europe	53.986	-2.628	3	8.0	1322	1.180	126.97	9.50
23	look.us*	USA	N Amer.	44.205	-122.128	4	4.8	1898	1.170	332.69	7.20
24	marc.ar	Argent.	S Amer.	-37.715	-57.425	1	13.9	838	NA	953.79	11.90
25	mcla.us*	USA	N Amer.	38.864	-122.406	4	13.5	867	NA	554.20	5.33
26	mtca.au*	AUS	Australia	-31.782	117.611	4	17.3	330	0.092	115.40	14.66
27	pape.de	Germany	Europe	53.086	7.473	4	8.9	783	0.190	1292.78	5.00
28	rook.uk	UK	Europe	51.406	-0.644	4	9.8	706	NA	233.19	10.92
29	sage.us*	USA	N Amer.	39.430	-120.240	4	5.7	882	0.714	159.92	12.36
30	saline.us	USA	N Amer.	39.050	-99.100	4	11.8	605	NA	490.44	10.75
31	sava.us*	USA	N Amer.	33.344	-81.651	4	17.3	1194	0.018	393.80	10.30
32	sereng.tz*	Tanzania	Africa	-2.255	34.513	3	22.1	854	0.133	362.90	12.58
33	sgs.us*	USA	N Amer.	40.817	-104.767	4	8.4	364	0.081	129.08	6.89
34	sier.us*	USA	N Amer.	39.236	-121.284	4	15.6	935	0.171	378.29	8.32
35	smith.us*	USA	N Amer.	48.207	-122.625	4	9.8	597	0.521	440.24	20.67
36	spin.us*	USA	N Amer.	38.136	-84.501	4	12.5	1140	0.261	425.16	9.53
37	trel.us*	USA	N Amer.	40.075	-88.829	3	11.0	982	0.273	1976.39	4.22
38	tyso.us	USA	N Amer.	38.519	-90.565	2	12.5	997	0.261	599.34	10.33
39	unc.us*	USA	N Amer.	36.008	-79.020	4	14.7	1162	0.162	427.24	11.73
40	valm.ch*	Switz.	Europe	46.631	10.372	4	0.3	1098	0.498	253.20	26.85

Nutrient Network sites with 1 to 4 years of experimental manipulations of both nutrient supply and herbivore access to plots. Control plot mass and control plot richness, the mean total biomass and mean number of species per m² in un-manipulated plots across all sample years; experiment years, the number of years of experimental data collected at each site for the current analyses; mean soil %N, the average percentage of nitrogen in soil of the site (across all plots, measured before establishment of experimental treatments); MAP is mean annual precipitation; and MAT is mean annual temperature. Lat. and Long. provide geographic coordinates of each site.

* Sites used in the main text analyses (year 3 measurements of richness, biomass and photosynthetically active radiation (PAR)).

Extended Data Table 2 | Statistical model for treatment effects on richness after 3 years of treatment ($n = 29$) as a function of fertilization by N, P and K and micronutrients, herbivore exclusion by fencing, and their interaction

	Value	Std.Error	DF	t-value	p-value
(Intercept)	11.965	1.085	264	11.031	<0.0001
fertFERTILIZED	-1.987	0.391	264	-5.075	<0.0001
excloseFENCE	-0.321	0.397	264	-0.809	0.4194
fertFERTILIZED:excloseFENCE	-0.166	0.561	264	-0.296	0.7677

Linear mixed-effects model was fit by maximum likelihood. Random effects in model were 'site' (s.d. = 5.60) and 'block within site' (s.d. = 1.22). The intercept is the estimated mean value of the control plots (no fence, no nutrients). This model is shown in Fig. 2a.

Extended Data Table 3 | Statistical model for treatment effects on biomass after 3 years of treatment ($n = 29$) as a function of fertilization by N, P and K and micronutrients, herbivore exclusion by fencing, and their interaction

	Value	Std.Error	DF	t-value	p-value
(Intercept)	5.803	0.143	264	40.497	<0.0001
fertFERTILIZED	0.379	0.061	264	6.235	<0.0001
excloseFENCE	0.027	0.062	264	0.438	0.6619
fertFERTILIZED:excloseFENCE	0.113	0.087	264	1.296	0.1961

Linear mixed-effects model was fit by maximum likelihood. Random effects in model were 'site' (s.d. = 0.73) and 'block within site' (s.d. = 0.20). The intercept is the estimated mean value of the control plots (no fence, no nutrients). This model is shown in Fig. 2b.

Extended Data Table 4 | Statistical model for treatment effects on proportion of photosynthetically active radiation (PAR) reaching ground level after 3 years of treatment ($n = 29$) as a function of fertilization by N, P and K and micronutrients, herbivore exclusion by fencing, and their interaction

	Value	Std.Error	DF	t-value	p-value
(Intercept)	0.399	0.046	264	8.615	<0.0001
fertFERTILIZED	-0.109	0.023	264	-4.850	<0.0001
excloseFENCE	-0.060	0.023	264	-2.614	0.0095
fertFERTILIZED:excloseFENCE	-0.009	0.032	264	-0.290	0.7721

Linear mixed-effects model was fit by maximum likelihood. Random effects in model were 'site' (s.d. = 0.23) and 'block within site' (s.d. = 6.24×10^{-6}). The intercept is the estimated mean value of the control plots (no fence, no nutrients). This model is shown in Fig. 2c.

Extended Data Table 5 | Statistical model for biomass effects on ground-level proportion of photosynthetically active radiation (PAR) after 3 years of treatment ($n = 29$) as a function of total plot-scale biomass

	Estimate	Std.Error	z-value	Pr(> z)
(Intercept)	-0.584	0.395	-1.479	0.1391
fertFERTILIZED	-1.108	0.361	-3.073	0.0021
excloseFENCE	-0.993	0.363	-2.736	0.0062
fertFERTILIZED:excloseFENCE	0.166	0.551	0.302	0.7626

Generalized linear mixed-effects model with logit link and binomial errors was fit by maximum likelihood. Random effects in model were 'site' (s.d. = 1.68) and 'block within site' (s.d. = 1.06×10^{-5}). The intercept is the estimated mean value of the control plots (no fence, no nutrients). This model is shown in Fig. 2d.

Extended Data Table 6 | Effects of climate, nitrogen deposition, soil nitrogen and site productivity on change in ground-level light across experimental fencing treatments after 3 years of treatment

	Estimate	Std. Error	Adjusted SE	z value	p-value	Relative Importance
(Intercept)	-0.30123	0.07368	0.07827	3.849	<0.001	1.00
Change in mass across fence	-0.56329	0.19684	0.20635	2.730	0.006	0.98
Annual Precipitation Variability	0.29938	0.16493	0.17463	1.714	0.086	0.51
Wet Quarter Temperature	-0.42281	0.28903	0.29826	1.418	0.156	0.40
Mean Annual Temperature	-0.51396	0.46975	0.48080	1.069	0.285	0.36
Maximum Temperature	0.53099	0.35922	0.37327	1.423	0.155	0.35
Minimum Temperature	-0.28435	0.43556	0.44519	0.639	0.523	0.29
Dry Quarter Temperature	-0.14111	0.54170	0.55158	0.256	0.798	0.18
Annual Temperature Variability	0.12017	0.39288	0.40263	0.298	0.765	0.17
Annual N-Deposition Rate	-0.14619	0.18187	0.19180	0.762	0.446	0.08
Rainfall Potential Evapotranspir.	-0.06077	0.22652	0.23682	0.257	0.797	0.06
Net primary production in Y3	-0.05213	0.16746	0.17748	0.294	0.769	0.04

Summary results of change in site-level means of ground-level light after model averaging; all factors are normalized. Soil nitrogen was included in the original models, but was never significant so was dropped from final models because of missing values.

Extended Data Table 7 | Effects of climate, nitrogen deposition, soil nitrogen and site productivity on site-level mean biomass change across experimental fencing treatments after 3 years of treatment

	Estimate	Std. Error	Adjusted SE	z value	p-value	Relative Importance
(Intercept)	0.12111	0.04966	0.05247	2.308	0.021	1.00
Dry Quarter Temperature	-0.66911	0.26088	0.27013	2.477	0.013	1.00
Annual Temperature Variability	-0.58513	0.28798	0.29564	1.979	0.048	0.63
Annual Precipitation Variability	-0.10096	0.13851	0.14446	0.699	0.485	0.63
Minimum Temperature	0.65583	0.29851	0.30830	2.127	0.033	0.52
Wet Quarter Temperature	-0.28870	0.29658	0.30660	0.942	0.346	0.29
Mean Annual Temperature	0.34511	0.40053	0.40959	0.843	0.400	0.29
Net primary production in Y3	-0.11616	0.10543	0.11130	1.044	0.297	0.15
Mean Annual Precipitation	-0.01959	0.11602	0.12206	0.160	0.873	0.10
Rainfall Potential Evapotranspir.	-0.06785	0.16203	0.16898	0.402	0.688	0.09
Annual N-Deposition Rate	-0.09961	0.14467	0.15200	0.655	0.512	0.09

Summary results of site-level means of biomass off-take after model averaging; all factors are normalized. Soil nitrogen was included in the original models, but was never significant so was dropped from final models because of missing values.

Extended Data Table 8 | Effects of climate, nitrogen deposition, soil nitrogen, site productivity, and change in light on change in site-level mean plant species richness across experimental fencing treatments after three years of treatments

	Estimate	Std. Error	Adjusted SE	z value	p-value	Relative Importance
(Intercept)	-0.05642	0.03317	0.03511	1.607	0.108	1.00
Change in light across fence	0.21878	0.08325	0.08734	2.505	0.012	1.00
Minimum Temperature	-0.16634	0.20331	0.20831	0.798	0.425	0.21
Maximum Temperature	0.15296	0.14054	0.14489	1.056	0.291	0.19
Change in mass across fence	-0.0941	0.08964	0.09495	0.991	0.322	0.13
Annual Temperature Variability	-0.0571	0.26403	0.26864	0.213	0.832	0.13
Rainfall Potential Evapotranspir.	-0.2268	0.32134	0.32656	0.695	0.487	0.13
Mean Annual Temperature	-0.17278	0.18625	0.19128	0.903	0.366	0.11
Annual N-Deposition Rate	-0.063	0.08599	0.09065	0.695	0.487	0.08
Mean Annual Precipitation	0.18256	0.28651	0.29187	0.625	0.532	0.07
Annual Precipitation Variability	0.05612	0.07807	0.08242	0.681	0.496	0.06
Dry Quarter Temperature	0.05108	0.12828	0.13300	0.384	0.701	0.06
Wet Quarter Temperature	0.03975	0.07086	0.07498	0.530	0.596	0.04
Net primary production in Y3	0.04017	0.07414	0.07845	0.512	0.609	0.04

Summary results of change in site-level means of plant richness after model averaging; all factors are normalized. Soil nitrogen was included in the original models, but was never significant so was dropped from final models because of missing values.