

Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory

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Although the impacts of the loss of biodiversity on ecosystem functioning are well established, the importance of the loss of biodiversity relative to other human-caused drivers of environmental change remains uncertain. Results of 11 experiments show that ecologically relevant decreases in grassland plant diversity influenced productivity at least as much as ecologically relevant changes in nitrogen, water, CO₂, herbivores, drought, or fire. Moreover, biodiversity became an increasingly dominant driver of ecosystem productivity through time, whereas effects of other factors either declined (nitrogen addition) or remained unchanged (all others). In particular, a change in plant diversity from four to 16 species caused as large an increase in productivity as addition of 54 kg·ha⁻¹·y⁻¹ of fertilizer N, and was as influential as removing a dominant herbivore, a major natural drought, water addition, and fire suppression. A change in diversity from one to 16 species caused a greater biomass increase than 95 kg·ha⁻¹·y⁻¹ of N or any other treatment. Our conclusions are based on >7,000 productivity measurements from 11 long-term experiments (mean length, ~ 13 y) conducted at a single site with species from a single regional species pool, thus controlling for many potentially confounding factors. Our results suggest that the loss of biodiversity may have at least as great an impact on ecosystem functioning as other anthropogenic drivers of environmental change, and that use of diverse mixtures of species may be as effective in increasing productivity of some biomass crops as fertilization and may better provide ecosystem services.

biogeochemistry | community ecology

Numerous experiments have found that biodiversity influences the primary productivity of ecosystems and other aspects of ecosystem functioning (1–6). It also is well established experimentally that productivity of many terrestrial ecosystems depends on the availability of limiting resources, such as soil nitrogen, water, and CO₂, on herbivory and disease, and on disturbances such as fire and drought. However, little work has compared the magnitude of biodiversity effects on productivity to those of other drivers of ecosystem productivity. Indeed, the importance of biodiversity has been questioned recently because of some seemingly divergent results provided by observational vs. experimental studies of the effects of biodiversity on ecosystem functioning (1–3, 7–16). A recent observational study (10) concluded that “the influence of small-scale diversity on productivity in mature natural systems is a weak force, both in absolute terms and relative to the effects of other controls on productivity.” A comparative study of 48 grassland sites on five continents found no consistent relation between diversity and productivity (9). Other studies have been interpreted as suggesting that biodiversity effects may be smaller than resource effects (12, 14), and perhaps dependent on trophic interactions (15, 17) or other ecosystem features (18). Thus, the importance of biodiversity relative to other potential driving variables remains uncertain.

Because ecosystem responses to such variables may depend on the type of ecosystem, its species composition and soils, abiotic variables including climate, and the magnitude of the change in

drivers, the resolution of this debate will require approaches that control for these potentially confounding factors. Here we compare effects on primary productivity of biodiversity with those of nitrogen addition, watering, elevated CO₂, fire, and herbivory by using results from 11 experiments that manipulated one or more of these factors over a period of 5 to 28 y (Tables 1 and 2). We controlled for many potentially confounding variables by performing all experiments on upland well-drained sandy soils of east-central Minnesota, and by using perennial grassland ecosystems of similar plant species compositions. We evaluate the relative importance of these drivers of ecosystem functioning by comparing the productivity of ecosystems in response to environmentally or societally relevant magnitudes of experimental changes in each driver.

Results and Discussion

Biodiversity affected annual biomass production at least as much as any other factor that we considered (Fig. 1). The greatest biomass difference observed on average across all years of the 11 experiments was from the comparison of reference plots planted with 16 species to plots planted with one species. It was significantly greater than all other responses ($P < 0.01$, Tukey contrasts) and 40% greater than the treatment with the next largest biomass difference, addition of 95 kg·ha⁻¹·y⁻¹ of N compared with reference plots receiving no N (Fig. 1A). The biomass difference for 95 kg·ha⁻¹ of N was significantly greater than for 34 kg·ha⁻¹ of N, CO₂ enrichment, drought, water addition, herbivore exclusion, or fire. A suite of treatments—biodiversity treatments of 16 vs. two species and 16 vs. four species, N addition of 54 and 34 kg·ha⁻¹, CO₂ enrichment, drought, water addition, and herbivore exclusion—had statistically indistinguishable biomass differences on average across all years (Fig. 1A).

Analyses of log response ratios of treatments (Fig. 1B) gave similar results on average across all years. The log response ratio for the 16 vs. one species comparison was significantly greater than for all other treatments ($P < 0.01$, Tukey contrast). Addition of 95 kg·ha⁻¹ of N had the next largest response. It differed ($P < 0.01$) from addition of 34 kg·ha⁻¹ of N, CO₂ enrichment, and fire suppression. Other treatments gave intermediate log response ratios that were generally indistinguishable ($P > 0.05$; Fig. 1B).

Our long-term experiments allow us to test for temporal shifts in the relative importance the treatments. Whether measured as biomass differences or log response ratios, we found that biodiversity effects increased over time, whereas effects of all other factors were time-independent or decreased (N addition). In particular, ANOVAs that used data from all years to determine effects of treatment, log(year) and the treatment × log(year) interaction on biomass difference or log ratios were highly significant overall (biomass difference, $R^2 = 0.63$, $F_{21,203} = 16.50$,

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Table 1. Summary of field experiments (N = 11)

Experimental variable	Variables used in analyses	Experiment period (no. years)	Experiment no./name	Source
Plant diversity	1, 2, 4 or 16 species	1994–2010 (15 y)	E120	25
Plant diversity	1, 4 or 16 species (only unfertilized and ambient CO ₂ plots)	1998–2010 (13 y)	E141 "BioCON"	3
Nitrogen addition	0, 34, 54 or 95 kg N·ha ⁻¹ ·y ⁻¹	1982–2004 (23 y)	E001	26
Nitrogen addition	0, 34, 54 or 95 kg N·ha ⁻¹ ·y ⁻¹	1982–1991 (10 y)	E002; Initial Disturbance	26
Water addition	Ambient rain or ~50% increase via watering (unfertilized plots only)	2007–2011 (5 y)	E248	20
Water addition	Ambient rain or ~50% increase via watering	1982–1991 (6 y)	E003	27
Drought	Ambient rain vs. ~50% decrease during 1987–1988 drought	1982–1990 (2 y)	E001	22
Herbivory	Unfenced or deer enclosure (unfertilized plots only)	2004–2010 (6 y)	E001-C	Present study*
Herbivory	Unfenced or insect and deer enclosure	1989–1995 (2 y; first and last years)	E062	28
Herbivory	Unfenced or deer enclosure (unfertilized plots only)	1982–1995 (1 y; last year)	E004-D plus Fenced Plots	29
Fire	Unburned or annual fire (unfertilized plots only)	1992–2004 (9 y)	E098	†
Fire	Unburned or annual fire	1983–2010 (5 y)	E012	30
CO ₂	Ambient CO ₂ or 560 ppm CO₂ via "FACE" (only 9 or 16 species plots that were unfertilized)	1998–2010 (13 y)	E141 "BioCON"	3

Variables listed in boldface are those with greater mean biomass; Cedar Creek experimental number or name; and sources of detailed methods for each experiment. See www.cedarcreek.umn.edu/research/data for additional information and for data.

*See *SI Methods*.

†See www.cedarcreek.umn.edu/research/data/All_Experiment_Methods.php?input=e098.

$P < 0.0001$; log ratio, $R^2 = 0.71$, $F_{21,203} = 24.06$, $P < 0.0001$). They also had strong treatment effects (biomass difference, $F_{10,203} = 25.71$, $P < 0.0001$; log ratio, $F_{10,203} = 38.39$, $P < 0.0001$), and significant treatment \times log(year) interactions (biomass difference, $F_{10,203} = 8.85$, $P < 0.0001$; log ratio, $F_{10,203} = 12.03$, $P < 0.0001$). Log(year) effects were not significant (biomass difference, $F_{1,203} = 0.95$, $P = 0.33$; log ratio, $F_{1,203} = 1.02$, $P = 0.31$). The biodiversity treatment effects (16 vs. one, two, or four species) increased (Fig. 2), whereas the N addition treatment effects (95, 54, and 34 kg N·ha⁻¹) decreased (Fig. 2) over time [treatment \times log(year) interaction, $P < 0.05$ for all cases]. There were no temporal trends for any other factors [treatment \times log(year) interactions, $P > 0.10$ for all cases] except that the log response ratio for herbivory increased over time ($P < 0.001$).

To further explore these temporal trends qualitatively, we determined the rank order of each the 11 treatments during different time segments of the experiments. When using data for the first 5 y of each experiment, the three biodiversity treatments (16 vs. one, 16 vs. two, and 16 vs. four species) ranked second, fifth, and sixth, respectively, for biomass differences and second, sixth, and seventh for log ratios (Tables S1 and S2). In contrast, on average from the sixth year and on, the three biodiversity treatments ranked first, second, and third for both biomass differences and log ratios, and were also first, second, and third for both measures for the ninth year and on (Tables S1 and S2).

These field experiments show that plant diversity is at least as influential as any of the other driving variables long known to impact ecosystem functioning. As would be expected, the effects

Table 2. Treatment categories used in analyses

Treatment category and reference for comparison	Plot-years		Treatment-years
	Treatment	Control	
CO ₂ : 560 ppm vs. ambient (9–16 species)	195	195	13
Diversity: 1 vs. 16 species	870	680	28
Diversity: 2 vs. 16 species	416		15
Diversity: 4 vs. 16 species	861		28
Drought: 1988 drought vs. before or after	23	46	8
Herbivory: fenced vs. unfenced	92	98	9
Fire: annually burned vs. unburned	96	96	14
Nitrogen addition: 34 kg·ha ⁻¹ vs. 0	709	1,238	33
Nitrogen addition: 54 kg·ha ⁻¹ vs. 0	709		33
Nitrogen addition: 95 kg·ha ⁻¹ vs. 0	709		33
Water: irrigation vs. ambient	79	79	11
Total	4,759	2,432	225

Each reported response compared growing-season peak aboveground living biomass of a treatment with its control (reference) as listed below. Analyses presented in this paper averaged all replicates of a treatment in a given year and experiment, and compared that mean to the average of all replicates of the reference plots for that same year and experiment. For our analyses, each year of an experiment contributed one such data point per treatment. Our analyses thus are based on 225 data points, which is the total number of treatment-years of data derived from a total of 7,191 plot-level treatment and reference data points.

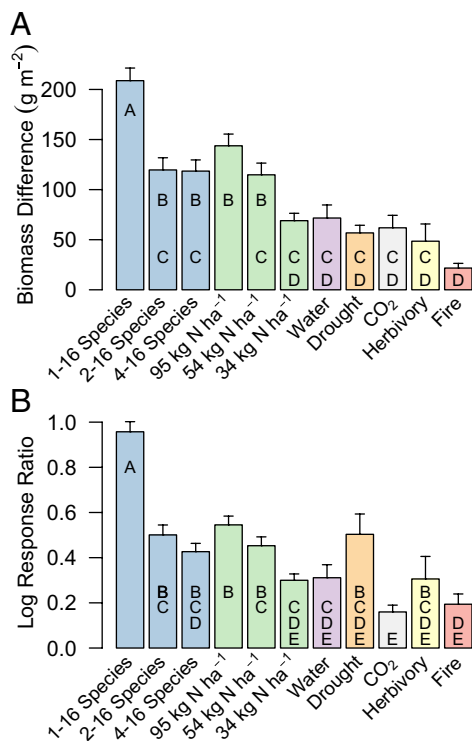


Fig. 1. Relative influences of biotic and abiotic factors on productivity. Productivity effects are shown as (A) biomass differences and (B) relative change (log response ratio). Treatment effect means significantly differed on both scales (biomass difference, $F_{10,214} = 18.81$, $P < 0.0001$; log response ratio, $F_{10,214} = 25.33$, $P < 0.0001$). Bars with the same letter within each panel do not significantly differ at the $P < 0.01$ level based on Tukey contrasts (corrected for multiple comparisons).

of treatments depended on the magnitude of the manipulation (Fig. 1). For these grassland communities, a change in plant diversity from four to 16 species led to as large an increase in plant productivity as the increase that resulted from annual addition of 54 kg·ha⁻¹ of N, and was as influential as removing a dominant herbivore, a major natural drought, water addition, and fire suppression. Moreover, the change in diversity from one to 16 species caused a greater plant biomass increase than did annual addition of 95 kg·ha⁻¹ of fertilizer N or any other treatment.

These comparisons should be evaluated in the context of the native grassland ecosystems of this region and of the natural differences and anthropogenic impacts they experience. Native savanna grasslands at our site average 10 plant species per 0.5-m² quadrat (19), 16.3 species per 1.0-m² quadrat (20), and 45 species per 0.375 ha (19). In contrast, 20 former prairie sites (21) that had been farmed and then restored to grassland through the Conservation Reserve Program had a median of three species per 1.0-m² quadrat, a mean of 3.5 species, and a range of one to eight species per 1.0 m². Furthermore, monocultures of perennial grassland plant species are increasingly studied as potential sources of biomass for biofuels. The 16 species treatment is thus representative of high-diversity native vegetation, whereas one, two, and four species treatments have diversity similar to potential biomass crops (i.e., grasses grown as monocultures) and to other regional grasslands of anthropogenic origin (but might have lower productivity than biomass crops chosen because they have high productivity). Because soil N mineralization rates at our site (22) range from ~34 to 80 kg N·ha⁻¹·y⁻¹, addition of as much as ~50 kg N·ha⁻¹·y⁻¹ would move a system from low to high soil N status. The five driest years of the past 150 y had growing season precipitation approximately 50% less than the mean, and the five

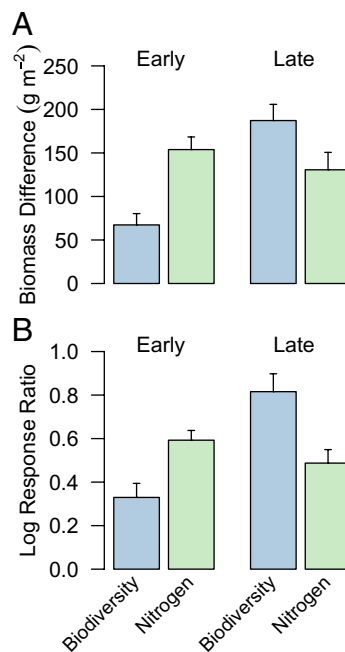


Fig. 2. Temporal trends in effect sizes. Effects of biodiversity on productivity increased through time whereas those of N decreased, switching their relative importance. Because all biodiversity treatments had similar increases through time and all N treatments had similar temporal declines, their treatments levels were combined for this analysis. For biomass difference (A) and log response ratio (B), means and SEs are shown for years 1 to 3 (early) and years 11 to 13 (late). Biodiversity treatments are blue bars (16:1, 16:2, and 16:4 treatment levels combined) and N treatments are green bars (95, 54, and 34 kg·ha⁻¹·y⁻¹ of N treatment levels combined). Treatment-year interactions were significant ($P < 0.0001$; statistical details are provided in the text).

wettest approximately 50% greater than the mean (23), placing our water treatments within this range of observed climatic variation. Our CO₂ treatments compare current levels with 560 ppm of CO₂, a level projected for late this century (3). Our herbivory treatment compares the presence or absence of the remaining large herbivore, deer; however, it does not consider effects of bison and elk, now regionally extirpated. Our fire treatment compares the absence of fire, currently common because of fire suppression, vs. annual fires, which were common before European settlement. Treatments that fall within the ranges imposed by natural and anthropogenic processes (i.e., all treatments except 95 kg N·ha⁻¹·y⁻¹ and perhaps one vs. 16 species because biofuel crops are rarely grown at present) show that diversity and nitrogen have the largest average effects across all years of the experiments, but often do not significantly differ from other treatments.

Conclusions

Our experimental finding that biodiversity is as important a determinant of grassland productivity as abiotic variables, disturbance, and herbivory may seem, on its surface, to contradict patterns reported in some comparisons across natural plant communities (9, 10). Although more research will be needed to determine the causes of these apparent differences, we offer a few speculations.

First, most natural plant communities have high plant diversity, which limits the ability of observations to reveal the effects of a change from high to low diversity. For example, native savanna grassland at our site that averaged 16.3 species per 1.0-m² quadrat and had only 8% of plots with <12 species and none with fewer than five species (20). Second, diversity effects may be amplified or nullified by other factors, such as

food web structure (15, 17, 24), the effects of which may be as great as those of plant diversity. For example, although algal biomass production increased with algal diversity in a study of a benthic marine community, this effect was masked when herbivores were present because, in this case, the increased production was consumed by herbivores (15). Third, the potential effects of biodiversity on productivity may at least partially result from the effects of diversity on abiotic factors, such as the higher levels of soil N and C that accumulated in the higher plant diversity treatments (11). Analyses of observational data that do not properly allow for such indirect paths could misattribute causation. Fourth, many observational studies are performed across much larger spatial scales than biodiversity experiments. Because climate and soils are likely to be highly similar among plots of a given biodiversity experiment, but to differ greatly in large-scale observational studies, the former seem more likely to detect biodiversity effects and the latter to detect climate and soil effects on productivity. Finally, we must also note that diversity and species composition are approximately equally important determinants of productivity (1–4, 16). If low-diversity natural communities or monoculture biomass crops tended to contain the more productive species, their productivity would not differ as much from the productivity of high-diversity communities as biodiversity experiments would predict because biodiversity experiments have been designed to consider random species loss. The nonrandom loss of species provides a fifth possible explanation for the differences between observational and experimental studies of biodiversity and productivity.

Our long-term experiments show that changes in diversity of the magnitude being imposed by human actions can have at least as great an effect on primary productivity as anthropogenic changes in atmospheric CO₂, the availability of a limiting soil resource, herbivory, fire, and variation in water availability. Although natural plant communities are limited by different abiotic and biotic forces in different regions (24), and although additional experiments are needed to determine the generality of our results, our results strongly suggest that contemporary biodiversity declines are among the dominant drivers of changes in ecosystem functioning, and that restoration of biodiversity in managed and seminatural ecosystems may be an efficient way to restore desired ecosystem services.

Methods

The 11 long-term field experiments were all performed at Cedar Creek Ecosystem Science Reserve, Bethel, MN. Our experiments manipulated one or more of the following variables: biodiversity, nitrogen, water, CO₂, fire, and herbivory (Table 1). Responses to treatments were often measured annually. In addition, plots in one experiment were used to record effects of a major drought by comparing biomass 1 y before drought began (1986) with biomass during the peak drought year (1988) and that attained 1 y after the drought ended (1990).

All analyses presented here use, for each year of a given experiment, the mean of the aboveground biomass production across all replicates (from two to >30) of a treatment (Table 2). We test for long-term consistent differences between drivers by comparing multiple years of such annual treatment means. In particular, for each sampled year of each experiment, we use mean production across all replicates of a treatment to derive two metrics. The first metric, the biomass difference, is the absolute value of [(mean treatment biomass) – (mean reference plot biomass)], where reference plots were unmanipulated or otherwise had more natural conditions, such as high diversity and ambient CO₂. The second metric, the log response ratio, is the absolute value of $\log_e[(\text{mean treatment biomass}) / (\text{mean reference plot biomass})]$. It measures, on a log scale, the proportional change in treatment plots relative to reference plots. Each metric has one value per treatment per year for each experiment, for a total of 225 observations that summarize annual values derived from >4,700 biomass measurements across all years of all treatment plots and from >2,400 reference plots (Table 2). The use of absolute values made all differences from the control plot values be positive numbers. Because each treatment had, with a few inconsequential exceptions for CO₂ and fire, year-to-year consistency in the sign (i.e., + or –) of its biomass differences from its control, the use of absolute values did not bias analyses and allowed comparison of effect sizes among treatments whether the effects were increases or decreases relative to the natural conditions represented by the controls. We used ANOVA to test for treatment effects and Tukey contrasts to correct for multiple comparisons. For detailed methods and original data see www.cedarcreek.umn.edu/research/data/.

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Supporting Information

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SI Methods

Some of our experiments manipulated a single factor, such as the rate of N addition (1), water addition (2), drought (3), herbivory (4, 5), fire frequency (6), or diversity (1, 7), whereas others were factorial manipulations of water and N (8), N and herbivory, N and fire, or biodiversity, CO₂, and N (9). Responses reported here focus on effects of single factors. In multifactor experiments, we calculate factor effects only from those plots in which other variables were unmanipulated or otherwise at “natural levels.” For example, for the diversity/CO₂/N experiment (9), reported diversity effects are just from plots at ambient CO₂ with no N addition; CO₂ effects are for high biodiversity (n = 9 or 16 species) plots with no N addition. Because N was added at a different rate (40 kg N·ha⁻¹ y⁻¹) in the diversity/CO₂/N ex-

periment (9) than in our other N addition experiments, we did not include the N addition data from the diversity/CO₂/N experiment in the analyses we present. Inclusion of these data by placing them in the closest category, 34 kg N·ha⁻¹ y⁻¹, lowered the mean biomass difference and log ratio values for this category approximately 10%, had no qualitative effect on results or comparisons of the effect sizes of the different treatments.

Herbivory experiment E001-C was established by D.T. in fall 2004 by enclosing in deer fences three randomly selected plots from the six replicates of each control and each treatment in the N addition experiment in field C. Plant biomass samples have been clipped, sorted to species, dried, and weighed annually, in late July, beginning in 2005. Here we compare aboveground living plant biomass in plots receiving no N that were fenced or unfenced.

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Table S1. Effects of the biodiversity treatments increased through time

Treatment	Years 1–5		Years 6+		Years 9+	
	Rank	Mean	Rank	Mean	Rank	Mean
Biomass difference						
Diversity 16 vs. 1	2	158	1	237	1	236
Diversity 16 vs. 4	6	71	2	145	2	146
Diversity 16 vs. 2	5	74	3	143	3	139
N addition 95 kg/ha	1	208	4	116	4	118
N addition 54 kg/ha	3	139	5	104	5	118
Water	7	65	6	89	6	104
Fenced (herbivory)	10	19	7	85	7	90
CO ₂	9	52	8	68	8	68
N addition 34 kg/ha	4	98	9	56	9	60
Drought	8	64	10	50	10	50
Fire	11	19	11	24	11	18
Log response ratio						
Diversity 16 vs. 1	2	0.74	1	1.08	1	1.12
Diversity 16 vs. 2	6	0.33	2	0.59	2	0.60
Diversity 16 vs. 4	7	0.26	3	0.52	3	0.54
Fence (herbivory)	8	0.25	8	0.38	4	0.50
N addition 95 kg/ha	1	0.77	5	0.45	5	0.44
N addition 54 kg/ha	4	0.57	7	0.40	6	0.44
Drought	3	0.58	6	0.43	7	0.43
Water	9	0.25	4	0.49	8	0.38
N addition 34 kg/ha	5	0.43	9	0.24	9	0.25
Fire	11	0.14	10	0.23	10	0.21
CO ₂	10	0.15	11	0.17	11	0.17

For each response variable, treatments are listed in order from the greatest to lowest mean as observed for years 9 and on.

Table S2. Mean aboveground biomass (in $\text{g}\cdot\text{m}^{-2}$) for each time interval for control and treatment plots associated with each treatment

Treatment	Years 1–5		Years 6+		Years 9+	
	Control	Treatment	Control	Treatment	Control	Treatment
Diversity 16 vs. 1	300	142	360	123	350	114
Diversity 16 vs. 2	257	183	322	179	310	171
Diversity 16 vs. 4	300	229	360	215	350	205
N addition 95 kg/ha	180	388	198	314	213	331
N addition 54 kg/ha	180	319	198	302	213	330
Fenced (herbivory)	118	135	188	273	140	230
Water	248	308	157	245	227	331
CO ₂	314	366	409	435	398	399
N addition 34 kg/ha	180	278	198	254	213	272
Drought	164	100	150	100	150	100
Fire	128	136	112	109	108	90

Note that the “diversity 16 vs. 1” and the “diversity 16 vs. 4” treatments occurred in both the E120 Bio-diversity Experiment and in the E141 BioCON experiment, but that the “diversity 16 vs 2” treatment occurred only in E120. In a few cases, the difference between the mean control and treatment values does not equal the biomass differences in Table S1 because the latter values are means of the absolute values of the biomass differences. If annual differences are negative some years and positive others, means would be less than the means of their absolute values, which occurs late in the experiment for CO₂ and early for fire.