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

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Contributed by David Tilman, May 15, 2012 (sent for review March 30, 2012)

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 yr⁻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 yr⁻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.

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 yr⁻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, R² = 0.63, F₂₇,₂₀₃ = 16.50, P = 0.0001).

Author contributions: D.T. and P.B.R. designed research; D.T. and P.B.R. performed research; D.T., P.B.R., and F.I. analyzed data; and D.T., P.B.R., and F.I. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.orglookup/suppl/doi:10.1073/pnas.1208240109/-DCSupplemental.
Table 1. Summary of field experiments (N = 11)

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

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 × 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 × log(year) interaction, P < 0.05 for all cases]. There were no temporal trends for any other factors [treatment × log(year) interactions, P > 0.10 for all cases] except that the log response ratio for herbivory increased over time (P < 0.0001).

Table 2. Treatment categories used in analyses

<table>
<thead>
<tr>
<th>Treatment category and reference for comparison</th>
<th>Plot-years</th>
<th>Treatment-years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>Control</td>
<td></td>
</tr>
<tr>
<td>CO2: 560 ppm vs. ambient (9–16 species)</td>
<td>195</td>
<td>195</td>
</tr>
<tr>
<td>Diversity: 1 vs. 16 species</td>
<td>870</td>
<td>680</td>
</tr>
<tr>
<td>Diversity: 2 vs. 16 species</td>
<td>416</td>
<td>15</td>
</tr>
<tr>
<td>Diversity: 4 vs. 16 species</td>
<td>861</td>
<td>28</td>
</tr>
<tr>
<td>Drought: 1988 drought vs. before or after</td>
<td>23</td>
<td>46</td>
</tr>
<tr>
<td>Herbivory: fenced vs. unfenced</td>
<td>92</td>
<td>98</td>
</tr>
<tr>
<td>Fire: annually burned vs. unburned</td>
<td>96</td>
<td>96</td>
</tr>
<tr>
<td>Nitrogen addition: 34 kg ha^{-1} vs. 0</td>
<td>709</td>
<td>1,238</td>
</tr>
<tr>
<td>Nitrogen addition: 54 kg ha^{-1} vs. 0</td>
<td>709</td>
<td>33</td>
</tr>
<tr>
<td>Nitrogen addition: 95 kg ha^{-1} vs. 0</td>
<td>709</td>
<td>33</td>
</tr>
<tr>
<td>Water: irrigation vs. ambient</td>
<td>79</td>
<td>79</td>
</tr>
<tr>
<td>Total</td>
<td>4,759</td>
<td>2,432</td>
</tr>
</tbody>
</table>

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.

To further explore these temporal trends qualitatively, we determined the rank order of each of 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 of biodiversity...
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 N·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 suppression. Moreover, the change in diversity from one to 16 species 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 N·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 N·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 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 biotic factors on productivity. Effects of a change from high to low diversity. 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).

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 savannah 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 her-
ivores were present because, in this case, the increased pro-
duction 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 di-
versity 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 expres-
sions were generally designed to consider random species loss.
The nonrandom loss of species provides a fifth possible expla-
nation for the differences between observational and experi-
mental 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 of 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 de-
clines 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 bio-
mass 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 differ-
ences between drivers by comparing multiple years of such annual treat-
ment 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). 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 few inconsistent 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.cedarreek.unl.edu/researchdata/.

ACKNOWLEDGMENTS.
The authors thank Troy Mielke, Dan Bahauddin, Kally Worm, and many summer interns for their assistance with this research; and Belinda Befort for assistance in preparing the manuscript. This work was supported by National Science Foundation (NSF) Long-Term Ecological Research Network Grants 9411972, 0080382, and 0620652; NSF Biocomplex-
ity Grant 0322057; NSF Long-Term Research in Environmental Biology Grant 0716587; US Department of Energy Grants DE-FG02-96ER62291 and DE-
FC02-06ER64158; the Andrew Mellon Foundation; and the Minnesota Envi-
noment and Natural Resources Trust Fund.

current knowledge. Ecol Monogr 75:3–35.
5. Balvanera P, et al. (2006) Quantifying the evolution for biodiversity effects on eco-
7. Duffy JE (2009) Why biodiversity is important to the functioning of real-world eco-
8. Wardle DA, Johnson NM (2010) Biodiversity effects in real ecosystems - a response to
11. Fornara DA, Tilman D (2009) Ecological mechanisms associated with the positive
influence of resource ‘availability’ from resource ‘imbalance’ on productivity-diversity
and composition are of similar importance for grassland productivity. PLoS ONE 6:e17434.
19. Peterson DW, Reich PB (2008) Fire frequency and tree canopy structure influence
20. Tilman D (1997) Community invisibility, recruitment limitation, and grassland bio-
28. Ritchie M, Tilman D, Knops JMH (1998) Herbivore effects on plant and nitrogen dy-
29. Knops JMH, Ritchie M, Tilman D (2000) Selective herbivory on a nitrogen fixing le-
gume (Lathyrus vernus) influences productivity and ecosystem nitrogen pools in an
Supporting Information

Tilman et al. 10.1073/pnas.1208240109

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, \(\text{CO}_2\), 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/\(\text{CO}_2\)/N experiment (9), reported diversity effects are just from plots at ambient \(\text{CO}_2\) with no N addition; \(\text{CO}_2\) 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/\(\text{CO}_2\)/N experiment (9) than in our other N addition experiments, we did not include the N addition data from the diversity/\(\text{CO}_2\)/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.


### Table S1. Effects of the biodiversity treatments increased through time

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Years 1–5</th>
<th>Years 6+</th>
<th>Years 9+</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rank</td>
<td>Mean</td>
<td>Rank</td>
</tr>
<tr>
<td>Biomass difference</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diversity 16 vs. 1</td>
<td>2</td>
<td>158</td>
<td>1</td>
</tr>
<tr>
<td>Diversity 16 vs. 4</td>
<td>6</td>
<td>71</td>
<td>2</td>
</tr>
<tr>
<td>Diversity 16 vs. 2</td>
<td>5</td>
<td>74</td>
<td>3</td>
</tr>
<tr>
<td>N addition 95 kg/ha</td>
<td>1</td>
<td>208</td>
<td>4</td>
</tr>
<tr>
<td>N addition 54 kg/ha</td>
<td>3</td>
<td>139</td>
<td>5</td>
</tr>
<tr>
<td>Water</td>
<td>7</td>
<td>65</td>
<td>6</td>
</tr>
<tr>
<td>Fenced (herbivory)</td>
<td>10</td>
<td>19</td>
<td>7</td>
</tr>
<tr>
<td>CO2</td>
<td>9</td>
<td>52</td>
<td>8</td>
</tr>
<tr>
<td>N addition 34 kg/ha</td>
<td>4</td>
<td>98</td>
<td>9</td>
</tr>
<tr>
<td>Drought</td>
<td>8</td>
<td>64</td>
<td>10</td>
</tr>
<tr>
<td>Fire</td>
<td>11</td>
<td>19</td>
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<tr>
<td>Log response ratio</td>
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<td>Diversity 16 vs. 1</td>
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<td>0.74</td>
<td>1</td>
</tr>
<tr>
<td>Diversity 16 vs. 2</td>
<td>6</td>
<td>0.33</td>
<td>2</td>
</tr>
<tr>
<td>Diversity 16 vs. 4</td>
<td>7</td>
<td>0.26</td>
<td>3</td>
</tr>
<tr>
<td>Fence (herbivory)</td>
<td>8</td>
<td>0.25</td>
<td>8</td>
</tr>
<tr>
<td>N addition 95 kg/ha</td>
<td>1</td>
<td>0.77</td>
<td>5</td>
</tr>
<tr>
<td>N addition 54 kg/ha</td>
<td>4</td>
<td>0.57</td>
<td>7</td>
</tr>
<tr>
<td>Drought</td>
<td>3</td>
<td>0.58</td>
<td>6</td>
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<tr>
<td>Water</td>
<td>9</td>
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<tr>
<td>N addition 34 kg/ha</td>
<td>5</td>
<td>0.43</td>
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<tr>
<td>Fire</td>
<td>11</td>
<td>0.14</td>
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</tr>
<tr>
<td>CO2</td>
<td>10</td>
<td>0.15</td>
<td>11</td>
</tr>
</tbody>
</table>

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 g·m⁻²) for each time interval for control and treatment plots associated with each treatment

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Years 1–5</th>
<th></th>
<th></th>
<th>Years 6+</th>
<th></th>
<th></th>
<th>Years 9+</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Treatment</td>
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<td>Treatment</td>
<td>Control</td>
<td>Treatment</td>
<td>Control</td>
<td>Treatment</td>
</tr>
<tr>
<td>Diversity 16 vs. 1</td>
<td>300</td>
<td>142</td>
<td>360</td>
<td>123</td>
<td>350</td>
<td>114</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diversity 16 vs. 2</td>
<td>257</td>
<td>183</td>
<td>322</td>
<td>179</td>
<td>310</td>
<td>171</td>
<td></td>
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<tr>
<td>Diversity 16 vs. 4</td>
<td>300</td>
<td>229</td>
<td>360</td>
<td>215</td>
<td>350</td>
<td>205</td>
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</tr>
<tr>
<td>N addition 95 kg/ha</td>
<td>180</td>
<td>388</td>
<td>198</td>
<td>314</td>
<td>213</td>
<td>331</td>
<td></td>
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</tr>
<tr>
<td>N addition 54 kg/ha</td>
<td>180</td>
<td>319</td>
<td>198</td>
<td>302</td>
<td>213</td>
<td>330</td>
<td></td>
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</tr>
<tr>
<td>Fenced (herbivory)</td>
<td>118</td>
<td>135</td>
<td>188</td>
<td>273</td>
<td>140</td>
<td>230</td>
<td></td>
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<tr>
<td>Water</td>
<td>248</td>
<td>308</td>
<td>157</td>
<td>245</td>
<td>227</td>
<td>331</td>
<td></td>
<td></td>
</tr>
<tr>
<td>CO₂</td>
<td>314</td>
<td>366</td>
<td>409</td>
<td>435</td>
<td>398</td>
<td>399</td>
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<tr>
<td>N addition 34 kg/ha</td>
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<td>278</td>
<td>198</td>
<td>254</td>
<td>213</td>
<td>272</td>
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<tr>
<td>Drought</td>
<td>164</td>
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<td>150</td>
<td>100</td>
<td>150</td>
<td>100</td>
<td></td>
<td></td>
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<tr>
<td>Fire</td>
<td>128</td>
<td>136</td>
<td>112</td>
<td>109</td>
<td>108</td>
<td>90</td>
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</table>

Note that the “diversity 16 vs. 1” and the “diversity 16 vs. 4” treatments occurred in both the E120 Biodiversity 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.