

genetics and genomics tools, water striders provide a model to reconstruct the genetic and adaptive paths to morphological diversity.

References and Notes

1. G. Arnqvist, L. Rowe, *Sexual Conflict* (Princeton Univ. Press, Princeton, NJ, 2005).
2. G. Arnqvist, L. Rowe, *Nature* **415**, 787 (2002).
3. R. Bonduriansky, S. F. Chenoweth, *Trends Ecol. Evol.* **24**, 280 (2009).
4. D. Hosken, R. Snook, *Am. Nat.* **165** (suppl. 5), S1 (2005).
5. T. Tregenza, N. Wedell, T. Chapman, *Philos. Trans. R. Soc. London Ser. B* **361**, 229 (2006).
6. T. M. Williams, S. B. Carroll, *Nat. Rev. Genet.* **10**, 797 (2009).
7. D. J. Emlen, L. Corley Lavine, B. Ewen-Campen, *Proc. Natl. Acad. Sci. U.S.A.* **104** (suppl. 1), 8661 (2007).
8. A. P. Moczek, D. J. Rose, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 8992 (2009).
9. T. M. Williams *et al.*, *Cell* **134**, 610 (2008).
10. L. Rowe, G. Arnqvist, *Evolution* **56**, 754 (2002).
11. L. Rowe, K. Westlake, D. C. Currie, *Can. Entomol.* **138**, 568 (2006).
12. K. P. Westlake, L. Rowe, D. C. Currie, *Syst. Entomol.* **25**, 125 (2000).
13. A. Beermann *et al.*, *Development* **128**, 287 (2001).
14. A. Khila, M. Grbić, *Dev. Genes Evol.* **217**, 241 (2007).
15. G. Panganiban, *Dev. Dyn.* **218**, 554 (2000).
16. G. Panganiban *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 5162 (1997).
17. E. F. Kirkness *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 12168 (2010).
18. J. Damgaard *et al.*, *Syst. Entomol.* **30**, 289 (2005).
19. L. Rowe, G. Arnqvist, A. Sih, J. J. Krupa, *Trends Ecol. Evol.* **9**, 289 (1994).
20. D. R. Angelini, T. C. Kaufman, *Dev. Biol.* **286**, 57 (2005).
21. A. Khila, E. Abouheif, L. Rowe, *PLoS Genet.* **5**, e1000583 (2009).
22. T. Werner, S. Koshikawa, T. M. Williams, S. B. Carroll, *Nature* **464**, 1143 (2010).
23. F. W. Buaas, P. Val, A. Swain, *Hum. Mol. Genet.* **18**, 2989 (2009).
24. R. Clifford *et al.*, *Development* **127**, 5265 (2000).
25. K. Tanaka, O. Barmina, L. E. Sanders, M. N. Arbeitman, A. Kopp, *PLoS Biol.* **9**, e1001131 (2011).

Acknowledgments: Supported by the Canada Research Chairs program and the Natural Sciences and Engineering Research Council of Canada (L.R. and E.A.) and by ATIP-Avenir program CNRS France (A.K.). We thank G. Arnqvist, A. Bruce, and M. Sokolowski for comments; H. Rodd and A. Agrawal for sharing their high-speed camera; and S. B. Carroll for the Dll antibody. DNA sequences were deposited in GenBank (accession nos. JQ639098, JQ639093, JQ639097, JQ639094, JN936863, JQ639092, JQ639096, and JQ639095).

Supplementary Materials

www.sciencemag.org/cgi/content/full/336/6081/585/DC1
Materials and Methods
Figs. S1 to S9
Table S1
Movies S1 to S3
References (26, 27)

30 November 2011; accepted 23 March 2012
10.1126/science.1217258

Impacts of Biodiversity Loss Escalate Through Time as Redundancy Fades

Peter B. Reich,^{1,2} David Tilman,^{3,4} Forest Isbell,³ Kevin Mueller,³ Sarah E. Hobbie,³ Dan F. B. Flynn,⁵ Nico Eisenhauer^{1,6}

Plant diversity generally promotes biomass production, but how the shape of the response curve changes with time remains unclear. This is a critical knowledge gap because the shape of this relationship indicates the extent to which loss of the first few species will influence biomass production. Using two long-term (≥ 13 years) biodiversity experiments, we show that the effects of diversity on biomass productivity increased and became less saturating over time. Our analyses suggest that effects of diversity-dependent ecosystem feedbacks and interspecific complementarity accumulate over time, causing high-diversity species combinations that appeared functionally redundant during early years to become more functionally unique through time. Consequently, simplification of diverse ecosystems will likely have greater negative impacts on ecosystem functioning than has been suggested by short-term experiments.

Experiments in grasslands regularly indicate strong plant diversity effects on biomass production (1–16), and some analyses indicate that relatively few of the species in any diverse mixture promote productivity (1, 5). However, many important temporal aspects of the diversity-productivity relationship remain obscure, including whether and how its shape changes over time, because most biodiversity experiments have been short (≤ 4 years typically, median ≈ 2 years) (10).

Prior studies have characterized the response of plant biomass to species richness as saturating (1, 7) or as continuously increasing, but in a decelerating manner (6, 8, 9). A recent meta-analysis (1) showed that saturating Michaelis-Menten curves were often the best statistical fit to the diversity-productivity relationship, suggesting losses of one or a few species at high richness levels could have minimal consequences for productivity.

Several experiments showed that the positive effects of species richness on biomass and productivity increased over time (6, 8, 10, 12–15), but implications of such changes for the shape of the diversity-productivity relationship are unknown. Two possibilities can be distinguished: (i) differences between low and intermediate diversity levels grow, resulting in an elevated but saturating response curve (fig. S1, scenario I); or (ii) diversity effects become progressively greater at higher diversity, resulting in an elevated and more linear response curve (fig. S1, scenario II,

nonsaturating response curve). These scenarios have fundamentally different implications for the consequences of biodiversity loss. If response curves become less saturating over time, losses of even very few species from diverse assemblages could cause substantial declines in productivity.

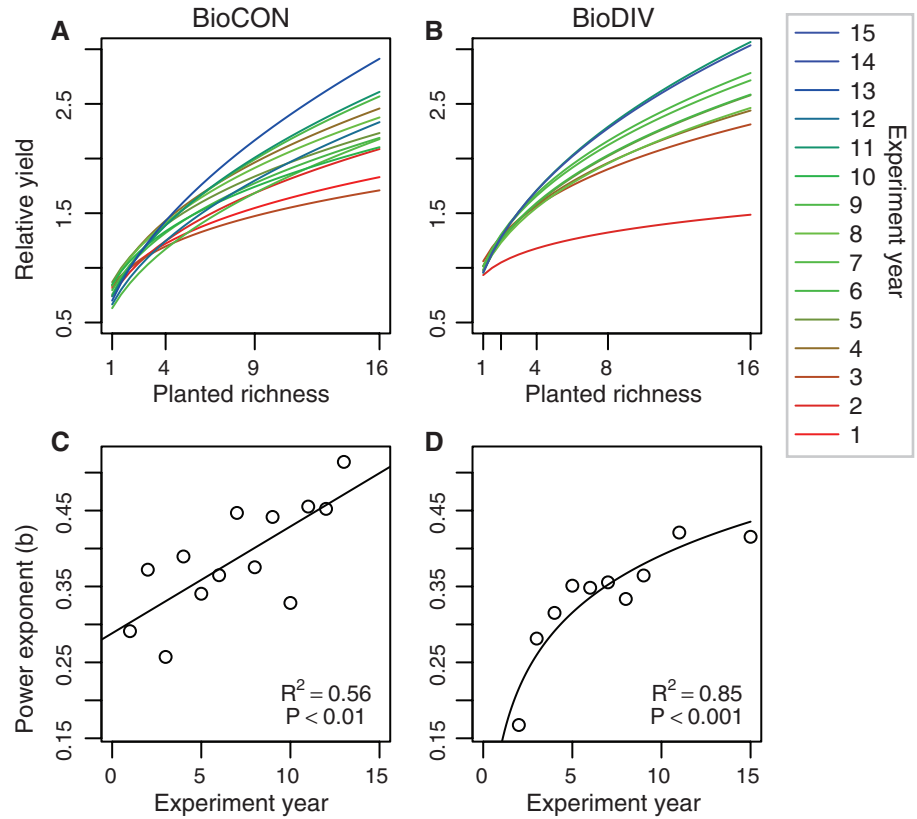
Several studies have assessed how biodiversity influences multiple functions within 1 year or across multiple years (2, 4, 5), but identifying what proportion of the available species pool contributes to multifunctionality does not address the question of whether species are redundant with respect to a single function, such as productivity, in a single year, let alone how that changes with time. We examined this latter issue by considering how the influence of biodiversity on productivity within each year changes from the early to the late years of two long-term experiments.

We present data from two long-running (≥ 13 years) grassland biodiversity experiments in Minnesota, USA: the “Cedar Creek Biodiversity Experiment” (BioDIV), planted in 1994–1995, and the “Biodiversity, CO₂, and N Experiment” (BioCON), planted in 1997 (6, 17–21). These independent, comparable experiments allow us to assess temporal variation in the response of biomass to planted and realized species richness. Species pools differed somewhat in the two experiments, although both include many of the same C3 and C4 grasses, and nitrogen (N)-fixing and nonfixing dicotyledonous herbs. BioCON included elevated carbon dioxide and enriched N treatments (18, 19), but only the ambient plots are considered here to facilitate comparison with BioDIV. In both experiments, the species richness across treatments ranged from 1 to 16 species, spanning the typical range observed from disturbed to native grassland (17).

In both experiments, the number of planted species explained an increasingly greater fraction of the variance in total plant biomass over time and had a larger effect on total plant biomass over time (Fig. 1, Table 1, and table S1). More-

¹Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA. ²Hawkesbury Institute for the Environment, University of Western Sydney, Penrith NSW 2753, Australia. ³Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA. ⁴Bren School of the Environment, University of California, Santa Barbara, CA 93106, USA. ⁵Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich 8057, Switzerland. ⁶Department of Ecology and Ecosystem Management, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany.

Fig. 1. (A and B) The power function of the relative yield of total biomass (above- plus belowground, 0 to 20 or 0 to 30 cm depth, respectively) in relation to planted species richness, across years in the BioCON and BioDIV experiments. Relative yield was defined by dividing plot-level values by the mean monoculture yield, averaged across all monoculture plots within each year. Details of all fits are provided in Table 1. (C and D) The exponent of the power function in relation to experimental years.



over, the relationship became increasingly non-saturating (17) over the range of species richness levels used (Fig. 1 and Table 1). The increasing linearity is illustrated first by comparing the Akaike Information Criterion (AIC) values of saturating functions (Michaelis-Menten) with decelerating functions. The saturating function is the best model by AIC only in the first few years in BioCON and is a poorer model than decelerating functions (especially the power function) in most years late in both experiments (table S1). Second, the exponent from the power function fits (“b”) increased over time in both experiments (Fig. 1 and Table 1), with increases from 0 toward 1, indicating that the diversity-productivity relationship is becoming more linear and less strongly decelerating. Consequently, we also observed increases over time for estimates of the number of planted species required to yield 90% of the biomass in 16 species plots (the number of species required to generate most of the diversity effect on biomass in a given year) (fig. S2). Results were similar when we considered aboveground or belowground biomass separately, when we considered absolute biomass, and when we considered observed richness instead of planted richness (figs. S3 to S5 and tables S2 and S3).

Because the statistical fits for the biodiversity functions are imperfect at establishing the precise shape of the relations, directly comparing across species-richness treatments illuminates the role

Table 1. Model fit statistics for the power function describing the relationship between relative biomass yield (Y) and planted richness (S). Relative biomass yield was defined by dividing plot-level values by the mean monoculture yield, averaged across all monoculture plots within each year.

Study	DF	Year	Power: $\ln(Y) = a + b \times \ln(S)$			
			R^2	P value	a	b
BioCON	71	1998	0.24	1.3×10^{-5}	-0.20	0.29
	72	1999	0.24	9.0×10^{-6}	-0.30	0.37
	72	2000	0.19	1.2×10^{-4}	-0.18	0.26
	71	2001	0.34	5.1×10^{-8}	-0.18	0.39
	72	2002	0.38	5.9×10^{-9}	-0.14	0.34
	72	2003	0.34	6.3×10^{-8}	-0.23	0.36
	70	2004	0.23	2.3×10^{-5}	-0.46	0.45
	70	2005	0.40	2.9×10^{-9}	-0.18	0.38
	71	2006	0.34	6.1×10^{-8}	-0.28	0.44
	64	2007	0.35	1.4×10^{-7}	-0.17	0.33
	64	2008	0.39	1.7×10^{-8}	-0.30	0.46
64	2009	0.31	1.2×10^{-6}	-0.41	0.45	
63	2010	0.39	2.2×10^{-8}	-0.36	0.51	
BioDIV	150	1997	0.08	3.3×10^{-4}	-0.07	0.17
	150	1998	0.24	2.3×10^{-10}	0.06	0.28
	150	1999	0.31	1.2×10^{-13}	0.02	0.32
	150	2000	0.37	6.5×10^{-17}	-0.03	0.35
	150	2001	0.39	8.3×10^{-18}	-0.02	0.35
	150	2002	0.43	6.3×10^{-20}	0.01	0.36
	150	2003	0.38	2.1×10^{-17}	-0.02	0.33
	150	2004	0.45	5.6×10^{-21}	0.01	0.36
	150	2006	0.48	2.8×10^{-23}	-0.05	0.42
	150	2010	0.52	1.3×10^{-25}	-0.04	0.42

that different levels of richness played in biodiversity effects at different times during the experiments (Fig. 2 and figs. S6 and S7). In the first 4 years of both experiments, the effect on biomass (shown as \log_{10} [biomass ratios]) of an increase in richness from one to four species was strong (Fig. 2C), whereas the increase in richness from medium (eight or nine species) to high (16 species) diversity was negligible (Fig. 2B). However, over time the log of the ratio of biomass in plots with four versus one species remained stable but became progressively larger for plots with 16 versus 1 species (Fig. 2, A and C). The latter result was because the difference in biomass between plots with highest richness (16 species) versus medium richness (eight or nine species) grew over time (Fig. 2B and fig. S8). Because the 16-, 9-, and 8-species plots were all planted with similar proportions of legumes, the increase over time in the biomass differences between them is not a

result of differences in legume presence in their original species pools (fig. S7). Additionally, although the shifts in biomass in different diversity treatments occurred in different ways in the two studies (17), the results in aggregate suggest that all species contribute to increasing biomass at higher diversity, especially so over time. Hence, simplification of even diverse ecosystems should be considered a possible threat to their long-term productivity.

What caused the diversity-biomass function to grow larger and less saturating over time? Evidence suggests this was due to the accumulating effects of complementarity of resource acquisition and use and of ecosystem feedback effects, such as on soil N cycling. By partitioning diversity effects into those associated with species complementarity versus selection (10, 12, 22), we show that the substantial and rising diversity effect is due largely to complementarity (Fig. 3,

A to D). The complementarity effect may be driven by increasing functional diversity (FD) (23, 24) and/or the replacement of species by functionally dissimilar ones (25). Within each level of species richness in BioCON, an abundance-weighted index of FD (FDA) increased over time (Fig. 3E). An alternative abundance-weighted functional diversity metric, Rao's Q, yields similar results, with less increase over time but greater separation across richness levels (fig. S9).

Complementarity can involve many traits, but important ones in an N-limited system might involve N cycling and availability. If diverse plots gradually accumulated more N in soil organic matter and plant biomass than less diverse plots, and this additional N subsequently becomes available through decomposition of plant litter and soil organic matter (13), then the diversity-productivity relationship could be boosted by in-

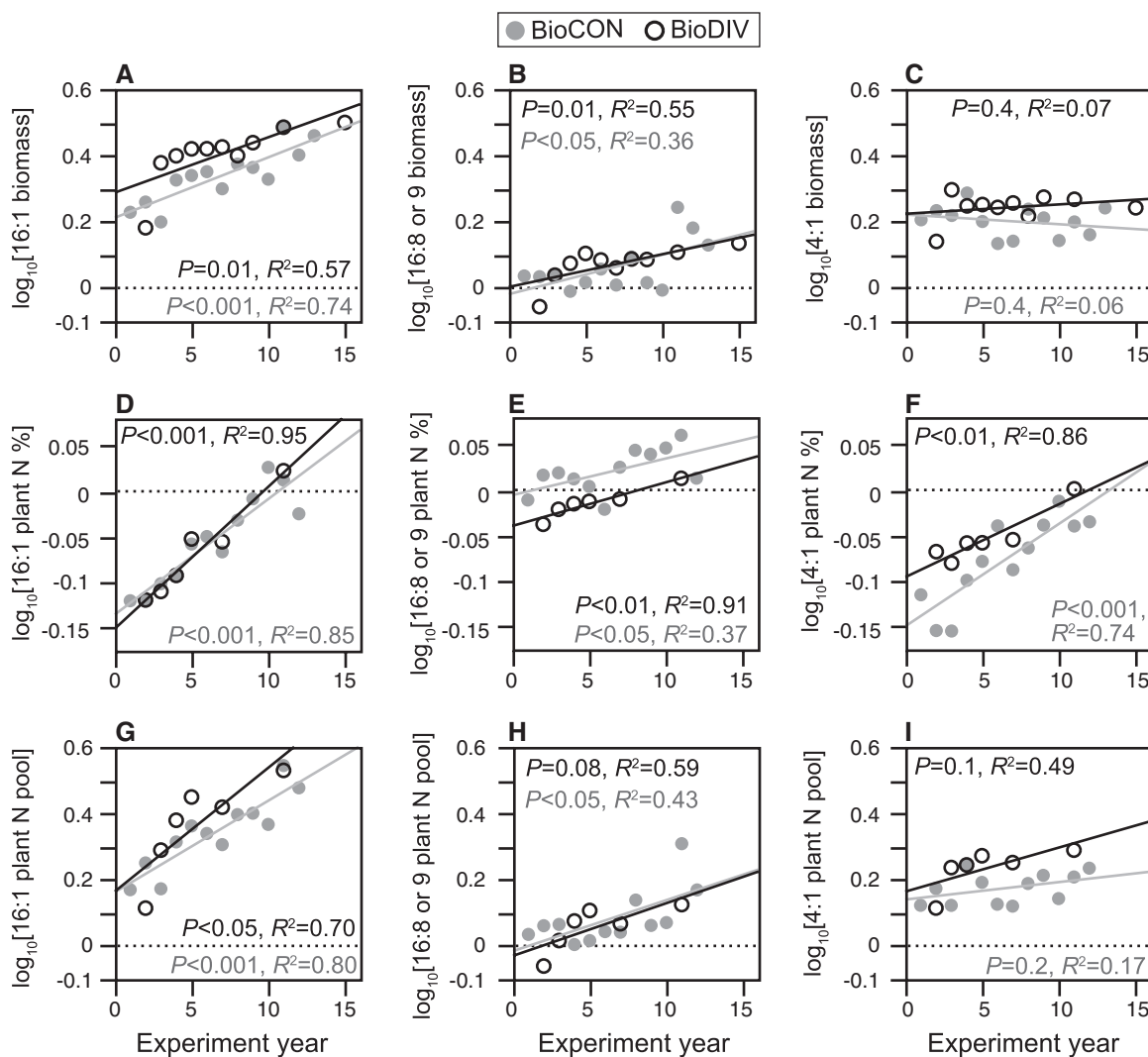


Fig. 2. The \log_{10} ratio of total biomass, tissue nitrogen concentration (plant N percent), and plant N pools (all above- and belowground, 0 to 20 or 0 to 30 cm depth), comparing means from treatments planted with different numbers of species [(A), (D), and (G), 16:1; (B), (E), and (H), 16:8 or 16:9; and (D), (F), and

(I), 4:1], across years, in the BioCON and BioDIV experiments. Values above zero represent a positive diversity effect; values below zero a negative effect [following (10)]. Similar trends were observed when comparing trends in absolute differences between species-richness levels instead of log ratios (not shown).

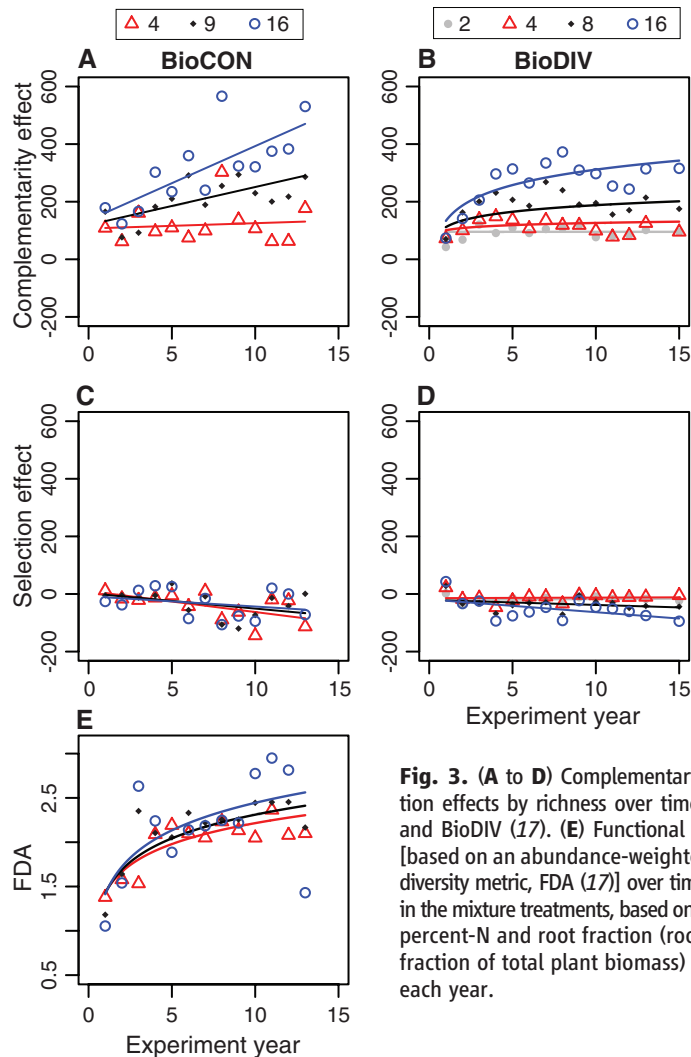


Fig. 3. (A to D) Complementarity and selection effects by richness over time for BioCON and BioDIV (17). (E) Functional trait diversity [based on an abundance-weighted functional diversity metric, FDA (17)] over time for BioCON in the mixture treatments, based on aboveground percent-N and root fraction (root biomass as fraction of total plant biomass) trait data for each year.

creased N availability in later years. Other biotic effects of diversity, including reduced disease (7, 26) and decreased abundances of herbivores (27), could also change over time and contribute to the growing diversity effects on productivity and nutrient cycling.

Species-rich plots became more N-rich over time relative to species-poor plots. Data from BioCON show an increasingly positive effect of diversity over time on rates of net N mineralization and concentrations of ammonium in soil (fig. S6; similar data are not available for BioDIV). For both experiments, diversity effects on community plant tissue N concentrations and plant N pools (Fig. 2) also became more positive, indicating an increase in N stocks, uptake, and/or supply rates in species-rich plots. Earlier reports showed only negative impacts of diversity on tissue percent-N (12, 19), but here we show diversity effects switched to neutral or slightly positive after ≈ 10 years (Fig. 2, D to F). In addition, variation among species in leaf percent-N, but not root fraction (root biomass as a fraction of total plant biomass), increased in higher-diversity plots. These observations indicate that in species-rich

plots, communities became more differentiated in their spread along the leaf economics spectrum (28). Last, the increasingly positive effects of diversity on N availability over time were not due solely to the presence of N-fixers. Soil N cycling and tissue percent-N were increasingly enhanced by higher species richness (16 versus 4 planted species) when legume presence was accounted for by examining only plots in which legumes were one-fourth of the original seed pool (fig. S8).

Over ≥ 13 years, both BioCON and BioDIV showed increasingly positive and nonsaturating relationships between biomass and species richness. These findings suggest that shorter-term studies could be misleading by incorrectly indicating functional redundancy and therefore undervaluing biodiversity. In BioCON and BioDIV, the relationship of biomass to species richness became stronger and less asymptotic as a result of increasing complementarity among species (for example, via increasing functional trait diversity) and increasingly positive impacts of diversity on soil N availability and plant N pools and tissue percent-N. Our long-term results show

that changes in diversity at high levels of richness have much larger effects than those shown by short-term studies. Thus, diversity matters for productivity not just in species-depauperate contexts (as in comparing monocultures to two- or four-species mixtures), but also, and increasingly over time, at high plant species richness. Hence, because of reduced cumulative feedback and complementarity effects, even the loss of a few species from mature diverse communities could lead in the long term to decreases in biomass production and the sustainability of ecosystem functioning.

References and Notes

1. B. J. Cardinale *et al.*, *Am. J. Bot.* **98**, 572 (2011).
2. E. S. Zavaleta, J. R. Pasari, K. B. Hulvey, G. D. Tilman, *Proc. Natl. Acad. Sci. U.S.A.* **107**, 1443 (2010).
3. P. Balvanera *et al.*, *Ecol. Lett.* **9**, 1146 (2006).
4. F. Isbell *et al.*, *Nature* **477**, 199 (2011).
5. A. Hector, R. Bagchi, *Nature* **448**, 188 (2007).
6. D. Tilman *et al.*, *Science* **294**, 843 (2001).
7. S. A. Schnitzer *et al.*, *Ecology* **92**, 296 (2011).
8. E. Marquard *et al.*, *Ecology* **90**, 3290 (2009).
9. A. Hector *et al.*, *Science* **286**, 1123 (1999).
10. B. J. Cardinale *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 18123 (2007).
11. A. Hector *et al.*, *PLoS ONE* **6**, e17434 (2011).
12. J. Fargione *et al.*, *Proc. Biol. Sci.* **274**, 871 (2007).
13. D. A. Fornara, D. Tilman, *Ecology* **90**, 408 (2009).
14. F. I. Isbell, H. W. Polley, B. J. Wilsey, *Ecology* **90**, 1821 (2009).
15. J. van Ruijven, F. Berendse, *Oikos* **118**, 101 (2009).
16. J. van Ruijven, F. Berendse, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 695 (2005).
17. Materials and methods are available as supplementary materials on Science Online.
18. P. B. Reich *et al.*, *Nature* **440**, 922 (2006).
19. P. B. Reich *et al.*, *Nature* **410**, 809 (2001).
20. D. Tilman *et al.*, *Science* **278**, 1866 (1997).
21. D. Tilman, P. B. Reich, J. M. H. Knops, *Nature* **441**, 629 (2006).
22. M. Loreau, A. Hector, *Nature* **412**, 72 (2001).
23. D. U. Hooper, P. M. Vitousek, *Ecol. Monogr.* **68**, 121 (1998).
24. A. Kahmen, C. Renker, S. B. Unsicker, N. Buchmann, *Ecology* **87**, 1244 (2006).
25. E. Allan *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 17034 (2011).
26. J. S. Petermann, A. J. F. Fergus, L. A. Turnbull, B. Schmid, *Ecology* **89**, 2399 (2008).
27. N. M. Haddad, G. M. Crutsinger, K. Gross, J. Haarstad, D. Tilman, *Ecol. Lett.* **14**, 42 (2011).
28. I. J. Wright *et al.*, *Nature* **428**, 821 (2004).

Acknowledgments: We thank the U.S. Department of Energy Program for Ecosystem Research (DE-FG02-96ER62291) and the National Institute for Climatic Change Research (DE-FC02-06ER64158); the National Science Foundation Long-Term Ecological Research (DEB-9411972, DEB-0080382, and DEB-0620652), Biocomplexity Coupled Biogeochemical Cycles (DEB-0322057) and Long-Term Research in Environmental Biology Programs (DEB-0716587), and the University of Minnesota for supporting this research. The data sets used in this study are available at the Cedar Creek Ecosystem Science Reserve Web site. The authors declare no conflicts of interest.

Supplementary Materials

www.sciencemag.org/cgi/content/full/336/6081/589/DC1
Materials and Methods

Figs. S1 to S9

Tables S1 to S3

References (29–40)

14 December 2011; accepted 15 March 2012
10.1126/science.1217909