2100. For case 2, the net GHG balance is +57 Pg CO_2eq through 2050 and +679 through 2100. We estimate that by the year 2100, biofuels production accounts for about 60% of the total annual N_2O emissions from fertilizer application in both cases, where the total for case 1 is 18.6 Tg N yr^{-1} and for case 2 is 16.1 Tg N yr^{-1}. These total annual land-use N_2O emissions are about 2.5 to 3.5 times higher than comparable estimates from an earlier study (8). Our larger estimates result from differences in the assumed proportion of nitrogen fertilizer lost as N_2O (21) as well as differences in the amount of land devoted to food and biofuel production. Best practices for the use of nitrogen fertilizer, such as synchronizing fertilizer application with plant demand (22), can reduce N_2O emissions associated with biofuels production.

The CI of fuel was also calculated across three time periods (Table 1) so as to compare with displaced fossil energy in a LCFS and to identify the GHG allowances that would be required for biofuels in a cap-and-trade program. Previous CI estimates for California gasoline (3) suggest that values less than ~96 g CO_2eq MJ^{-1} indicate that blending cellulosic biofuels will help lower the carbon intensity of California fuel and therefore contribute to achieving the LCFS. Entries that are higher than 96 g CO_2eq MJ^{-1} would raise the average California fuel carbon intensity and thus be at odds with the LCFS. Therefore, the CI values for case 1 are only favorable for biofuels if the integration period extends into the second half of the century. For case 2, the CI values turn favorable for biofuels over an integration period somewhere between 2030 and 2050. In both cases, the CO_2 flux has approached zero by the end of the century when little or no further land conversion is occurring and emissions from decomposition are approximately balancing carbon added to the soil from unharvested components of the vegetation (roots). Although the carbon accounting ends up as a nearly net neutral effect, N_2O emissions continue. Annual estimates start high, are variable from year to year because they depend on climate, and generally decline over time.

One of the perplexing issues for policy analysts has been predicting the dynamics of the CI over different integration periods [supporting online material (SOM) text]. If one integrates over a long enough period, biofuels show a substantial greenhouse gas advantage, but over a short period they have a higher CI than fossil fuel (3). Drawing on previous analyses (5, 23), we argue that a solution need not be complex and can avoid valuing climate damages by using the immediate (annual) emissions (direct and indirect) for the CI calculation. In other words, CI estimates should not integrate over multiple years but rather simply consider the fuel offset for the policy time period (normally a single year). This becomes evident in case 1. Despite the promise of eventual long-term economic benefits, a substantial penalty—in fact, possibly worse than with gasoline—in the first few decades may render the near-term cost of the carbon debt difficult to overcome in this case.

In case 2, in which there is less willingness to convert land, the economics of biofuels would be favorable sooner. Greater measures to protect forests could make the economics and CI of biofuels even more favorable because improved management on low-quality or degraded land can lead to carbon accumulation in the soil rather than a carbon loss (fig. S3). Our results suggest that tropical regions that are currently suffering substantial amounts of deforestation may also be the most competitive producers of biofuels. Our suggested strategy of not integrating over future fuel offsets increases the near-term CI of biofuels unless forested lands globally are better protected. Success in avoiding deforestation will be reflected in lower estimates of indirect emissions and lower carbon penalties.

References and Notes

1. J. Fargione et al., Science **319**, 1235 (2008).
2. T. Searchinger et al., Science **319**, 1238 (2008).
3. California Environmental Protection Agency (EPA), "Proposed regulation to implement the low carbon fuel standard," vol. 1 (EPA, Sacramento, CA, 2009); www.arb.ca.gov/fuels/lcfs/030409lcfs_isor_vol1.pdf.
4. E. Gallagher, The Gallagher Review of the Indirect Effects of Biofuels Production (Renewable Fuels Agency, East Sussex, UK, 2008).
5. J. Reilly et al., in Greenhouse Gas Sinks, D. S. Reay, C. N. Hewitt, K. A. Smith, J. Grace, Eds. (CABI Publishing, Wallingford, UK, 2007), chap 8, pp. 115–142.
6. M. Wise et al., Science **324**, 1183 (2009).
7. R. Leemans, A. van Amstel, C. Battjes, E. Kreileman, S. Toet, Glob. Environ. Change **6**, 335 (1996).
8. B. Strengers, R. Leemans, B. Eickhout, B. de Vries, L. Bouwman, GeoJournal **61**, 381 (2004).
9. M. R. Raupach et al., Proc. Natl. Acad. Sci. U.S.A. **104**, 10288 (2007).
10. A. Gurgel, J. M. Reilly, S. Paltsev, J. Agric. Food Ind. Org. www.bepress.com/jafio/vol5/iss2/art9.
11. J. Melillo et al., "Unintended environmental consequences of a global biofuels program" [Report 168, MIT Joint Program on the Science and Policy of Global Change (JPSPGC), Cambridge, 2009]; http://globalchange.mit.edu/files/document/MITJPSPGC_Rpt168.pdf.
12. S. Paltsev et al., "The MIT emissions prediction and policy analysis (EPPA) model: version 4" (MIT JPSPGC, Cambridge, 2005); http://globalchange.mit.edu/files/document/MITJPSPGC_Rpt125.pdf.
13. J. Melillo et al., Nature **363**, 234 (1993).
14. B. Felzer et al., Tellus **56B**, 230 (2004).
15. A. Sokolov et al., J. Clim. **21**, 3776 (2008).
16. Materials and methods are available as supporting material on Science Online.
17. G. Hurtt et al., Glob. Change Biol. **12**, 1208 (2006).
18. P. A. Sanchez, Science **295**, 2019 (2002).
19. B. Felzer et al., Clim. Change **73**, 345 (2005).
20. X. Wang, thesis, MIT (2008); available at http://globalchange.mit.edu/files/document/Wang_PhD_08.pdf.
21. P. J. Crutzen, A. R. Mosier, K. A. Smith, W. Winiwarter, Atmos. Chem. Phys. **8**, 389 (2008).
22. G. P. Robertson, in Ecology in Agriculture, L. Jackson, Ed. (Academic Press, New York, 1997), pp. 347–365.
23. H. Herzog et al., Clim. Change **59**, 293 (2003).
24. This research was supported in part by the David and Lucile Packard Foundation to the MBL, Department of Energy, Office of Science (BER) grants DE-FG02-94ER61937, DE-FG02-93ER61677, and DE-FG02-08ER64648; EPA grant XA-83240101; NSF grant BCS-0410344; and the industrial and foundation sponsors of the MIT JPSPGC.

Elevated CO_2 Reduces Losses of Plant Diversity Caused by Nitrogen Deposition

Peter B. Reich

The interactive effects of rising atmospheric carbon dioxide (CO_2) concentrations and elevated nitrogen (N) deposition on plant diversity are not well understood. This is of concern because both factors are important components of global environmental change and because each might suppress diversity, with their combined effects possibly additive or synergistic. In a long-term open-air experiment, grassland assemblages planted with 16 species were grown under all combinations of ambient and elevated CO_2 and ambient and elevated N. Over 10 years, elevated N reduced species richness by 16% at ambient CO_2 but by just 8% at elevated CO_2. This resulted from multiple effects of CO_2 and N on plant traits and soil resources that altered competitive interactions among species. Elevated CO_2 thus ameliorated the negative effects of N enrichment on species richness.

Two global change factors likely to have widespread influence on plant communities are nitrogen (N) deposition and rising atmospheric carbon dioxide (CO_2) levels (1–7). Levels of N deposition and CO_2 have risen in recent decades and are expected to increase further (8). Because increased CO_2 and N supply often drive plant stoichiometry in opposite directions but productivity in the same direction, and as plant resources are primarily available above-

Department of Forest Resources, University of Minnesota, 1530 Cleveland Avenue North, St. Paul, MN 55108, USA. E-mail: preich@umn.edu

ground versus below ground, there are many possible ways in which competitive or other biotic interactions that influence biodiversity might be affected (2–7, 9–11). Although increasing N supply frequently results in declining species diversity (1, 6, 7, 9), there has been less research about (4, 5, 10), and no consensus regarding, how rising CO_2 levels will influence species diversity. Even less is known about the influence of rising CO_2 on the effects of N deposition on diversity (4, 5).

Experimental and observational studies in terrestrial ecosystems have typically shown that increases in N availability increase productivity and decrease plant diversity, and this has been explained by a variety of mechanisms (1, 6, 7, 9, 12–16). Investigations in different study systems have provided evidence that a decline in diversity under elevated N can result from resource preemption (i.e., from either belowground resource or light competition) and associated competitive exclusion, shifts in competitive intensity aboveground versus belowground, alterations of soil acidity, a switch from one limiting resource to another, and/or a shift in niche dimensionality (1, 6, 7, 9, 12–16). Therefore, although the suppression of diversity by increasing N availability is almost ubiquitous, no single mechanism is universally responsible.

In contrast, evidence and theory about CO_2 effects on species richness are less well developed. Much like enriched N, elevated CO_2 could result in decreasing species richness as it also commonly increases productivity (2, 17–19), potentially leading to competitive exclusion following resource preemption. Alternatively, as rising CO_2 levels change plant stoichiometry (17, 20), potentially resulting in greater relative limitations by other dominant resources such as N (18, 19, 21), elevated CO_2 could reduce competitive exclusion and lead to increased species richness. Evidence of CO_2 effects on species richness is scarce (4, 5, 10, 22) and shows mixed results, with positive, neutral, and negative responses seen in the few published reports.

Equally important to impacts of multiple global change agents is whether their effects are interactive (2–4, 18, 19), as it will bode poorly for future biodiversity conservation if rising CO_2 exacerbates the considerable negative impacts of N deposition on community-scale species richness (1, 6, 7, 13, 14). However, a plethora of possible mechanisms suggests that synergistic, additive, or antagonistic interactive outcomes of joint CO_2 and N effects are plausible (23).

To address the issues raised above, species richness was measured in 48 experimental grassland plots (each 2 m by 2 m) planted in 1997 with 16 perennial species and treated since 1998 with all combinations of ambient and elevated atmospheric CO_2 (ambient and +180 μmol mol^{-1} delivered by means of a free-air CO_2 enrichment technique) and ambient and enriched N (ambient and +4 g N m^{-2} year^{-1} delivered as ammonium nitrate in three equal doses each year) (11, 19, 23). This experiment, called BioCON, is conducted in an ecosystem co-limited by CO_2 and N (11, 19)

and dominated by belowground interactions (24, 25). Although wet and dry N deposition to terrestrial ecosystems is primarily of atmospheric origin, the effects are largely mediated through belowground processes, because uptake by soil microbes and plant roots generally begins the incorporation of this N into the plant biogeochemical cycle. Species richness (the number of species observed in a plot), belowground and aboveground biomass, root C/N ratio, soil solution N concentration, percent soil water content, and percent light transmission were measured in each plot in all years from 1998 to 2007 (23) and used to evaluate treatment effects on species richness and the underlying mechanisms (Tables 1 and 2).

From 1998 to 2007, there were significant main effects of N treatment ($P < 0.001$) and year ($P < 0.0001$) on species richness, and a significant interaction between CO_2 and N treatments ($P = 0.02$) (Tables 1 and 3). On average, enriched N supply reduced species richness by 16% under ambient CO_2, but only by 8% under elevated CO_2 (Table 3 and Fig. 1). The N effect was consistently smaller under elevated than under ambient CO_2 from the second to tenth year of the experiment (Fig. 1). From the CO_2 effect perspective, elevated CO_2 had minimal impact (−2%) on observed species richness at ambient N, whereas at enriched N, elevated CO_2 modestly increased species richness by 7% (Table 3). The $CO_2 \times$ N interaction was more pronounced once the experimental plots were well established. For example, during the most recent 7 years, enriched N supply reduced species richness by 15% under ambient CO_2, but only by 5% under elevated CO_2.

What accounts for the more consistently negative effect of added N than of elevated CO_2 on species richness, and what caused the observed $CO_2 \times$ N interaction? To address these questions, it is useful to focus on elements of plot-scale structure or function that might be influenced by CO_2 and N and contribute to effects on species richness, asking (i) which plot-scale attributes were related to species richness, (ii) how did CO_2 and

N treatments influence those attributes, and (iii) were such responses consistent with observed treatment effects on species richness? Relevant measures (6, 7, 12, 13, 15, 24–26) include (i) total root biomass, an indication of productivity and potentially of capacity to preempt (competitively obtain) soil resources; (ii) soil solution N, an indication both of resource supply and of resource preemption; (iii) root C/N, which is an indication of species differences in root chemical stoichiometry and hence of both relative physiological limitation by N and of treatment-induced differences in soil N availability; (iv) percent soil water content, an indication both of resource supply and of resource preemption; and (v) percent light transmission, which can indicate variation in the level of asymmetric competition for this aboveground resource.

These five measures were not closely related among plots (23) and thus, in theory, each could serve to independently drive species richness. In bivariate relations, species richness was negatively related ($P < 0.001$) to increased soil solution N and root biomass, and positively related to root C/N ratios ($P < 0.001$) and percent soil water content ($P < 0.05$) (Fig. 2, A to D), but unrelated ($P > 0.50$) to percent light transmission. Moreover, all five of these attributes were significant predictors of species richness in multiple regression models (Table 2 and table S1), with residual plots from the full model (Fig. 2, E to H) similar to those for the bivariate relationships for the four belowground attributes (Fig. 2, A to D). This similarity indicates that the associations seen in bivariate relations are also significant (and in the same direction) once the effects on species richness of other important driving variables are accounted for. The question then is whether these attributes responded to CO_2 and N treatments in ways that would "drive" species richness in the observed patterns.

Table 2. Species richness of the plant community as a function of total root biomass, root C/N ratio, soil solution N concentration, percent soil water content, and percent light transmission. Data are mean values for species richness, biomass, C/N ratio, soil solution N concentration, percent soil water content, and percent light transmission for each of 48 plots measured over 10 years (26). Model was selected based on Akaike's Information Criteria from a suite of models involving these variables and all possible interactions.

Variable	Whole-plot species richness	
	F value	P > F
Whole model R^2	0.65	<0.0001
Effect		
Root biomass	9.85	0.0031
Root C/N	6.06	0.0182
Soil solution N	13.91	0.0006
Soil water	3.12	0.0850
Light transmission	6.09	0.0176
Root biomass × soil water	9.11	0.0044

Table 1. Repeated-measures analysis of variance of CO_2 and N effects on species richness. Effects of year, CO_2, and N, and all interactions, on species richness (the number of species observed in a plot during sampling) are shown.

Variable	Whole-plot species richness	
	F value	P > F
Whole-model R^2	0.70	<0.0001
Effect		
CO_2	0.23	0.655
N	49.43	<0.0001
Year	66.83	<0.0001
$CO_2 \times$ year	0.66	0.741
N × year	2.49	0.0089
$CO_2 \times$ N	5.61	0.0228
$CO_2 \times$ N × year	0.27	0.896

Total root biomass, root C/N, soil solution N, and percent soil water content were influenced by CO_2, N, and their combination in ways that were consistent with CO_2 and N effects on species richness, and with soil and root factor relations with species richness (Tables 1 to 3 and Figs. 1 and 2), whereas percent light transmission was not (23). For example, enriched N increased soil solution N concentration and root biomass, and decreased root C/N and percent soil water content (Table 3), all of which are consistent with decreased species richness given relations shown in Figs. 1 and 2. Treatments that made plants N-rich or productive, and soils N-rich or dry, also reduced diversity. Moreover, joint effects of CO_2 and N on biomass, C/N, and soil solution N mirrored their joint effects on species richness (i.e., enriched N effects were smaller at elevated than in ambient CO_2 treatments, significantly so for soil solution N; Table 3). Hence, the main and interactive effects on species richness of CO_2 and N in this experiment were apparently the result of impacts of CO_2 and N on several belowground drivers of species richness, perhaps, most importantly, soil solution N (Figs. 1 and 2 and Table 1), which itself showed a significant $CO_2 \times N$ interaction (Table 3).

The changes in species richness under CO_2 and N can also be viewed through the lens of individual species and functional group responses (4, 5, 10), given that all plots were initially planted with four species from four functional groups (11). The relative abundance of C_3 grasses increased markedly with N enrichment (by 69%) and was associated with a modest increase (+8%) in C_3 grass species richness (Table 3). In contrast, with enriched N, two of the three other functional groups had large decreases in relative abundance, and all three had lower species richness (Table 3), with this suppression more modest at elevated than at ambient CO_2, especially for the C_4 grasses ($P = 0.0006$ for the $CO_2 \times N$ interaction). Additionally, changes in species richness in response to CO_2 and N and their interaction were little influenced by changes in frequency (fraction of plots in which they are present) of either the rarest or most frequent species; instead, a set of species of intermediate frequency and abundance played the major role in this regard (23).

These results suggest that changes in ecosystem attributes and in functional group relative abundances together explain the main and interactive effects on CO_2 and N on species richness in this system. The decreasing species richness under enriched N likely resulted from competitive exclusion of other functional groups by increasingly abundant C_3 grasses, and was associated with greater root biomass, lower root C/N, greater soil solution N, and lower percent soil water content under enriched N. At this site, increased C_3 grass biomass under N enrichment can reduce soil water availability, leading to increased mortality of other species (26), and the BioCON C_4 grasses show reduced relative abundance in simulated drought treatments (23). These enriched N effects were

somewhat muted under elevated compared to ambient CO_2, because enriched N-induced increases in root biomass, decreases in root C/N, and especially increases in soil solution N were smaller in the enriched CO_2 treatment (Table 3). Given the relations of species richness to each of these potential drivers (Fig. 2), the smaller responses of these attributes to enriched N (in elevated than in ambient CO_2) likely contributed to the smaller N-induced declines in species richness (Tables 1 to 3 and Figs. 1 and 2) in elevated than in ambient CO_2.

In summary, elevated CO_2 had modest effects on species richness (compared to N enrichment), in part because CO_2 effects on key drivers of species richness were smaller and sometimes offsetting. For instance, CO_2-induced increases (Table 3) in root C/N and percent soil water content, which were linked to increases in species richness, counteract biomass productivity effects

Table 3. Percent response (average, 1998 to 2007) of community and ecosystem variables to elevated CO_2 at both ambient and enriched N, as well as to enriched N under both ambient and elevated CO_2 levels. Variables include species richness, root biomass, root C/N ratio, soil solution N, percent soil water content, percent light transmission (all at plot scale), and species richness and relative abundance of each functional group (defined as the fraction of total aboveground biomass). Also shown is whole-model R^2 and significance levels for analysis of variance for each variable in relation to CO_2, N, and their interaction.

Variable	CO_2 effect (% change)		Significance			N effect (% change)		Whole-model R^2
	Ambient N	Enriched N	CO_2	N	$CO_2 \times N$	Ambient CO_2	Elevated CO_2	
Species richness (plot)	−2.2	+6.9		***	*	−15.9	−8.1	0.64
Root biomass (plot)	+11.0	+19.6	**	***		+33.3	+23.7	0.47
Root C/N (plot)	+4.0	+9.7	†	***		−10.4	−5.4	0.31
Soil solution N (plot)	+37.7	−29.2		***	**	+391.1	+152.5	0.60
Percent soil water content	+10.0	+11.3	**	*		−6.8	−5.6	0.24
Percent light transmission (plot)	−1.2	−2.1		***		+17.1	+16.1	0.31
Species richness, C_4 grass	−11.7	+11.1		***	***	−32.7	−15.4	0.78
Species richness, C_3 grass	−1.7	+1.9		***		+5.7	+9.6	0.40
Species richness, N fixer	−6.2	+0.4		***		−26.4	−21.1	0.66
Species richness, forb	+25.5	+31.1	†	*		−18.4	−14.8	0.39
Relative abundance, C_4 grass	−12.3	−8.4		*		−28.3	−25.2	0.48
Relative abundance, C_3 grass	−3.2	−6.6		***		+72.0	+65.9	0.77
Relative abundance, N fixer	+6.3	+12.4		***		−42.5	−39.2	0.25
Relative abundance, forb	+1.0	+11.0				−1.9	+7.8	0.69

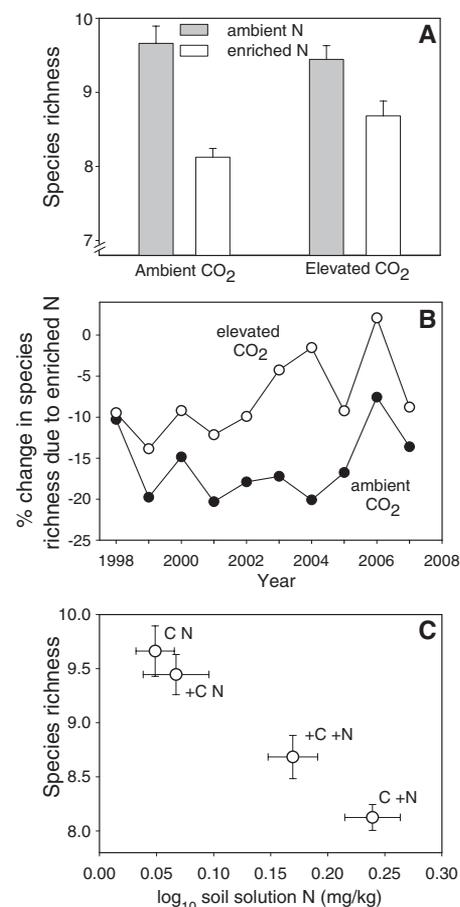$†P < 0.10$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Fig. 1. (**A**) Species richness (±SE among plots) of experimental plots ($n = 48$), under four combinations of CO_2 and N ($n = 12$ plots for each), averaged from 1998 to 2007. (**B**) The percent effect of enriched N treatment on species richness under ambient CO_2 (filled circle) and elevated CO_2 (open circle) conditions from 1998 to 2007. (**C**) Mean species richness (±SE) and soil solution N (mg/kg, 0 to 20 cm depth) (±SE) from 1998 to 2007 for ambient and elevated CO_2-treated plots under ambient and enriched N conditions. Relevant statistics for all panels are shown in Tables 1 to 3 and the text.
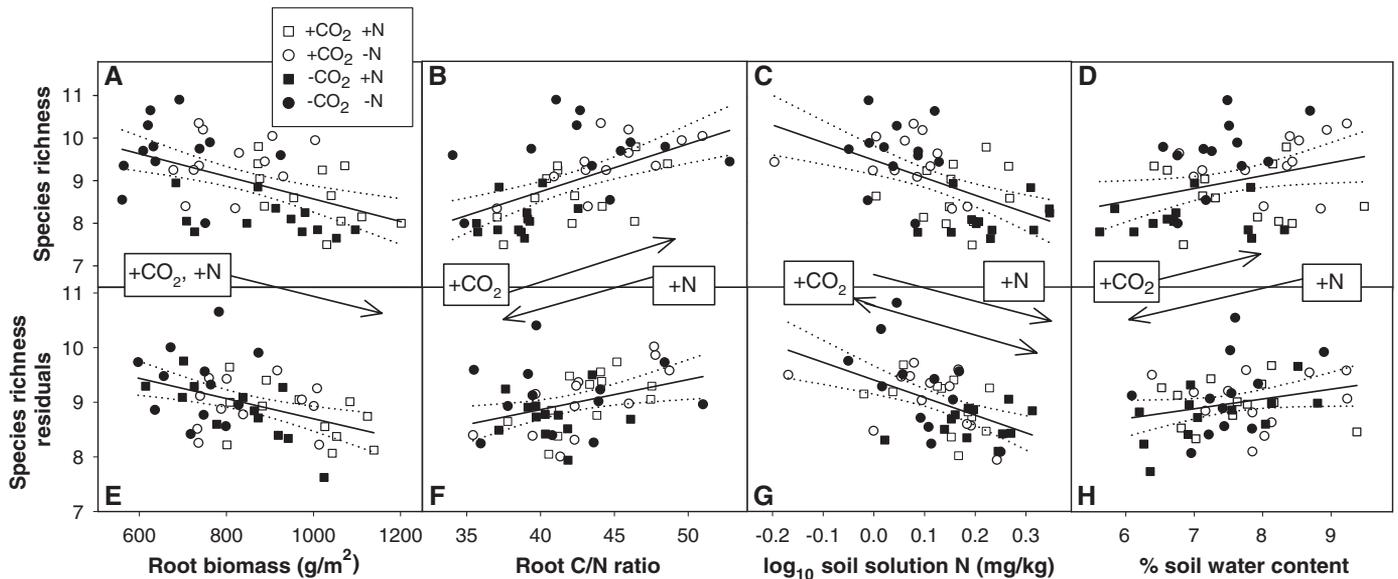
Fig. 2. The relation of mean species richness per plot versus root biomass (0 to 20 cm, g m^{-2}), root C/N ratio, soil solution N (mg/kg, 0 to 20 cm depth), and percent soil water content (0 to 20 cm depth) for all plots ($n = 48$), each averaged over 10 years [(**A** to **D**), all relations significant $P < 0.05$], as well as the partial residual relationship (**E** to **H**) for each of these from the full multiple regression model. The arrows show directional effects of enriched N (+N) or elevated CO_2 (+CO_2) on both species richness and the ecosystem attribute shown in each panel. Confidence intervals (95%) for the model fit are shown with the dotted lines. Multiple regression model details are provided in Tables 1 and 2.

(which decrease species richness) (Fig. 2). In contrast, enriched N has a consistent negative effect on species richness because its effects on productivity, soil solution N, soil moisture, and root C:N ratio all individually suppress species richness (Fig. 2). Moreover, because the effects of CO_2 and N on the drivers of species richness differ depending on the particular combinations of levels of CO_2 and N, the joint effects of enriched CO_2 and enriched N were nonadditive, i.e., could not be predicted from knowledge of each alone. These results for a temperate perennial grassland contrast with results of a study of multiple global change effects in annual Mediterranean grassland, where such impacts were predictable from knowledge of each alone (*4*). Competition for soil N, for which soil solution N may be a surrogate, and for soil water may be particularly important in BioCON, as (i) there were $CO_2 \times N$ interactions on soil solution N as well as on species richness, (ii) enriched N and CO_2 treatments drove percent soil water content in opposite directions, and (iii) competition for N and water have been shown to influence the outcomes of competition of these species and functional groups at Cedar Creek (*7, 23–25*). Indeed, when averaged over the entire experiment for the four contrasting CO_2 and N levels, the correspondence between species richness and soil solution N was pronounced (Fig. 1)—with treatments diverging along a single species richness and soil solution N axis.

Results of this study have important implications for natural ecosystems under global change, because they demonstrated that within 2 years and persisting for 10, altered CO_2 and N regimes had significant, interactive, impacts on species diversity. From a biodiversity conservation perspective, there was no evidence to support the worst-case

scenario in which rising CO_2 and N deposition each suppresses diversity and jointly do so additively or synergistically. Instead, their joint interaction ameliorated the diversity loss due to N enrichment that occurs under ambient CO_2. However, in viewing the possible implications of these results at broad scales and in other ecosystems, it is uncertain whether rising CO_2 and N deposition will generally cause changes in plant biomass, plant or soil stoichiometry, soil chemistry, or soil moisture or other drivers of biotic interactions in ways that lead to the same nonlinear interactive effect on species richness. Regardless, the sensitivity of species richness to factors that themselves were sensitive to CO_2 and N suggests that predicting responses of species richness at local community scales may be challenging, as responses to multiple global change drivers are perhaps not generally predictable from the responses to each alone. Given that humankind is enriching the biosphere in both CO_2 and N (*8*) and that species diversity is a key ecological attribute providing ecosystem services, such uncertainty further contributes to our concern about systemic impacts of global environmental change on Earth's ecological sustainability.

References and Notes
1. C. J. Stevens, N. B. Dise, J. O. Mountford, D. J. Gowing, *Science* **303**, 1876 (2004).
2. R. Oren *et al.*, *Nature* **411**, 469 (2001).
3. M. R. Shaw *et al.*, *Science* **298**, 1987 (2002).
4. E. S. Zavaleta, M. R. Shaw, N. R. Chiariello, H. A. Mooney, C. B. Field, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 7650 (2003).
5. P. A. Niklaus, C. Körner, *Ecol. Monogr.* **74**, 491 (2004).
6. K. N. Suding *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 4387 (2005).
7. C. M. Clark, D. Tilman, *Nature* **451**, 712 (2008).
8. IPCC (Intergovernmental Panel on Climate Change), *Climate Change 2007: The Physical Science Basis: Summary for Policymakers* (IPCC Secretariat, February 2007).
9. L. Gough, C. W. Osenberg, K. L. Gross, S. L. Collins, *Oikos* **89**, 428 (2000).
10. C. Potvin, L. Vasseur, *Ecology* **78**, 666 (1997).
11. P. B. Reich *et al.*, *Nature* **410**, 809 (2001).
12. T. K. Rajaniemi, V. J. Allison, D. E. Goldberg, *J. Ecol.* **91**, 407 (2003).
13. M. J. Crawley *et al.*, *Am. Nat.* **165**, 179 (2005).
14. C. J. Stevens, N. B. Dise, D. J. G. Gowing, J. O. Mountford, *Glob. Change Biol.* **12**, 1823 (2006).
15. Y. Hautier, P. A. Niklaus, A. Hector, *Science* **324**, 636 (2009).
16. W. S. Harpole, D. Tilman, *Nature* **446**, 791 (2007).
17. E. A. Ainsworth, S. P. Long, *New Phytol.* **165**, 351 (2005).
18. P. B. Reich, B. A. Hungate, Y. Luo, *Annu. Rev. Ecol. Evol. Syst.* **37**, 611 (2006).
19. P. B. Reich *et al.*, *Nature* **440**, 922 (2006).
20. A. M. Novotny *et al.*, *Oecologia* **151**, 687 (2007).
21. R. W. Sterner, J. J. Elser, Eds., *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere.* (Princeton Univ. Press, Princeton, NJ, 2002).
22. R. T. Belote, J. F. Weltzin, R. J. Norby, *New Phytol.* **161**, 827 (2004).
23. Materials, methods, and supplemental information are available as supporting material on *Science* Online.
24. D. Wedin, D. Tilman, *Ecol. Monogr.* **63**, 199 (1993).
25. R. Dybzinski, D. Tilman, *Am. Nat.* **170**, 305 (2007).
26. M. Davis *et al.*, *Plant Ecol.* **145**, 341 (1999).
27. Funding was provided by the U.S. Department of Energy, National Institute for Climate Change Research; and the NSF, Long Term Ecological Research (LTER), Biocomplexity, and Long Term Research in Environmental Biology (LTREB) programs. Thanks to S. Hobbie, K. Worm, J. Trost, and D. Bahauddin in particular, and to many others for their contributions to the BioCON project; and to R. Dybzinski, K. Suding, I. Woodward, and B. Medlyn for critiquing an earlier version of the manuscript.

ERRATUM

Post date 12 February 2010

Reports: "Elevated CO_2 reduces losses of plant diversity caused by nitrogen deposition" by P. B. Reich (4 December 2009, p. 1399). The 0.70 and 0.65 values and corresponding <0.0001 values in the first row of Tables 1 and 2, respectively, are the R^2 values and significance values for the whole models (and should not have been placed in the columns labeled "F value" and "$P > F$," respectively).