

ECOSYSTEM MANAGEMENT

The economic value of grassland species for carbon storage

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Carbon storage by ecosystems is valuable for climate protection. Biodiversity conservation may help increase carbon storage, but the value of this influence has been difficult to assess. We use plant, soil, and ecosystem carbon storage data from two grassland biodiversity experiments to show that greater species richness increases economic value: Increasing species richness from 1 to 10 had twice the economic value of increasing species richness from 1 to 2. The marginal value of each additional species declined as species accumulated, reflecting the nonlinear relationship between species richness and plant biomass production. Our demonstration of the economic value of biodiversity for enhancing carbon storage provides a foundation for assessing the value of biodiversity for decisions about land management. Combining carbon storage with other ecosystem services affected by biodiversity may well enhance the economic arguments for conservation even further.

INTRODUCTION

The rise of photosynthesis nearly 4 billion years ago initiated the transfer of carbon dioxide in the atmosphere to organic carbon, much of which is now contained in rocks (1). This transfer helped create Earth's modern atmosphere and climate, as well as the accumulation of oxygen that allowed aerobic life to thrive, and the proliferation of the thousands of different species of plants that now inhabit Earth. This biodiversity, "the variety of living [photosynthetic] organisms, the genetic differences among them, and the communities and ecosystems in which they occur" (2), is therefore essential for carbon storage on Earth, for our oxygen-dependent existence, and for regulation of global climate.

What happens to carbon storage in ecosystems when their photosynthetic biodiversity declines, as biological communities become simplified (3)? Syntheses of experiments across different ecosystems indicate that biomass accumulation tends to decline as local species richness decreases (4). This decline can occur because species differ in resource use in space or time, leading to greater use of total available resources (niche complementarity), facilitation of some species by others, or greater probability of the presence of highly effective species as the number of total species increases (sampling, or selection, effects). Observations in forests also indicate that local species richness contributes to carbon gain across broad gradients of climate and soil conditions (5–7). Reduced carbon gain as species diversity declines reduces carbon input to soil and, in some longer-term experiments, reduces soil carbon stocks (8). Thus, species richness may influence climate regulation, a service provided by natural ecosystems upon which humans strongly rely.

Policies have developed over the past several decades that place an economic value on protecting the climate system. In carbon markets, buyers pay for sellers to build renewable energy systems to reduce greenhouse gas emissions, to capture and store greenhouse gases from emission sources, or in some cases, to manage natural ecosystems to promote carbon storage. These activities are quantified by how much they prevent emissions of carbon dioxide to the atmosphere, and these avoided emissions can be assigned a value where carbon-valuation mechanisms exist, such as emissions trading schemes, carbon taxes, and voluntary markets. Despite challenges, the valuation of carbon is expanding rapidly (9): Over the past decade, there has been a three-fold increase in the number of national and local jurisdictions that put a price on carbon (10). Many regulated and voluntary markets value carbon accumulation in forests (11–13) despite issues with additionality, permanence, and leakage (14). Although we are unaware of regulated markets explicitly valuing land carbon uptake in grassland ecosystems, protocols have been developed (15), and the potential is clear (16, 17).

This context sets the stage for the question addressed here: What is the value of plant species richness in terms of carbon storage? Our approach to this question offers a quantitative monetized view of one of the values of biodiversity that contrasts with the typically qualitative nature of most other assessments of biodiversity value (18–20). Valuation also provides a quantitative foundation for assessing decisions about land use involving trade-offs (21), and, as described above, it is relevant to existing and developing carbon markets. Any exercise to place a value on species is fraught with challenges of interpretation: The service of carbon storage is but one of the many facets of a species' value, and biodiversity may have intrinsic value beyond utility for humans. Even so, estimating the monetized value of species richness with respect to one particular ecosystem service, carbon storage, provides a tractable focus for quantifying one dimension of the value of biodiversity (species richness) and one that is relevant to the pressing environmental concerns of species loss and carbon storage.

We drew upon long-term experimental manipulations of species richness to assess its marginal value with respect to grassland carbon storage, including consideration of both the plant and soil carbon pools. We analyzed data from two experiments, performed in a North American grassland where species richness had been manipulated for

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over a decade periodic measurements of plant and soil carbon content in this site over time have suggested that both factors increase with species richness (8, 22), despite some evidence that species richness also stimulates soil carbon turnover (23). We utilized these data to assess the marginal increase in carbon content with increasing species richness and estimated the economic value of the carbon storage conferred. For plants, we used observed changes in plant carbon content. For soils, we used data on soil carbon and plant productivity to model carbon accumulation as a function of increasing species richness over a 50-year period. This time horizon is sufficient to capture effects of species richness on soil carbon, which accumulates slowly; however, it is also short enough to represent a tractable target, consistent with time horizons discussed for carbon management and climate protection (24). Although there are many studies of plant carbon storage beyond those used here that have experimentally manipulated the diversity of plant species, we focused on these particular experiments because they are by far the longest-running biodiversity experiments and are among the few to also estimate soil carbon, the largest carbon reservoir in most grasslands. We calculated the marginal change in carbon content with increased richness next, we calculated the economic value of species richness for carbon storage in grasslands, using a wide range of estimates of the social cost of carbon compiled by the Interagency Working Group in a recent synthesis used by U.S. federal agencies when estimating the benefits of carbon reductions from application of federal rules and regulations [mid-range estimate, \$137.26 per metric

ton C (MT C^{-1}), ranging from a low estimate of \$41.94 to a high estimate of \$400.33 MT C^{-1} ; see Materials and Methods] (25).

RESULTS

Adding species increased cumulative carbon storage in plant, soil, and ecosystem carbon pools (Fig. 1): The marginal change in 50-year carbon storage caused by adding species was positive for both experiments and across the full range of species richness evaluated, from 1 to 16 plant species. The marginal increase in cumulative carbon storage declined as plant species accumulated, reflecting the commonly observed positive but nonlinear relationship between plant species richness and biomass (4). As a result, the largest marginal values of cumulative carbon storage occurred at low levels of species richness, and the smaller marginal values occurred at the high richness levels. For example, increasing richness from five to six plant species increased carbon storage projected after a 50-year time period by 1.02 MT C ha^{-1} species $^{-1}$ (averaged over the two experiments); that change was only 0.15 MT C ha^{-1} species $^{-1}$ —nearly an order of magnitude less—when increasing richness from 15 to 16 species. Carbon accumulation slowed during the 50-year simulation (Fig. 2). Annual marginal carbon accumulation and annual marginal value were highest early in the 50-year simulation and declined over time.

Total marginal present value tracked cumulative marginal carbon content, highest at low initial species richness and declining as richness increased (Fig. 3). Although the values declined with increasing diversity, at no point did the 95% confidence limit overlap zero: There was always a positive economic value for carbon storage to increasing species richness up to 16 species. On the scale of a single hectare and averaged across experiments using the medium estimate of the social cost of carbon, adding a 2nd species increased the value of carbon storage by \$804.55 ha^{-1} species $^{-1}$, the 3rd species added an

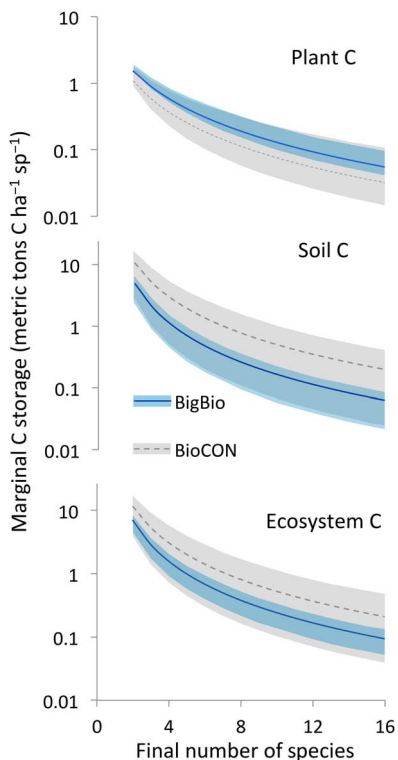


Fig. 1. Marginal carbon storage, which is the incremental change in cumulative carbon storage over 50 years caused by adding one additional species, as a function of final species richness, estimated from two grassland experiments (BioCON shown in gray; BigBio in blue). Means are shown in solid lines, with shaded regions indicating 95% confidence intervals estimated from bootstrapping for plant carbon (top), soil carbon (middle), and total ecosystem carbon (bottom).

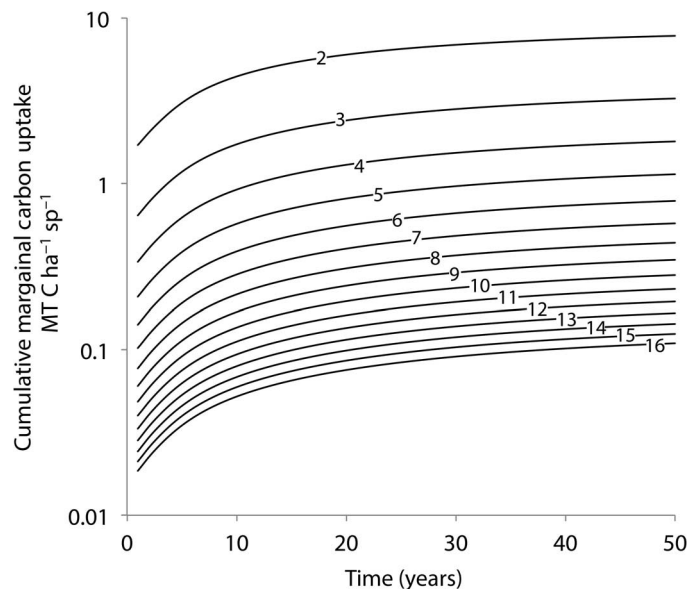


Fig. 2. Marginal carbon accumulation over time at different levels of species richness. Each line shows the additional carbon accumulated over time caused by increasing species richness by one species. Numeric labels on each curve indicate the specific increment in species richness, with “2” indicating the marginal carbon accumulation caused by increasing S from 1 to 2, “3” indicating the marginal carbon accumulation caused by increasing S from 2 to 3, etc., up to 16.

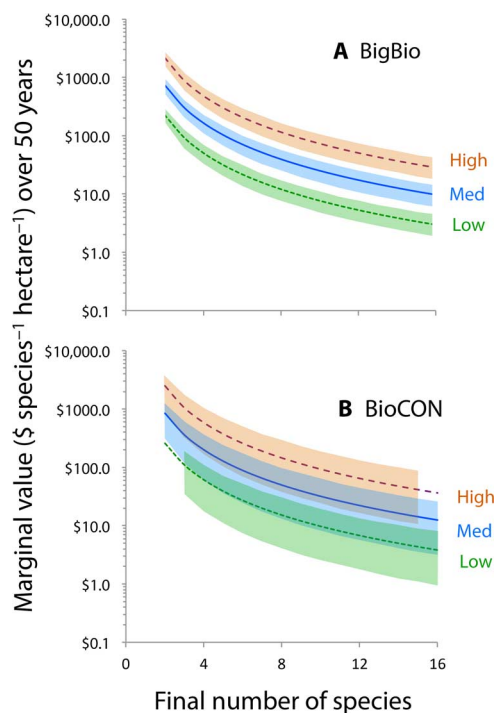


Fig. 3. Marginal present discounted economic value over 50 years from adding one species as a function of final species richness, using three estimates of the social cost of carbon: low (green), medium (blue), and high (purple) estimates described by the U.S. government (25) and in Materials and Methods. Marginal values were estimated from the two grassland experiments shown in Fig. 1 and are expressed here as USD (2010) per species per hectare, integrated over 50 years. (A) The marginal values for BigBio. (B) The marginal values for BioCON. Lines indicate means for each of the three estimates for the social cost of carbon. Shaded regions indicate 95% confidence intervals. For ease of visualization of values for BioCON, the confidence interval for the high estimate of the social cost of carbon is truncated at species richness of 15, and the confidence interval for the low estimate of the social cost of carbon begins at species richness of 3. For orientation, the position on the y axis (ordinate) corresponding to the x axis (abscissa) value of 5 shows the marginal value of adding the fifth species to a grassland initially containing four species.

additional \$333.38 ha⁻¹ species⁻¹, whereas the 10th added an additional \$28.51 ha⁻¹ species⁻¹ (Table 1).

DISCUSSION

On the basis of these estimates of the economic value of species richness from small-scale experiments, we explore their implications on larger scales, first, using the current ranges of the species included in the grassland experiments to quantify the potential marginal cost of species loss, and, second, considering how changes in species diversity might add value to grassland restoration projects through the Conservation Reserve Program (CRP) (16, 17). The species included in the experiments we assessed currently occupy ranges in the conterminous United States as small as 8400 ha (*Petalostemum villosum*) to as large as 9.6 million ha (*Achillea millefolium*), with a median range of 61,400 ha (S2). For the median current range occupied by these species, preventing species richness from declining from five to four, for example, would confer a marginal value for carbon storage of \$7.1 million species⁻¹ (calculated as the product of the median area, 61,400 ha and the marginal value for the fifth species for the medium price scenario; Table 1).

Preventing species richness declining from 16 to 15 would confer a marginal value of carbon storage of \$681,000 species⁻¹. These scenarios are hypothetical because species richness is not uniformly distributed, because species loss does not occur independently of other shifts in community and ecosystem processes, and because the selection of the median range is arbitrary, given the large variation among species and the marked reduction in the ranges of grassland species due to extensive historical conversion of grasslands to agriculture (26). These all challenge the simple translation of the loss of one species over its full geographic range to the experimentally derived relationship between richness and value (Fig. 3). The estimates are offered here in the spirit of exploring the context of the marginal value of species richness for carbon storage.

In the second example, consider the CRP of the U.S. Department of Agriculture (USDA), where land owners receive federal payments for restoring previously cultivated lands to grasslands. Across the conterminous United States, approximately 12.34 million ha of land under cultivation have been converted to CRP grasslands, increasing land C uptake by approximately 6.54 teragrams C year⁻¹ [area and C uptake estimates averaged from (17, 27–30)]. We synthesized published estimates of species richness in CRP grasslands and paired reference native grasslands (16, 31–34) and found that species richness in CRP grasslands ($S = 6.5 \pm 1.1$) was lower than in adjacent remnant grassland sites ($S = 11.4 \pm 1.8$), indicating the potential for CRP restoration to achieve higher species richness and associated ecosystem services. Directly extrapolating economic value determined from the Minnesota grassland experiments, the marginal value of gaining one additional species over this entire CRP area (increasing species richness from $S = 6$ to $S = 7$), would amount to ~\$722 million. Restoring species richness on CRP grasslands to levels observed for the remnant grasslands (from $S = 6$ to $S = 11$) would confer a value for the increased carbon storage of ~\$2.350 billion (calculated as the area of CRP lands, 12.34 million ha, multiplied by the sum of the marginal values per unit area for the 7th through the 11th species shown in Table 1 for the mid-range estimate of the social cost of carbon, \$137.26 MT C⁻¹). Practices as simple as using more diverse seed mixes can promote higher species richness in prairie restoration (35, 36). Although this may be more expensive up front than seeding monocultures (37), the valuation shown here provides a means to evaluate the long-term economic benefits from carbon storage and other ecosystem services flowing from increased diversity compared to the higher up-front costs. This simple extrapolation extends the relationship between species richness and carbon storage developed in the Minnesota grassland experiments to the 12.34 million ha of the CRP, which is unlikely to be a precise translation, given differences in climate zones and soil types across the region; the certainty of our estimates obviously declines with increasing spatial scale. It is also worth noting that converting marginal or recently abandoned agricultural land (with typically very low soil C and species richness) to diverse prairie (for example, 11 species) would result in even greater increases in C storage than increasing CRP grasslands from 6 to 11 species (38).

This example illustrates how the valuation approach presented here could inform choices about land use. For example, assessing the role that biodiversity plays in the value of ecosystems to store carbon relative to other land use choices would highlight the opportunity costs of a grassland that is kept as a prairie rather than converted to an alternative land use. Similarly, assuming that higher forest species richness also enhances C storage (5, 6), incorporating this information into the C storage valuation of conversion of marginal or abandoned agricultural land into forests (17) (where forests rather than grasslands are the

Table 1. Marginal values of carbon stored by additional species to a grassland ecosystem for three carbon prices capturing the range summarized by the Interagency Working Group on the Social Cost of Carbon (25). Values are means and 95% confidence intervals in $\$ \text{sp}^{-1} \text{ha}^{-1}$ for ecosystem carbon (soil and plants) averaged across the BigBio and BioCon grassland experiments. Values are in 2010 U.S. dollar (USD).

| Number of species | Medium estimate of social cost of C (\$137.26 MT C ⁻¹) | Low estimate of social cost of C (\$41.94 MT C ⁻¹) | High estimate of social cost of C (\$400.33 MT C ⁻¹) |
|-------------------|--|--|--|
| 2 | \$804.55 (\$524.3–\$1059.54) | \$245.83 (\$160.2–\$323.74) | \$2346.54 (\$1529.16–\$3090.24) |
| 3 | \$333.38 (\$201.36–\$473.06) | \$101.87 (\$61.52–\$144.54) | \$972.33 (\$587.27–\$1379.72) |
| 4 | \$183.05 (\$107.8–\$268.18) | \$55.93 (\$32.94–\$81.94) | \$533.89 (\$314.41–\$782.17) |
| 5 | \$115.83 (\$67.21–\$174.15) | \$35.39 (\$20.54–\$53.21) | \$337.84 (\$196.03–\$507.94) |
| 6 | \$79.94 (\$45.83–\$123.40) | \$24.43 (\$14.00–\$37.71) | \$233.15 (\$133.66–\$359.91) |
| 7 | \$58.50 (\$33.19–\$91.64) | \$17.88 (\$10.14–\$28.00) | \$170.63 (\$96.81–\$267.26) |
| 8 | \$44.68 (\$25.15–\$70.43) | \$13.65 (\$7.68–\$21.52) | \$130.31 (\$73.35–\$205.43) |
| 9 | \$35.24 (\$19.71–\$56.20) | \$10.77 (\$6.02–\$17.17) | \$102.77 (\$57.50–\$163.90) |
| 10 | \$28.51 (\$15.87–\$45.89) | \$8.71 (\$4.85–\$14.02) | \$83.14 (\$46.29–\$133.83) |
| 11 | \$23.54 (\$13.05–\$38.06) | \$7.19 (\$3.99–\$11.63) | \$68.64 (\$38.06–\$111.00) |
| 12 | \$19.76 (\$10.92–\$32.08) | \$6.04 (\$3.34–\$9.80) | \$57.63 (\$31.85–\$93.56) |
| 13 | \$16.83 (\$9.27–\$27.41) | \$5.14 (\$2.83–\$8.37) | \$49.08 (\$27.04–\$79.93) |
| 14 | \$14.50 (\$7.97–\$23.68) | \$4.43 (\$2.44–\$7.24) | \$42.30 (\$23.25–\$69.08) |
| 15 | \$12.63 (\$6.93–\$20.67) | \$3.86 (\$2.12–\$6.32) | \$36.83 (\$20.20–\$60.30) |
| 16 | \$11.10 (\$6.07–\$18.20) | \$3.39 (\$1.86–\$5.56) | \$32.36 (\$17.72–\$53.09) |

typically native vegetation) would also advance our knowledge about economic consequences of management decisions. Hence, at the very least, determining the additional C storage value gained with species richness should be taken into account in comparing different land use management options.

The assessment of economic value offered here is limited in a number of ways. For example, our analysis assessed the value of species richness for carbon storage in one ecosystem type only and only in one part of the world. Although the pattern of increasing plant carbon storage (and thus value) with plant species richness may be general, reflecting the well-documented relationship between plant species richness and plant productivity (4), it is possible that biome-specific estimates of the value of species richness will reflect variation in the relationships between species richness and carbon storage. Relationships between species richness and soil carbon, for which we currently have the least information, may vary with region, driven by climate, edaphic factors, dominant vegetation type (for example, trees, shrubs, grasses, or forbs), or characteristics of dominant species.

Moreover, species identities influence ecosystem services (39), such that the order in which species are lost from ecosystems could influence the quantitative responses of ecosystem services, like carbon storage. For example, in grasslands, C4 grasses and legumes tend to promote greater soil carbon accumulation (8). Our approach evaluates changes in species richness on average, irrespective of the impacts of individual species, because currently, we do not have the knowledge to predict which species are at greatest risk of extinction in these systems. Thus, our assessment focused on the average expectations at each level of richness.

Nevertheless, our estimates of the value of species richness may be conservative. Our data are based on experiments where carbon storage and, thus, economic values are nonlinear functions of species richness (Fig. 3), such that changes in richness at lower levels of diversity have greater influence on net primary production, which in turn influences carbon storage. However, the typically saturating relationship between plant richness and net primary production can become more monotonically increasing the longer the studies proceed. For example, in the experiments assessed here—among the longest-running biodiversity experiments in grasslands—the effects of species richness are growing stronger through time and have yet to reach a steady state (40). Thus, our estimates of biodiversity effects on carbon storage may underestimate the long-term relationships. In the absence of 50-year-long biodiversity experiments, our study provides a first-cut valuation of the carbon storage provided by species richness that can guide further refinements.

Furthermore, carbon storage is only one ecosystem service among many that species contribute to ecosystems, and therefore, our economic valuation likely underestimates the total value of species richness. Plant species provide a wide variety of benefits, including products, like wood, food, and biofuels, as well as services, like recreation, water purification, buffers against floods, and support for other sources of biodiversity—all of which have their own economic values. Although there is evidence for trade-offs among species in the functions they perform and services they provide (41), no single species appears to be “best” at providing a wide variety of benefits to society (42). Optimizing the variety of services ecosystems provide to humanity will almost certainly require conserving a greater number of species, and the value of each species will likely be the sum of its contributions

across multiple processes. Integrating our approach with robust estimates of diversity effects on multiple ecosystem processes (43) and of their value remains an important task for future studies.

Despite widespread claims about the economic value of biodiversity for ecosystem services (18–20), quantitative assessments of the relationship between biodiversity and specific services are rare. Our work demonstrates positive marginal value of species richness for carbon storage, which, by offering actual assessments of value, helps move beyond mere speculation about the economic importance of biodiversity and lends an economic argument to biodiversity preservation for climate protection. Other ecosystem services are sensitive to the simplification of biological communities, and including these other factors in future assessments can build upon the framework for valuing the biodiversity presented here.

MATERIALS AND METHODS

Estimating C storage in grasslands

We estimated grassland carbon storage based on two experiments that have examined how the richness of herbaceous plants affects plant biomass production and soil carbon in the Cedar Creek Ecosystem Reserve in Minnesota, United States. Experiment 120 (E120), called Biodiversity II or BigBio due to its larger-than-average spatial scale for manipulations of biodiversity, was started in 1994. E120 contained 342 plots laid out as 13-m × 13-m squares with the central 9 m × 9 m actively maintained for the specified species and plant diversity (44). Plots were planted with grassland perennials that represented C4 grasses, C3 grasses, legumes, and other forbs. The species composition of plots was chosen by separate random draws of 1, 2, 4, 8, or 16 plant species from a pool of 18 species, with each level replicated in 30 or more plots. E141, called BioCON, started in 1997 to explore how plant communities respond concurrently to three forms of environmental change: increasing nitrogen deposition, increasing atmospheric CO₂, and decreasing biodiversity (45). For the work conducted here, only data from the ambient CO₂ and ambient N treatments were used. Species richness was manipulated in subplots (2 m × 2 m) located within the three 20-m-diameter ambient CO₂ plots, with 32 randomly assigned replicates for the 1-species treatments (2 replicates per each of 16 species), 15 for those planted to 4 species, 15 for 9 species, and 12 for 16 species. Different functional groups of plants are present in both experiments (for example, C4 grasses, C3 grasses, legumes, and other forbs) and are represented at all levels of species richness. Thus, any influence of functional groups on carbon accumulation (8, 46) are distributed across treatment levels in our analysis. These experiments—and our analyses of them—excluded large vertebrate grazers, which can influence grassland carbon storage (47) and, thus, its economic value; our assessment focused solely on species richness and did not consider grazing or other influences on grassland carbon accumulation.

In both experiments, soils were treated before initiation of the manipulations. Before planting, methyl bromide was applied to soils in the BioCON experiment, and the uppermost layer of the soil (0 to 5 cm) was relocated off plot for BigBio, to reduce the influence of the seed bank on species composition of the experimental plots in both cases. Differences in these pretreatments may contribute to differences between the experiments in rates of carbon accumulation.

Soil carbon equilibrates slowly with changes in plant production, such that measured changes in soil carbon even after 10 years of experimental manipulation will be smaller than what can be reasonably expected over time scales appropriate for carbon management for cli-

mate protection (for example, 50 years). Thus, for each of the two grassland experiments, we used data collected from each plot to estimate parameters for a model that projects soil C accumulation over a 50-year time frame, using first-order kinetics to describe soil C accumulation for surface (0 to 20 cm) and deep (20 to 100 cm) soil C

$$C_{it} = C_{0i} \times e^{-k_i t} + I_i \times (1 - e^{-k_i t})/k_i \quad (1)$$

where C_0 and C_t are soil C (g C m⁻²) at the beginning of the experiment and at time t (year), k is the decomposition rate constant (year⁻¹), I is the annual input of C to soil (g C m⁻² year⁻¹), and the subscript i indicates that the model is constructed for both shallow ($i = 1$) and deep ($i = 2$) soil carbon. To fit the model and obtain plot-level parameter estimates of I and k , we used all available soil C data from the Cedar Creek Ecosystem Science Reserve website (available publicly from www.cbs.umn.edu/explore/cedarcreek). For E120, surface soil data (0 to 20 cm) were available from years 0, 1, 5, 7, 9, and 11 for all plots, and from year 10 for some plots, and data for 0 to 100 cm were available for years 0 and 11. For E141, soil C data were available for each plot at the beginning of the experiment (year 0) and after 5 and 10 years of experimental treatment (0- to 60-cm depth); we scaled soil C data to 0- to 100-cm depth for E141 using soil C depth distributions for E120 (20-cm increments to 1-m depth) to determine the proportion of C in the top meter of soil contained in the 60- to 100-cm depth, and then we used this proportion with observed soil C data for each plot to estimate total C to 1 m. To find the best-fit parameters [I and k that explained the change in observed soil C over time (Eq. 1)], we used a global optimization procedure with a Markov chain Monte Carlo approach. In this approach, the model parameters I and k are estimated at the same time, repeatedly, to produce a joint probability density function. Each time the parameters are estimated, the cost function, J , was calculated, which determines the difference between observed and modeled soil C

$$J = \sum_{i=1}^n (C_m(t_i) - C_{\text{obs}}(t_i))^2 \quad (2)$$

where n is the number of times soil C was sampled, t_i for $i = 1, 2, \dots, n$, t is time (years) after the start of the biodiversity experiment, and C_m and C_{obs} are the modeled and observed soil C at time t_i . After each iteration of parameter estimates, the Metropolis-Hastings algorithm was used to determine whether the current parameter estimates resulted in a closer match to the observed data. In the end, the Metropolis-Hastings algorithm generates a distribution of accepted I and k values wherein their means coincide with the minimal value of J (that is, the best fit to the observed data). Soil C content for each plot was projected to 50 years using the mean parameter estimates I and k and measured C_0 for both depths (that is, soil C at start of the experiment). During this fitting process, we constrained total I to be within 30% of the sum of the following variables that comprised our proxies for current input: (i) annual root C increment, (ii) an estimate of turnover [the product of measured maximum root C content and 0.55 year⁻¹, which is an average value for root turnover in grasslands (48)], and (iii) average aboveground C content (reasonable, because all aboveground biomass dies back each year in these perennial plants). I was partitioned into surface soil and deep soil based on the proportion of total root biomass that occurred in the 0- to 20-cm depths versus the 20- to 100-cm depths. The 30% bounds were chosen on the basis of our opinion that this represents a

reasonable measurement error such that actual C input to soil may be 30% lower or higher than the measurements we have available. The parameter k was constrained to fall between 0.0001 and 1.0 year⁻¹, which allows for a wide range of soil C mean residence times ranging from 1 to 10,000 years.

For each plot, total soil carbon (0 to 100 cm) was projected for each year of the 50-year simulation, to be used as input data for the procedure to relate C storage to species richness (see next section). For years where soil C was measured directly, modeled estimates of soil C for those years corresponded well with measurements (S1). Plant biomass C was determined for each plot as the product of biomass and C concentration (data available publicly from www.cbs.umn.edu/explore/cedarcreek).

Relating C storage to species richness

For each C pool, the relationship between species richness and C content was analyzed by bootstrapping, using a Michaelis-Menten function to describe the relationship between plant species richness and carbon content. Each bootstrap iteration also estimated cumulative and annual marginal carbon, and economic value, as described in more detail below. An example of the R code used for the bootstrapping procedure for total ecosystem C pools for the BioCON experiment (S4) and the function used to estimate the Michaelis-Menten parameters (S5) are included in the Supplementary Materials. Here, we refer to specific lines of code in the file (S4) in describing the steps used in the bootstrapping procedure.

For plants, one set of Michaelis-Menten parameter values was determined on the basis of measurements of plant biomass, and these were used to project a constant plant C pool over the 50-year period. For soils and total ecosystem C content, Michaelis-Menten parameter values were determined for each of the 50 years. The resampling procedure worked as follows (S4, lines 18 to 84): Samples, corresponding to replicate plots, were drawn with replacement, replicating the structure of the data set by drawing the same number of samples at each level of species richness as actually occurred in the grassland experiments (S4, lines 25 to 29). For each bootstrapped iteration, the resampled data were fit to the Michaelis-Menten function between S and total ecosystem carbon content, C

$$C = \frac{aS}{(b + S)} \quad (3)$$

where a and b are the parameter values for the Michaelis-Menten fit (S4, lines 32 to 40, which calls the function described in S5). The best-fit parameter values were obtained for each iteration by minimizing the sums of squares using the “optim” function in R (version 3.0.2) with the “Nelder-Mead” and a bounded “Broyden-Fletcher-Goldfarb-Shanno” algorithm (bounded such that both parameters could not be negative; see S5). For each bootstrapped iteration for each year, the parameter values a and b were used to estimate total soil and ecosystem C content for plots ranging from 1 to 16 species (S4, lines 41 to 49). Parameter values for year 50 are reported in the Supplementary Materials (S2).

Estimating the economic value of richness

The economic analysis of the carbon storage value of grassland plant species diversity considers the additional carbon storage that occurs as the number of species S increases by one unit (marginal C storage). Marginal carbon was computed for each of the 15 incremental steps in species richness described in the modeled data, from $S = 1$ to $S = 2$,

$S = 2$ to $S = 3$, ..., to $S = 15$ to $S = 16$, bounded by the actual data from the experiments where S varied from 1 to 16 in experimental plots. Cumulative marginal carbon storage was computed in the bootstrapping procedure as the added carbon stored, for a given year, in simulations with one additional species (S4, lines 50 to 56). Annual marginal carbon storage was determined by calculating the change in cumulative marginal carbon from year to year at each change in species richness considered (S4, lines 58 to 67).

Valuation of the estimated annual marginal changes in carbon storage as species richness increases was then estimated using the social costs of carbon, with the value discounted over time as carbon accumulation occurred over the 50-year simulation. The social cost of carbon is the damage done by emitting an additional unit of carbon dioxide (CO₂). To ensure a common unit across all greenhouse gases, researchers often express the social cost of carbon in terms of carbon dioxide (CO₂) equivalents. We converted CO₂ equivalents to metric tons of carbon (MT C) emissions, expressing the social costs of carbon in U.S. dollars per metric ton of carbon (\$ MT C⁻¹). If, as a result of increased plant species richness, carbon storage by grasslands rises, then the value of this additional carbon storage is the total damages avoided by removing greenhouse gases such as CO₂ from the atmosphere.

The estimates of the social cost of carbon we used were derived from the recent synthesis conducted by a consortium of U.S. federal agencies for regulatory impact analysis (25). These values, reported in \$ MT CO₂⁻¹ and USD 2007, were transformed to 2010 \$ MT C⁻¹ using the molecular formula of CO₂ and the U.S. gross domestic product deflator from the World Bank (49). We calculated the present value of future storage of a metric ton of carbon, V , as

$$V = \sum_{t=1}^{50} P m_t e^{-rt} \quad (4)$$

where r is the real discount rate for future “payments” (in terms of avoiding social damages from CO₂ emissions) to preserve grasslands for carbon storage, P is the social cost of carbon, t is year over the 50-year period, and m_t is the annual marginal carbon accumulation for year t in metric ton C per hectare per species per year, determined as described above. Equation 4 estimates the present value of carbon uptake over 50 years, where the value of carbon uptake is discounted over time. That is, a quantity of carbon in year 1 has a higher present value than the same quantity of carbon taken up in year 50. We assume that the long-run rate of r is 4%. We used three values for P from the Interagency Working Group that capture a broad range of estimates of the social cost of carbon (25), all based on simulations of the social cost of carbon from integrated assessment models with varied assumptions about factors such as the social discount rate. The low estimate is \$41.94 per metric ton C, the medium estimate is \$137.26 per metric ton C, and the high estimate is \$400.33 per metric ton C. All social cost estimates are in 2010 USD. The Interagency Working Group included a range of discount rates, from 2.5 to 5%, reflecting uncertainty about discounting over many generations. The highest estimate of the social cost of carbon was “included to represent higher-than-expected economic impacts from climate change” [(23), p. 12]. The estimates we selected span an order of magnitude, capturing a wide range of estimates of the social cost of carbon. The conversion of annual marginal carbon uptake to value occurs in lines 98 to 117 of the R code file (S4).

As a hypothetical exercise estimating the marginal value of the entire species for C storage, we estimated the marginal value of species for

carbon storage based on the median geographical ranges of all the species included in the Minnesota grassland experiments. We multiplied the areal-based marginal value calculated as described above ($\$ \text{sp}^{-1} \text{ha}^{-1}$) by the median range of species (ha) included in the grassland experiments (61,400 ha; S2). Species ranges were estimated using occurrence records extracted from the Global Biodiversity Information Facility (50), including synonymous records when relevant. Geo-referenced records were rasterized to a 1-km resolution grid, and the range for each species was estimated as the total number of grid cells in which a species occurred. To provide just one example of the resulting values, we used values for each species to estimate the median marginal value of preventing the loss of one species over its entire range, as a function of starting species richness. We also estimated the marginal value of species for carbon storage, using as an illustrative case study the lands in the conterminous United States registered through the USDA's Conservation Reserve Program (CRP), for which estimates are available for the effect of land conversion on species richness and carbon uptake. We gathered published surveys of species richness that compared restored grasslands to paired plots of remnant prairie. Our search yielded publications reporting data from restored grasslands and paired reference plots in the U.S. states of Colorado, Iowa, Kansas, Nebraska, New Mexico, Oklahoma, and Texas (16, 31–34). We calculated the mean species richness (\pm SEM) across studies for the CRP grasslands and paired reference plots. We then used the experimentally determined relationship between species richness and value from the Minnesota grassland experiments (Table 1) and the average area covered by the CRP program reported from the literature (17, 27–30). Given the exploratory nature of this exercise, we did not attempt to estimate error. Instead, we simply extrapolated on the basis of our calculated marginal value of species on a per hectare basis, shown in Table 1, using the average value for the medium social cost of carbon ($\$137.26 \text{ MT C}^{-1}$).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/4/e1601880/DC1>

- S1. Measured soil carbon in the BioCON and BigBio experiments compared to soil carbon modeled using data assimilation and the *I-k* model.
- S2. Michaelis-Menten parameters for plant, soil (at year 50), and total C (at year 50) as a function of species richness.
- S3. List of species (by binomial name, common name, and functional group) included in the BioCON and BigBio experiments at the Cedar Creek Long-Term Ecological Research (LTER) site.
- S4. R code for estimating marginal carbon and value for the BioCON experiment.
- S5. R code function for estimating Michaelis-Menten parameters relating species richness to carbon stocks.

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The economic value of grassland species for carbon storage

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