

Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity

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Society places value on the multiple functions of ecosystems from soil fertility to erosion control to wildlife-carrying capacity, and these functions are potentially threatened by ongoing biodiversity losses. Recent empirically based models using individual species' traits suggest that higher species richness is required to provide multiple ecosystem functions. However, no study to date has analyzed the observed functionality of communities of interacting species over multiple temporal scales to assess the relationship between biodiversity and multifunctionality. We use data from the longest-running biodiversity-functioning field experiment to date to test how species diversity affects the ability of grassland ecosystems to provide threshold levels of up to eight ecosystem functions simultaneously. Across years and every combination of ecosystem functions, minimum-required species richness consistently increases with the number of functions considered. Moreover, tradeoffs between functions and variability among years prevent any one community type from providing high levels of multiple functions, regardless of its diversity. Sustained multifunctionality, therefore, likely requires both higher species richness than single ecosystem functionality and a diversity of species assemblages across the landscape.

Cedar Creek | multifunctionality | species richness | tradeoffs

As human-driven ecosystem simplification and species losses accelerate worldwide, a growing body of experimental and theoretical literature has emerged to examine the effects of biodiversity losses on ecosystem functioning. Syntheses in this field suggest that the relationship between species richness and individual ecosystem functions is positive but often saturating (1–6). However, society places value on multiple attributes of ecosystems ranging from productivity and crop pollination to the maintenance of viable species populations (7). A critical need, therefore, exists to examine the effects of species losses on multiple ecosystem functions simultaneously (8–10). Although initial empirically based models using individual plant species' traits suggest that higher species richness is required to provide ecosystem multifunctionality (2, 11), this hypothesis remains untested in established communities of interacting species over time.

In multispecies assemblages, at least two important types of tradeoffs are likely to affect the relationship between biodiversity and ecosystem multifunctionality (8). First, certain functions could be difficult for a single assemblage to support, because the functions conflict. For example, productivity and stress tolerance can be negatively related and difficult or impossible to maximize jointly; species best suited for one of these functions often possess traits that lead to low levels of the other function (12, 13). Second, different functions could be maximized by communities of different species richness and composition (14). For example, resistance to different invasive species might be maximized by different resident species combinations. If either type of tradeoff proves important, then high levels of multifunctionality will require not just greater species richness within local assemblages but also a diversity of assemblages on the landscape.

We analyzed data from the longest-running biodiversity-ecosystem functioning manipulation to date at the Cedar Creek Ecosystem Science Reserve in Minnesota (15) to examine the ef-

fects of biodiversity on the provision of up to eight ecosystem functions simultaneously. We compare the capacities of 168 established grassland plant communities of differing richness to provide multiple ecosystem functions, ranging from invasion resistance to productivity to support for higher trophic levels. Unlike previous analyses of multifunctionality based on calculated (8) or regression-based estimates (11) of individual species' contributions to functioning, our approach is based on the observed levels of functioning provided by the actual species combinations included in the experiment. This allows us to detect and explore the effects of species interactions and the possibility of tradeoffs in the provision of different functions, both of which are critical to understanding how multifunctionality works in real ecosystems.

Results and Discussion

We assessed the ability of communities to achieve multifunctionality thresholds (T), which we defined as a set percentage of each function's observed maximum value (e.g., $T_5 = 30\%$ of maximum value for each of five functions). We began by asking what minimum species richness was required for most (>50%) assemblages at each richness level to exceed multifunctionality thresholds. The minimum species richness required for >50% of all communities to meet multifunctionality thresholds increased as the number of functions considered increased from one to seven, regardless of the year (1998, 2000, or 2002) or desired multifunctionality threshold ($T = 30\%$, 40%, or 50%). For each number of ecosystem functions considered, minimum species richness also increased as we raised T (Fig. 1).

We then tested how communities of differing richness performed at providing different numbers of functions at different T . The proportion of communities achieving T increased with higher species richness in most, but not all, years. In 1998, richness did not significantly affect the proportion of communities at that richness level that achieved multifunctionality at T values of 30%, 40%, 50%, and 60% (Table S1). In 2000 and 2002, both species richness and the number of functions considered influenced the overall proportion of communities of a given richness level that met or achieved T (ANOVA; $P < 0.001$) (Fig. 2 and Table S1). In the years 2000 and 2002 and at relatively low values of T ($T = 30\text{--}50\%$ in 2000 and $T = 30\text{--}40\%$ in 2002), communities of higher richness were more likely to meet or exceed T for all functions considered, from one to seven functions (ANOVA; $P < 0.001$).

After we considered higher levels of T , few communities were able to achieve threshold levels of more than four functions simultaneously, regardless of species richness. The strong positive interdependence of richness and multifunctioning at lower levels of T suggests that assemblages with higher richness than 16 species might be able to more frequently achieve high threshold levels for

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Table 1. Best-performing plot for each year (assessed across seven ecosystem functions) and multifunctionality achieved in each year by that plot

| Plot number (richness) | Rank (percentage of maximum multifunctionality) by year | | |
|-----------------------------|---|-------------|------------|
| | 1998 | 2000 | 2002 |
| 178 (8) | 1 (95.6%) | 5 (83.3%) | 27 (66.2%) |
| 273 (16) | 29 (68.8%) | 1 (105.0%)* | 13 (70.1%) |
| 206 (8) | 11 (71.6%) | 68 (64.8%) | 1 (77.7%) |
| Best-performing monoculture | 0 (72.4%) | 0 (67.3%) | 0 (65.9%) |

Percentage of maximum multifunctionality for a plot is computed as the mean percentage of the maximum that it achieved for each function when the maximum level for each function in a given year is taken from across all plots.

*Because the maximum level for each function was computed as a mean of the top eight plots, some individual plots achieve >100% of this level for one or more functions.

richness can alleviate the tradeoffs between certain functions in some years. This could occur simply because more species assemblages are more likely to contain more species that maximize each of the negatively correlated functions (sampling effect) (2).

In addition to negative correlations among functions, tradeoffs occurred, because different ecosystem functions were seldom maximized at the same species-richness levels (Fig. 3) and even more seldom by the same particular species mix in a given year. Thus, fewer plots achieved high-multifunctionality thresholds, because more functions were considered. Different species mixes and richness levels are also required in each year to maximize or provide high levels of multifunctionality (Table 1). In 1998, very few plots delivered high levels of functioning, even for individual functions. For instance, in 1998, fewer than one-half of the plots achieved $T = 50\%$ of maximum for even one function.

A frequent finding in biodiversity-ecosystem functioning experiments, and in related mathematical theory (4, 5), is an asymptotic relationship between species richness and a single ecosystem function with seeming “saturation” occurring at low diversity (typically <50% of total) (16). In these cases, as species numbers increase, each additional species contributes, on average, progressively less additional functioning, providing support for the possibility that only a subset of the species in a given community is necessary to maintain maximum levels of functioning (17). Several authors have argued that added layers of realism, such as temporal and spatial variability and spatial scale, would increase the number of species needed to saturate ecosystem functioning (2, 18, 19). Multifunctionality has been explored in this light (1, 9) and is shown to require higher species richness in analyses based on individual plant species’ traits (20).

Our results concur with others’ findings that the probability of sustaining multiple functions increases with species richness and that

low multifunctional redundancy across species increases the likelihood of functional consequences of species loss when more than one function is considered (8, 11). However, contrary to our results, one experimental dataset involving six functions by Gamfeldt et al. (8) found that communities were able to provide threshold levels of more than four functions. Our findings suggest that the added realism of considering multifunctionality over multiple years and in assemblages of established, interacting species increases the number of species required for functional saturation because of functional tradeoffs. For example, certain combinations of functions such as invasion resistance (maximized at high richness) and plant nitrogen content (maximized in certain monocultures) could not be achieved by any single community, and the optimal community composition to provide a given bundle of ecosystem functions varies from year to year. Others have observed that single-function or single-service analyses at any scale miss important tradeoffs (21). We show that such tradeoffs increase the importance of both species richness at the plot scale and biodiversity at larger scales for the sustained delivery of multiple ecosystem functions. For ecosystems to provide multiple functions, community diversity across a landscape and species diversity within neighborhoods are probably necessary.

Methods

We used 1998, 2000, and 2002 data from the Cedar Creek experiment in which 168 9×9 -m field plots were planted with randomized combinations of 1, 2, 4, 8, and 16 grassland species drawn out of a pool of 18 species in 1994 (n at each richness level = 29–39 plots) (15). We included data on eight measures of ecosystem functioning: invasion resistance (100% minus percentage of cover of invasive species); above ground net primary productivity; below ground biomass (0–30 cm); soil-nitrogen use (minimizing $\text{NO}_2 + \text{NO}_3$, 0–20 cm); insect species richness and abundance (in August); soil C (0–20 cm); and plant N (% N). Data for soil carbon and nitrate were not collected in 1998 and 2000, respectively. We defined maximum level of functioning (for each year and function) as the mean of the top-functioning eight (~5%) communities. For each community, by year, we computed the percentage of this maximum achieved for each function.

We assessed the ability of communities to simultaneously achieve at least a particular percentage (multifunctionality threshold or T) of each function’s observed maximum value across all communities and functions considered. We calculated minimum species richness required so that one-half of communities at that richness level exceeded T (for $T = 30\%$, 40% , and 50%) for all of n functions ($n = 1-7$). To calculate this, we first identified the proportion of plots (y) that achieved T for each unique combination of T (30%, 40%, or 50%), year (1998, 2000, or 2002), richness level (1, 2, 4, 11, or 19), and number of functions (1–7). Because y is a proportion of all 168 experimental plots, there is only one value per T per year per richness per number of functions combination and therefore, no error bars. For each combination of T , year, and number of functions, we fit a straight line ($y = mx + b$ where y is the proportion of plots and x is the species richness) between the two richness levels that bracketed $y = 0.5$. We fit these lines by solving for m and b using the known (x and y) for each of the two endpoints. We then set $y = 0.5$ and solved $y = mx + b$ for the critical level of species richness (x) at which one-half of plots of a given richness in a given year meet or exceed T for all n functions.

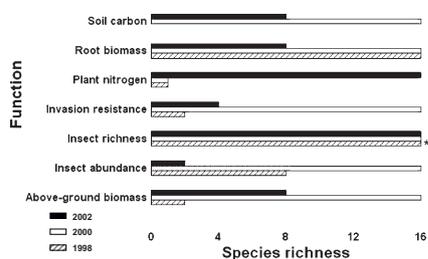


Fig. 3. Species richness at which each ecosystem function is maximized in each of the three study years. Data were not collected for soil nitrate in 2000 or soil carbon in 1998. Maximum insect richness in 1998 occurred in both single and 16-species communities (a tie). Soil-nitrate data are not shown for 1998 and 2002, because in each year, maximum soil-nitrate use was a tie among three or more richness levels.

For each richness level, we tallied the proportion of communities exceeding T values from 10% to 90% for all possible combinations of 1–7 (8 in 2002) functions. We conducted ANOVA on the proportion of communities in each year that met or exceeded T of 30–60% with species richness and number of functions as factors and an interaction term. The dependent variables (proportion of communities) were arcsine transformed for each of these four tests (for $T = 30\%$, 40%, 50%, and 60%) to improve data conformation with the assumptions of a parametric test. We did not perform post hoc tests on the results of these ANOVAs.

We computed Pearson correlation coefficients for all pairs of ecosystem functions for each year and across all richness levels to identify negatively correlated pairs. We then computed Pearson correlation coefficients within each richness level for those functions in negatively correlated pairs. We used ordinary least squares regression of correlation coefficients on richness level

to test the effect of species richness on degree of tradeoff between negatively correlated pairs of functions. We used Bonferroni-adjusted P values to account for multiple tests.

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- Balvanera P, et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning. *Ecol Lett* 9:1146–1156.
- Hooper DU, et al. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol Monogr* 75:3–35.
- Cardinale BJ, et al. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc Natl Acad Sci USA* 104: 18123–18128.
- Tilman D (1999) The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80:1455–1474.
- Lehman CL, Tilman D (2001) Biodiversity, stability, and productivity in competitive communities. *Am Nat* 156:534–552.
- Naeem S, Bunker DE, Hector A, Loreau M, Perrins C (2009) *Biodiversity, Ecosystem Functioning and Human Wellbeing* (Oxford University Press, Oxford).
- Hassan R, Scholes R, Ash N, eds (2005) *Ecosystems and Human Well-being: Current State and Trends, Volume 1. Findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment*, (Island Press, Washington, DC), pp vii–23.
- Gamfeldt L, Hillebrand H, Jonsson PR (2008) Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89:1223–1231.
- Hector A, Joshi J, Lawler SP, Spehn EM, Wilby A (2001) Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* 129:624–628.
- Turner RK, et al. (2003) Valuing nature: Lessons learned and future research directions. *Ecol Econ* 46:493–510.
- Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448: 188–190.
- Grime JP (1974) Vegetation classification by reference to strategies. *Nature* 250: 26–31.
- Diaz S, et al. (2004) The plant traits that drive ecosystems: Evidence from three continents. *J Veg Sci* 15:295–304.
- Vinebrooke RD, et al. (2004) Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. *Oikos* 104:451–457.
- Tilman D, Reich PB, Knops JMH (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- Schwartz MW, et al. (2000) Linking biodiversity to ecosystem function: Implications for conservation ecology. *Oecologia* 122:297–305.
- Gitay H, Wilson JB, Lee WG (1996) Species redundancy: A redundant concept? *J Ecol* 84:121–124.
- Rosenfeld JS (2002) Functional redundancy in ecology and conservation. *Oikos* 98: 156–162.
- Loreau M (2004) Does functional redundancy exist? *Oikos* 104:606–611.
- Gamfeldt L, Hillebrand H (2008) Biodiversity effects on aquatic ecosystem functioning—maturation of a new paradigm. *Int Rev Hydrobiol* 93:550–564.
- Carpenter S, et al. (2006) Ecology. Millennium Ecosystem Assessment: Research needs. *Science* 314:257–258.