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Productivity and sustainability influenced by biodiversity in grassland ecosystems

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THE functioning and sustainability of ecosystems may depend on their biological diversity^{1–8}. Elton's⁹ hypothesis that more diverse ecosystems are more stable has received much attention^{1,3,6,7,10–14}, but Darwin's proposal¹⁵ that more diverse plant communities are more productive, and the related conjectures^{4,5,16,17} that they have lower nutrient losses and more sustainable soils, are less well studied^{4–6,8,17,18}. Here we use a well-replicated field experiment, in which species diversity was directly controlled, to show that ecosystem productivity in 147 grassland plots increased significantly with plant biodiversity. Moreover, the main limiting nutrient, soil mineral nitrogen, was utilized more completely when there was a greater diversity of species, leading to lower leaching loss of nitrogen from these ecosystems. Similarly, in nearby native grassland, plant productivity and soil nitrogen utilization increased with increasing plant species richness. This supports the diversity–productivity and diversity–sustainability hypotheses. Our results demonstrate that the loss of species threatens ecosystem functioning and sustainability.

The diversity–productivity hypothesis is based on the assumption that interspecific differences in the use of resources by plants allow more diverse plant communities to utilize more fully limiting resources and thus attain greater productivity^{6,8,17,18}. A related hypothesis is that nutrient leaching losses from ecosystems should be a decreasing function of plant diversity because of greater nutrient capture and/or immobilization in more diverse ecosystems^{4,5,17}. Taken together, these lead to the diversity–sustainability hypothesis; that the sustainability of soil nutrient cycles and thus of soil fertility depends on biodiversity. But the relationships between biodiversity and ecosystem functioning remain controversial^{3,10,13,18–23} because existing field data are from studies that lacked direct experimental control of biodiversity or sufficient replication. Only direct control of diversity allows attribution of responses to diversity rather than to other correlated factors^{8,18,20–23}. Moreover, the species composition of plots must be

randomly determined to avoid biases caused by the traits of particular species^{20,21}.

Here we report results of a field experiment in which the number of plant species was experimentally controlled (Fig. 1 legend). Our 147 plots, located on nitrogen-limited soil²⁴, were planted with either 1, 2, 4, 6, 8, 12, or 24 species. The species assigned to each plot were chosen by a separate random draw of the appropriate number of species from a pool of 24 North American prairie species. The impacts of diversity on plant productivity, nutrient capture and nutrient leaching were observed during the second year of growth. We also sampled a native grassland to determine the relationships between these variables in an undisturbed mature ecosystem.

Treatments created an experimental biodiversity gradient. Plant species richness, Shannon diversity (H'), and effective species richness (e^H ; Fig. 1a) were all significantly correlated with the number of species seeded into the plots (Pearson's $r = 0.81$, $r = 0.74$, $r = 0.75$, respectively; $n = 147$, $P < 0.001$ for all). Two measures of peak standing crop (our estimate of plant productivity) were positively correlated with the species-richness treatment (total plant cover: $r = 0.39$, $n = 147$, $P < 0.001$, Fig. 1b; biomass estimated by light penetration: $r = 0.27$, $n = 147$, $P < 0.001$). Both estimates were similarly dependent on observed plot species richness ($r_{\text{cover}} = 0.55$, $r_{\text{biomass}} = 0.42$, $n = 147$, $P < 0.001$ for both) and effective species richness ($r_{\text{cover}} = 0.29$, $r_{\text{biomass}} = 0.29$, $n = 147$, $P < 0.001$ for both). Thus, greater plant diversity led to greater productivity during the second year of ecosystem establishment.

Rooting-zone extractable soil NO_3^- was a decreasing function of species richness (Fig. 1c). Extractable NH_4^+ had a similar pattern ($r = -0.18$, $n = 147$, $P = 0.03$). This indicates that more species-rich plots more fully utilized soil mineral nitrogen, the main limiting resource²⁴. Below the rooting zone, soil NO_3^- concentrations

TABLE 1 Factors influencing plant total cover (productivity) in the biodiversity experiment

Variable	Parameter	Student's <i>t</i>	<i>P</i>
Intercept	18.9	3.82	0.0002
Species richness	1.31	6.72	0.0001
Rooting zone NO_3^-	-26.6	-2.20	0.03
Rooting zone NH_4^+	7.82	1.65	0.10
Root mass	2.96	5.00	0.0001

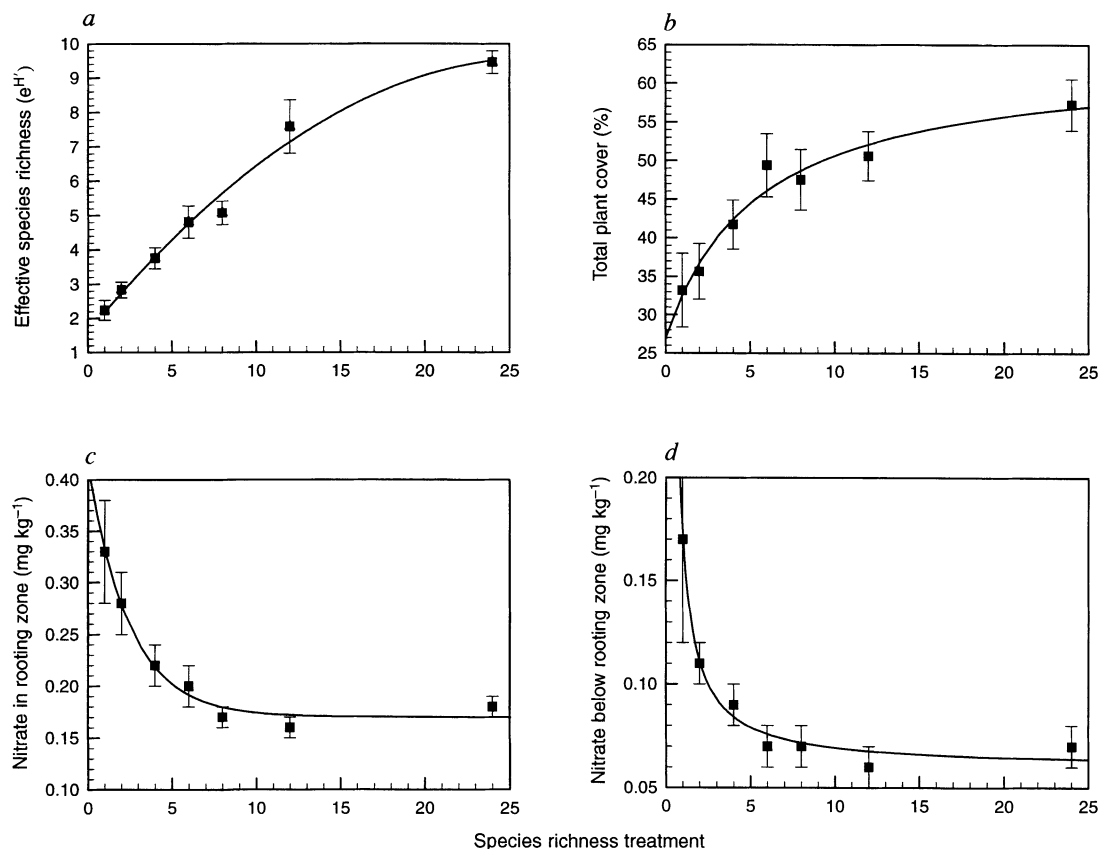
Multiple regression of total plant cover (dependent variable) on listed variables, each measured in all 147 plots. Overall $F_{4,142} = 28.5$, $P < 0.0001$, $R^2 = 0.45$.

TABLE 2 Factors influencing soil NO_3^- in the rooting zone in the biodiversity experiment

Variable	Parameter	Student's <i>t</i>	<i>P</i>
Intercept	0.33	12.0	0.0001
Species richness	-0.005	-2.74	0.007
Plant total cover	-0.001	-1.56	0.12
Root mass	0.003	0.14	0.89

Multiple regression of rooting zone soil NO_3^- on listed variables, each measured in all 147 plots. Overall $F_{3,143} = 7.39$, $P < 0.0001$, $R^2 = 0.13$.

FIG. 1 a, Effective species richness is $e^{H'}$, where H' is the Shannon diversity index; $e^{H'}$ is the number of equally abundant species required to give the observed H' . Curve is a simple second-order fit ($R^2 = 0.60$, $n = 147$, $P < 0.001$). b, Total plant cover is the sum of cover of all vascular species in a plot. Fitted curve is $y = 27 + 36.4x/(5.48 + x)$, $R^2 = 0.18$, $n = 147$, $P < 0.001$. c, Soil nitrate (as mg of N per kg of dry soil) at 0–20 cm depth, where 79.8% of roots occur. Fitted curve is $y = 0.17 + 0.24e^{-0.41x}$, $R^2 = 0.22$, $n = 147$, $P < 0.001$. d, Soil nitrate (as N) at 40–60-cm depth, where only 6.5% of roots occur. Fitted curve is $y = 0.06 + 0.091/x + 0.02/x^2$, $R^2 = 0.14$, $n = 147$, $P < 0.001$. All results plotted are means \pm s.e.m. METHODS. 147 plots, each 3×3 m, with 1-m walkways located at Cedar Creek in Minnesota²⁴, were randomly assigned to one of 7 species-richness treatments: seeding plots in May 1994 to 1, 2, 4, 6 or 8 species (20 replicates each), 12 species (23 replicates), or 24 species (24 replicates). Species used were *Achillea millefolium*, *Agropyron smithii*, *Andropogon gerardi*, *Anemone cylindrica*, *Asclepias tuberosa*, *Aster azureus*, *Astragalus canadensis*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Coreopsis palmata*, *Elymus canadensis*, *Euphorbia corollata*, *Koeleria cristata*, *Lespedeza capitata*, *Liatris aspera*, *Panicum virgatum*, *Petalostemum purpureum*, *Poa pratensis*, *Rudbeckia hirta*, *Schizachyrium scoparium*, *Solidago nemoralis*, *Sorghastrum nutans*, *Sporobolus cryptandrus* and *Vicia villosa*. Species added to each plot were chosen by separate random draws from these 24 prairie perennials. Each plot received 10 g m^{-2} seed in total, with equal masses of each species. To prepare soils for planting, pre-existing vegetation was treated with herbicide and burned in August 1993, the upper 6 to 8 cm of soil removed to reduce the seed bank, then plowed and repeatedly harrowed. Plots were watered twice a week and



weeded from an elevated boardwalk. All responses to treatments were measured after two seasons of growth, in August 1995, time of peak standing crop, a measure of productivity in these grasslands. Standing crop was estimated two ways. First, per cent cover of each species was determined in the same, predetermined 0.5×0.5 -m location in all plots for calculation of species richness, total plant cover, H' and $e^{H'}$. Second, light penetration through vegetation, measured 6 times per plot, was converted to biomass using a calibrated relationship. Soil nitrate and ammonium concentrations used 0.01 M KCl extractions, with two cores per plot. Root biomass data in regressions were from cores $5 \text{ cm diameter} \times 20 \text{ cm deep}$. Curves were chosen for simplicity and goodness of fit, and have much higher R^2 values than the corresponding Pearson (linear) correlations (see text).

were greater under low-diversity treatments (Fig. 1d), indicating greater leaching loss of soil nitrogen at lower plant diversity. Consistent with its low mobility in soil, NH_4^+ showed no such dependence ($r = 0.03$, $n = 147$, $P = 0.7$).

In summary, this experiment shows that both plant productivity and resource utilization were significantly greater at higher plant diversity in these developing grassland ecosystems. The greater nutrient utilization at higher species diversity resulted in lower leaching loss of soil nitrogen, which should contribute to the sustainability of nutrient cycling and soil fertility in these ecosystems.

Native, undisturbed grassland showed similar relationships. Total plant cover increased significantly with plant species richness (Fig. 2a). The most species-rich plots had total cover of about 80%, compared with about 60% in our experiment, indicating that cover may continue to increase in our experiment. However, soil fertility (that is, the total soil nitrogen level, N) was higher in the native grassland than in the experiment ($\text{N}: 686 \text{ mg kg}^{-1}$ compared with 406 mg kg^{-1}), which may explain this difference in plant cover. Rooting-zone extractable soil NO_3^- and NH_4^+ were both negatively correlated with plant-species richness in native grassland (NO_3^- : $r = -0.47$, $n = 120$, $P < 0.001$, Fig. 2b; NH_4^+ :

$r = -0.28$, $n = 120$, $P < 0.01$). As in the experiment (Fig. 1c), native vegetation showed higher variance in soil NO_3^- at lower species richness. Thus the relationships observed in our two-year field experiment also occurred in natural ecosystems, indicating that the effects of biodiversity observed during ecosystem establishment are maintained in mature ecosystems.

Compensatory competitive interactions^{6,7,14} might have played a role in causing these relationships in our experiment. Five species (*Andropogon gerardi*, *Achillea millefolium*, *Bouteloua gracilis*, *Lespedeza capitata*, and *Rudbeckia hirta*) had significantly ($P < 0.01$) greater abundance in higher-diversity plots than expected on the basis of their proportion in the seed mixture, indicating that, when present, they could compensate for poorly performing species. Multiple regression showed that total plant cover in the diversity experiment was negatively dependent on rooting-zone soil NO_3^- and positively dependent on root biomass (Table 1). But there remained a significant dependence of cover on species richness (Table 1), suggesting that additional factors related to species richness also were involved. Other multiple regressions showed that soil NO_3^- , both in the rooting zone (Table 2) and below, was independent of plant cover and surface root biomass, but remained dependent on species richness. Further

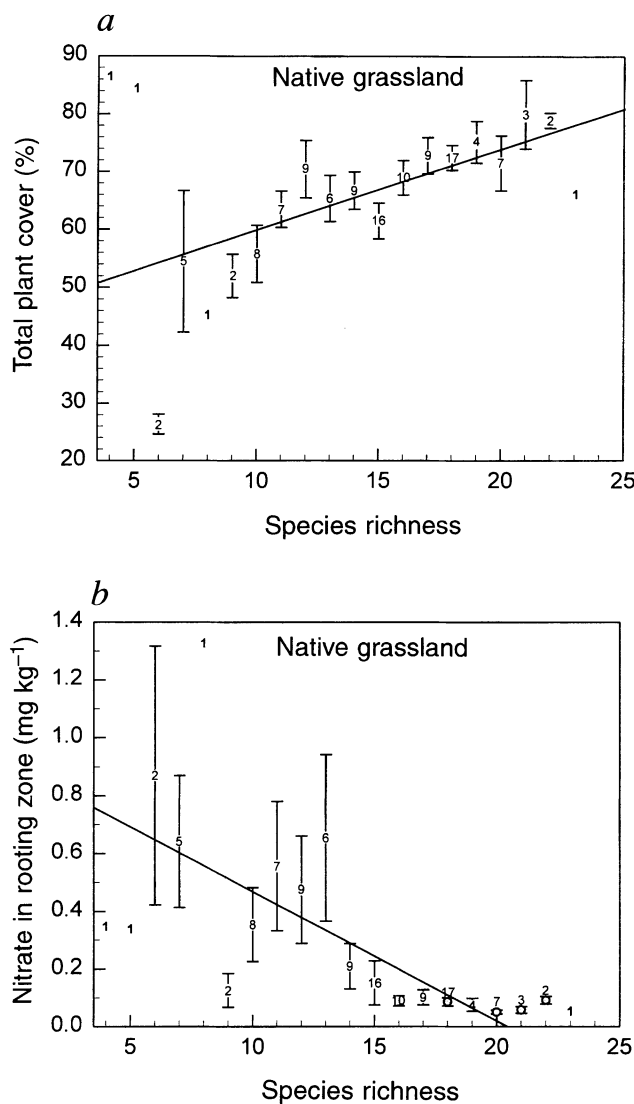


FIG. 2 a, Mean \pm s.e.m. of total plant cover (fitted curve: $y = 46.1 + 1.40x$, $R^2 = 0.16$, $n = 120$, $P < 0.001$) and b, soil nitrate in the rooting zone (fitted curve: $y = 0.92 - 0.045x$, $R^2 = 0.22$, $n = 120$, $P < 0.001$) both plotted against plant-species richness in 120 native grassland plots. Figures indicate the number of plots with a given level of plant species richness. Simple curvilinear fits were no better than lines. METHODS. Native, undisturbed grassland in Field D (ref. 24) was sampled for plant species cover and species richness (number of vascular plant species per plot) in 120 plots, each 1 m \times 1 m, with a block of 4 such plots in each of 30 localities. Four 0–20 cm soil cores per plot were extracted for measuring NO_3^- and NH_4^+ levels.

work is needed to determine how interspecific morphological and physiological differences^{25–27} influence the dependence of ecosystem functioning on biodiversity in this and other ecosystems.

It is known that soil fertility and productivity influence diversity^{28,29}. Our results demonstrate that the converse is also true: in our experiment using initially homogeneous soils, plant diversity had a significant effect on productivity, nutrient use, and nutrient retention. The establishment and functioning of these grassland ecosystems depended on their species richness, with more diverse ecosystems being more productive and having lower nutrient losses than less diverse ecosystems. This extends earlier results^{8,18} to the field, providing direct evidence that the current rapid loss of species on Earth³⁰, and management practices that decrease local biodiversity, threaten ecosystem productivity and the sustainability of nutrient cycling. Observational, laboratory and now field experimental evidence supports the hypotheses that bio-

diversity influences ecosystem productivity^{6,8,17,18}, sustainability^{4,5,17} and stability^{3,6,7,14}. □

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Allometry and simple epidemic models for microparasites

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SIMPLE mathematical models for microparasites offer a useful way to examine the population dynamics of different viral and bacterial pathogens. One constraint in applying these models in free-living host populations is the paucity of data with which to estimate transmission rates. Here we recast a standard epidemiological model by setting the birth and death rates of the host population and its density as simple allometric functions of host body weight. We then use standard threshold theorems for the model in order to estimate the minimum rate of transmission for the parasite to establish itself in a mammalian host population. Transmission rates that produce different comparable values of the parasites' basic reproductive number, R_0 , are themselves allometric functions of host body size. We have extended the model to show that hosts having different body sizes suffer epidemic outbreaks whose frequency scales with body size. The expected epidemic periods for pathogens in different mammalian populations correspond to cycles observed in free-living populations.

The basic microparasite model takes the form¹ $dS/dt = (v - \mu)(1 - S/K)S - \lambda(I)S$, and $dI/dt = \lambda(I)S - (\mu + \alpha)I$, where S and I are the density of susceptible and infected individuals respectively, K the carrying capacity in absence of the pathogen^{2,3},