The Influence of Functional Diversity and Composition on Ecosystem Processes

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Humans are modifying both the identities and numbers of species in ecosystems, but the impacts of such changes on ecosystem processes are controversial. Plant species diversity, functional diversity, and functional composition were experimentally varied in grassland plots. Each factor by itself had significant effects on many ecosystem processes, but functional composition and functional diversity were the principal factors explaining plant productivity, plant percent nitrogen, plant total nitrogen, and light penetration. Thus, habitat modifications and management practices that change functional diversity and functional composition are likely to have large impacts on ecosystem processes.

Although the organisms living in an ecosystem control its functioning (*1–4*), it has not been clear how much of this control is determined by the identities of the species present (*4, 5*), by the number of species present (*2, 4, 6, 7*), by the number of different functional roles that these species represent (*1, 2, 8*), or by which functional roles are represented (*4, 9*). The effects of species or functional diversity are expected to increase with the magnitude of the differences among species or functional groups (*10*). These differences are also expected to influence the magnitude of the effects caused by compositional differences. However, the relative effects attributable to diversity versus composition are unclear.

We performed a field experiment in which plant species diversity (defined as number of plant species added to plots), functional diversity (defined as number of functional groups added to plots), and functional composition (defined as which functional groups were added to plots) were directly controlled (*11*). Our 289 plots, each 169 m^2, were planted and weeded to have either 0, 1, 2, 4, 8, 16, or 32 perennial savanna-grassland species representing 0, 1, 2, 3, 4, or 5 plant functional groups. Grassland-savanna plants were classified into functional groups on the basis of intrinsic physiological and morphological differences, which influence differences in resource requirements, seasonality of growth, and life history. Legumes fix nitrogen, the major limiting nutrient at our site (*7*). Grasses with the three-carbon photosynthetic pathway (C_3) grow best during the cool seasons and have higher tissue N than do grasses with the C_4 pathway, which grow best during the warm season. Woody plants have high allocation to perennial stem and low growth rates, and forbs do not fix N and often have high allocation to seed.

When analyzed in separate univariate regressions, species diversity had significant effects on plant productivity (Fig. 1A) and on three of five other response variables measured in the third year of study (*12, 13, 14*). Functional diversity significantly influenced plant productivity (Fig. 1B) and all other variables (*13, 14*). Species diversity had a highly significant effect ($P < 0.001$) in a one-way multivariate analysis of variance (MANOVA) that included all six response variables, as did functional diversity in a similar MANOVA.

In multiple regressions of each of the six response variables on both species and functional diversity, functional diversity was significant in all six cases, but species diversity was not (Table 1) (*14*). Plant productivity and plant total N significantly increased, and soil NO_3, soil NH_4, plant percent N (% N), and light penetration significantly decreased as functional diversity increased. A two-way MANOVA that included all six response variables showed highly significant effects of functional diversity (Wilk's lambda $F = 7.58$; df = 6, 277; $P < 0.0001$) but no significant effects of species diversity (Wilk's lambda $F = 0.12$; df = 6, 277; $P = 0.99$). Similar results were obtained in alternative analyses (*14*), including a two-way MANOVA that used observed species and functional diversities from 1996 (*15*). Thus, the functional group component of diversity is a greater determinant of ecosystem processes than the species component of diversity.

The independent effects of functional composition can be tested by ANOVAs in which each of the 32 possible functional compositions (*16*) is nested within the appropriate level of functional diversity. There were highly significant effects of both functional diversity (Fig. 1B) and functional composition (Fig. 2) on plant productivity, plant % N, plant total N, and light penetration (Table 2). Soil NH_4 and soil NO_3 depended on functional diversity but not on functional composition. Thus, for four of the six variables, both functional composition and functional diversity had significant impacts. A two-way MANOVA that included all six variables found highly significant effects of both functional diversity and functional composition (*14, 17*).

On average, across the six ANOVAs of Table 1, species and functional diversity together explained 8% of the variance in response variables, whereas functional composition and diversity together explained 37% (Table 2), suggesting that composition is the greater determinant of ecosystem processes.

To determine if particular functional groups were responsible for the effects of

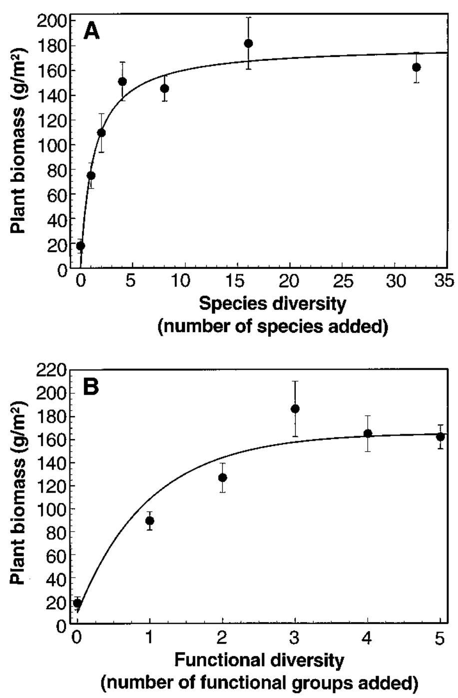

Fig. 1. (**A**) Dependence of 1996 aboveground plant biomass (that is, productivity) (mean and SE) on the number of plant species seeded into the 289 plots. (**B**) Dependence of 1996 aboveground plant biomass on the number of functional groups seeded into each plot. Curves shown are simple asymptotic functions fitted to treatment means. More complex curves did not provide significantly better fits.

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functional diversity, we repeated the multiple regressions of Table 1, but replaced functional diversity with five dummy variables, each describing a functional group as either absent from a plot or represented by at least one species. For each of the six ecosystem variables, there were significant ($P < 0.05$) effects of the presence of particular functional groups and no significant effects of species diversity. Only C_4 grasses and legumes significantly affected productivity (Fig. 2) and light penetration ($P < 0.001$ for each, overall $r^2 = 0.19$ for C_4 grasses and 0.27 for legumes). Plant % N depended on all five functional groups ($P < 0.05$ for all, $r^2 = 0.57$). The other ecosystem variables were significantly dependent only on either legumes (plant total N) or C_4 grasses (soil NH_4, soil NO_3). On average, across plots containing two, four, or eight species, the presence of one or more C_4 grass species led to a 40% increase in productivity, and the presence of one or more legume species led to a 59% increase. The greater biomass from legumes is consistent with their ability to fix N. The greater biomass from C_4 grasses is consistent with their lower tissue N concentrations.

Another multiway MANOVA, in which the five independent variables were the species diversity within each functional group (number of plant species within a functional group planted in a plot) and the dependent variables were the six ecosystem responses, showed significant ($P < 0.01$) effects of species diversity within each functional group except woody plants. Thus, both the presence of some functional groups and the number of species within most functional groups had significant effects on ecosystem processes.

Table 1. Dependence of ecosystem variables on diversity treatments as determined by multiple regression. Values shown are regression parameters. A separate regression was performed for each ecosystem variable. Regressions have df = 2, 283 to 2, 286. NS, $P > 0.05$; *, $0.05 \geq P > 0.01$; **, $0.01 \geq P > 0.001$; and ***, $P < 0.001$ for tests of significant difference of parameter value from 0.

Response variable	Regression parameters			Overall r^2	Overall *F* value
	Intercept	Species diversity	Functional diversity		
Productivity	81.1***	−0.19NS	20.0***	0.09	14.0***
Plant % N	1.24***	−0.0003NS	−0.072***	0.11	17.15***
Plant total N	104.3***	−0.193NS	12.06*	0.02	3.61*
Soil NH_4	1.07***	0.003NS	−0.082**	0.04	5.60**
Soil NO_3	0.37***	0.001NS	−0.041***	0.09	13.4***
Light penetration	0.75***	0.0001NS	−0.040***	0.11	18.3***

The increase in productivity with diversity was partially caused by overyielding of species, especially C_4 grasses, in high-diversity plots. Specifically, a regression for each species of log(percent cover) on log(species richness) revealed significant ($P < 0.05$) overyielding at high species diversity (that is, slopes significantly less negative than –1) for 14 of the 34 species, but significant underyielding at high diversity for only four species. All eight C_4 grasses significantly overyielded (*Andropogon gerardi*, *Bouteloua curtipendula*, *B. gracilis*, *Buchloe dactyloides*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and *Sporobolus cryptandrus*), as did the C_3 grass *Elymus canadensis*, the legumes *Lespedeza capitata* and *Petalostemum villosum*, the forb *Aster azureus*, and the woody plants *Quercus ellipsoidalis* and *Q. macrocarpa*. Thus, many species inhibited themselves in monoculture and low-diversity plots more than they were inhibited by other species in high-diversity plots. This is consistent with several mechanisms of niche differentiation and coexistence (*18*), suggesting that such mechanisms may explain the increase in productivity with diversity (*10*).

Other studies have shown that the number of species (*2, 6, 7, 19*), the number of functional groups (*8*), or ecosystem species composition (*20, 21*) influence various ecosystem processes. Our results show that composition and diversity are significant determinants of ecosystem processes in our grasslands. Given our classification of species into functional groups, functional diversity had greater impact on ecosystem processes than did species diversity. This suggests that the number of functionally different roles represented in an ecosystem may be a stronger determinant of ecosystem processes than the total number of species, per se. However, species diversity and functional diversity are correlated; each was significant by itself, as was species diversity within functional groups; and either species or functional diversity may provide a useful gauge of ecosystem functioning.

Our results show a large impact of composition on ecosystem processes. This means that factors that change ecosystem composition, such as invasion by novel organisms, nitrogen deposition, disturbance frequency, fragmentation, predator decimation, species extinctions, and alternative management practices (*20, 21*), are likely to strongly affect ecosystem processes. Our results demonstrate that all species are not equal. The loss or addition of species with certain functional traits may have a great impact, and others have little impact, on a particular ecosystem process, but different processes are likely to be affected by different species and functional groups.

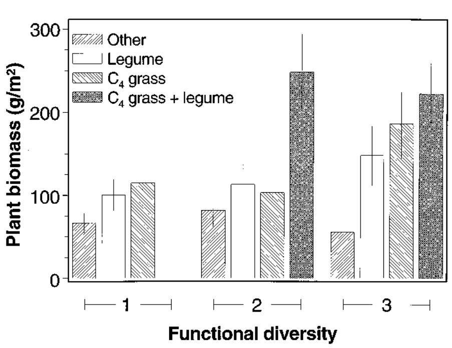

Fig. 2. Effects of functional composition on 1996 aboveground plant biomass (productivity) in plots containing at least one legume species (Legume), at least one C_4 grass species (C_4 grass), at least one of each (C_4 grass plus legume), or only species from other functional groups (Other). Mean and SE are shown, using all plots containing 1, 2, or 3 functional groups.

Table 2. Dependence of response variables on functional diversity treatments and functional composition based on ANOVAs. Functional composition was nested within each level of functional diversity. A separate analysis was performed for each ecosystem response variable.

Response variable	*F* values			Overall r^2
	Functional diversity (df = 5, 254)	Functional composition (df = 26, 254)	Overall model (df = 31, 254)	
Productivity	9.36***	2.87***	4.02**	0.33
Plant % N	22.2***	17.3***	17.4***	0.68
Plant total N	4.23**	3.92***	4.18***	0.34
Soil NH_4	2.40*	1.23NS	1.40NS	0.14
Soil NO_3	22.3***	1.17NS	4.57***	0.36
Light penetration	12.1***	3.21***	4.57***	0.36

REFERENCES AND NOTES

1. J. H. Lawton and V. K. Brown, in *Biodiversity and Ecosystem Function*, E.-D. Schulze and H. A. Mooney, Eds. (Springer-Verlag, Berlin, 1993), pp. 255–270.
2. P. M. Vitousek and D. U. Hooper, *ibid.*, pp. 3–14.
3. B. H. Walker, *Conserv. Biol.* **6**, 18 (1991).
4. F. S. Chapin III, J. Lubchenco, H. L. Reynolds, in *Global Biodiversity Assessment*, V. H. Heywood, Ed. (Cambridge Univ. Press, Cambridge, 1995), pp. 289–301.
5. T. J. Givnish, *Nature* **371**, 113 (1994).
6. S. J. McNaughton, in (*1*) , pp. 361–383; S. Naeem, L. J. Thompson, S. P. Lawler, J. H. Lawton, R. M. Woodfin, *Nature* **375**, 561 (1995).
7. D. Tilman, D. Wedin, J. Knops, *Nature* **379**, 718 (1996).
8. D. U. Hooper, *Ecol. Monogr*., in press.
9. P. M. Vitousek, *Oikos* **57**, 7 (1990); F. S. Chapin III, H. L. Reynolds, C. D'Antonio, V. Eckhart, in *Global Change in Terrestrial Ecosystems*, B. Walker, Ed., in press.
10. D. Tilman, C. L. Lehman, K. T. Thomson, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 1857 (1997).
11. To prepare for planting, a field at Cedar Creek Natural History Area, in Minnesota, was treated with herbicide and burned in August 1993, and had the upper 6 to 8 cm of soil removed to reduce the seed bank, was plowed and repeatedly harrowed, and divided into 342 plots, each 13 m by 13 m (only the inner 11 m by 11 m was sampled). Plots were seeded in May 1994 and again in May 1995. To test for effects of species diversity, we determined composition of each of 167 plots by random draws of 1, 2, 4, 8, or 16 species from a core pool of 18 species (four species each of C_3 grasses, C_4 grasses, legumes, and forbs; two woody species), with 29 to 35 replicates at each level of species diversity. To better distinguish between effects of species and functional diversity, we assigned combinations of 1, 2, or 3 functional groups containing 2, 4, or 8 species to 76 more plots, with compositions chosen by random draws of functional groups followed by species. When needed, we used a pool of 16 additional species (four in each of the nonwoody functional groups). Another 46 plots were created with 32 of these 34 species. Four plots were kept bare. These 289 plots uncouple species diversity, functional diversity, and functional composition, but have a weak correlation between these and species composition. There is no such correlation in the 167-plot random species subexperiment. The 289 plots have the following numbers of plots assigned to species and functional diversity classes:

Functional groups per plot	Species per plot: 0	1	2	4	8	16	32
0	4	–	–	–	–	–	–
1	–	34	11	12	14	–	–
2	–	–	33	13	14	–	–
3	–	–	–	20	14	–	–
4	–	–	–	10	18	1	16
5	–	–	–	–	11	34	30

12. Unless noted otherwise, all analyses use treatment species diversity, treatment functional diversity, and treatment functional composition. In each plot we estimated the percent cover of each species in four subplots (0.5 m by 1 m each). We measured peak aboveground living plant standing crop (an estimate of plant productivity) by clipping, drying, and weighing four 0.1 m by 3.0 m strips per plot. We measured % N in this aboveground biomass (plant % N), its total N (plant total N), soil NH_4 and soil NO_3 extractable in 0.01 KCl [four soil cores (2.5 cm by 20 cm depth) per plot], and the proportion of incident light (PAR) that penetrated to the soil surface. In 1996, plots contained mature, flowering plants, but the relative abundances of species may still be changing.
13. Linear regressions for effects of species diversity: productivity, r = 0.20, $P < 0.01$, $n = 289$; plant % N, r = −0.24, $P < 0.001$, $n = 286$; plant total N, r = 0.10, $P = 0.08$, $n = 286$; soil NH_4, r = −0.11, $P = 0.06$, $n = 289$; soil NO_3, r = −0.18, $P < 0.01$, $n = 289$, light penetration, r = −0.24, $P < 0.001$, $n = 288$. For effects of functional diversity: productivity, r = 0.30, $P < 0.001$, $n = 289$; plant % N, r = −0.33, $P < 0.001$, $n = 286$; plant total N, r = 0.16, $P < 0.01$, $n = 286$; soil NH_4, r = −0.19, $P = 0.01$, $n = 289$; soil NO_3, r = −0.29, $P < 0.001$, $n = 289$, light penetration, r = −0.34, $P < 0.001$, $n = 288$.
14. Regressions (as in *13*), multiple regressions (as in Table 1), ANOVAs (as in Table 2), and MANOVAs that used only the 167 plots of the random species subexperiment (*11*) had similar results and generally higher r^2 values, indicating that results are not caused by the weak correlation between diversity and species composition in the full 289-plot experiment.
15. The 1996 average percent cover of each species or functional group in each plot was used to calculate its effective species or functional diversity as $e^{H'}$, where H' is the Shannon-Wiener diversity index for species or functional groups. Trends found using treatment diversity variables also occurred when using 1996 effective diversity.
16. There were 32 different combinations of five functional groups drawn 0, 1, 2, 3, 4 or 5 at a time. All 32 combinations were represented in the experiment. For the nested ANOVAs, each plot with a given level of functional diversity was further classified by which of the 32 combinations it contained. Similar results occurred when plots with bare soil or with 32 species were excluded.
17. In the MANOVA, $P < 0.0001$ for both functional diversity and functional composition using Wilks' Lamba, Pillai's Trace, Hotelling-Lawley Trace, or Roy's Greatest Root.
18. J. L. Harper, *Population Biology of Plants* (Academic Press, London, 1977); D. Tilman, *Resource Competition and Community Structure, Monographs in Population Biology* (Princeton Univ. Press, Princeton, NJ, 1982).
19. J. J. Ewel, M. J. Mazzarino, C. W. Berish, *Ecol. Appl.* **1**, 289 (1991).
20. R. T. Paine, *Am. Nat.* **100**, 65 (1966); J. H. Brown, D. W. Davidson, J. C. Munger, R. S. Inouye, in *Community Ecology*, J. Diamond and T. Case, Eds. (Harper and Row, New York, 1986), pp. 41–61; S. R. Carpenter *et al.*, *Ecology* **68**, 1863 (1987); J. Pastor, J. D. Aber, C. A. McClaugherty, J. M. Melillo, *ibid.* **65**, 256 (1984); G. C. Daily, P. R. Ehrlich, N. M. Haddad, *Proc. Natl. Acad. Sci. U.S.A.* **90**, 592 (1993).
21. P. M. Vitousek, L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, P. A. Matson, *Science* **238**, 802 (1987).

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The Effects of Plant Composition and Diversity on Ecosystem Processes

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The relative effects of plant richness (the number of plant functional groups) and composition (the identity of the plant functional groups) on primary productivity and soil nitrogen pools were tested experimentally. Differences in plant composition explained more of the variation in production and nitrogen dynamics than did the number of functional groups present. Thus, it is possible to identify and differentiate among potential mechanisms underlying patterns of ecosystem response to variation in plant diversity, with implications for resource management.

Recent experiments have shown increasing net primary productivity (NPP) and nutrient retention in ecosystems as the number of plant species increases (*1, 2*). Ecosystem response to plant richness could occur via complementary resource use if plant species differ in the ways they harvest nutrients, light, and water (*3, 4*). Complementarity could happen in space, for example, because of differences in rooting depths; in time, for example, because of differences in phenology of plant resource demand; or in nutrient preference, for example, nitrate versus ammonium versus dissolved organic N. Greater plant diversity would then allow access to a greater proportion of available resources, leading to increased total resource uptake by plants, lower nutrient losses from the ecosystem, and increased NPP, if the resources in question are limiting growth. However, differences in plant composition (the identity of the species present) may have large effects on ecosystem processes if the traits of one or a few species dominate (*5*). For example, if one species or group of species reduces soil nutrients to a lower level than do other species, then this species (or group) may dominate pools of available soil nutrients in mixtures (*6*). Such effects of composition could also lead to lower soil nutrient pools and greater nutrient retention as diversity increases because of an increasing probability of including the dominant species at higher levels of richness. In this case, however, increased ecosystem nutrient retention results from the presence of only one species rather than from niche differentiation and complementary resource use among many.

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