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Species loss and ecosystem functioning: effects of species identity and community composition

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Losing a single species from an ecosystem may have large effects on community and ecosystem properties, but this may depend on characteristics of the species and the ecosystem. We examined the effect of losing a single species on productivity and nitrogen retention in experimental grassland communities, concentrating on how these effects varied with the functional identity of the species lost and the diversity and composition of the community from which it was lost. In one experiment, we constructed random plant assemblages that varied in species richness to measure the effect of diversity alone on productivity and nitrogen retention. In another experiment, we constructed plant assemblages to assess the effects of deleting an individual plant species from assemblages differing in their functional and species richness and composition. On average, as species richness declined, productivity decreased but nitrogen retention was unaffected. However, the magnitude and direction of change in ecosystem functioning with declining diversity depended on the identity of the species deleted and the composition of the community from which it was deleted. The functional identity of a species predicted the type of impact its loss had on productivity, but not on nitrogen retention.

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Several recent studies have shown a positive correlation between plant species richness and ecosystem productivity, stability, and sustainability (Naeem et al. 1994, 1995, 1996, Tilman and Downing 1994, Tilman 1996, Tilman et al. 1996). Because all species presumably have some impact on the ecosystem in which they live, it is not clear how much of this relationship is caused by species number per se versus the effects of individual species. The abundance of a single species may affect community and ecosystem properties such as the abundance of other species (e.g., Paine 1966, 1974, Power et al. 1985), nutrient cycling (Vitousek and Walker 1989), and susceptibility to disturbance (D'Antonio and Vitousek 1992). The magnitude of these impacts, however, seems to vary enormously among species, from those with keystone effects (sensu Paine 1969, Power et al. 1996) to those whose loss either has a negligible effect or is compensated for by other species in its functional group (Walker 1992, 1995, Lawton and Brown 1993, Frost et al. 1995).

Here we systematically investigate all of the species in an experimental community to determine individual species' impacts on ecosystem processes and how these impacts are related to species and community characteristics. Using a series of greenhouse grassland plant communities, we determined the effect of losing a single species on two ecosystem processes and investigated how these effects varied with the functional identity of the species and the diversity and composition of the community from which it was lost.

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Table 1. Treatments and species in Experiment I.

Treatment	Description	Species†				Number of replicates per combination
A	Monocultures of 16 species	*Pp, Ec, Es, Kp, Sts, Bd, Sn, Scs, Rh, Am, Anc, Lc, Amc, Vv, Dp, Lp*				4
B	All combinations of 4 species taken 2 at a time	*Pp, Bd, Rh, Lc*				4
		Species in full treatment				
		C3 grasses	C4 grasses	Forbs	Legumes	
C	4 species and all combinations with one species deleted	*Pp*	*Bd*	*Rh*	*Lc*	5
D	8 species and all combinations with one species deleted	*Pp, Ec, Es*	*Bd*	*Rh*	*Lc, Amc, Vv*	5
E	8 species and all combinations with one species deleted	*Pp*	*Bd, Sn, Scs*	*Rh, Am, Anc*	*Lc*	5
F	12 species and all combinations with one species deleted	*Pp, Ec, Es, Kp, Sts*	*Bd, Sn, Scs*	*Rh, Am, Anc*	*Lc*	5
G	12 species and all combinations with one species deleted	*Pp*	*Bd, Sn, Scs*	*Rh, Am, Anc*	*Lc, Amc, Vv, Dp, Lp*	5

† Abbreviations for species are as follows: *Am* = *Achillea millefolium*, *Amc* = *Amorpha canescens*, *Anc* = *Anemone cylindrica*, *Bd* = *Buchloe dactyloides*, *Dp* = *Dalea purpurea*, *Ec* = *Elymus canadensis*, *Es* = *Elytrigia smithii*, *Kp* = *Koeleria pyrimidata*, *Lc* = *Lespedeza capitata*, *Lp* = *Lupinus perennis*, *Pp* = *Poa pratensis*, *Rh* = *Rudbeckia hirta*, *Scs* = *Schizachyrium scoparium*, *Sn* = *Sorghastrum nutans*, *Sts* = *Stipa spartea*, *Vv* = *Vicia villosa*. Nomenclature follows Gleason and Cronquist (1991).

Materials and methods

Experimental design

We conducted two experiments, both using assemblages of plants from a pool of 16 North American grassland species (Table 1) consisting of four species in each of four functional groups (C3 grasses, C4 grasses, legumes, and other forbs). Experiment I assessed the effects of losing an individual plant species from each of several alternative assemblages that were designed to differ in their functional and plant species richness and composition. This experiment had 7 treatments. Treatment A consisted of monocultures of the 16 species in these experiments and had 4 replicates for each species. Treatment B consisted of all pairwise combinations of 4 particular species, with 4 replicates of each unique combination. The 4 species (*Poa pratensis*, *Buchloe dactyloides*, *Lespedeza capitata*, and *Rudbeckia hirta*) were chosen, one per functional group, by random draw. These same 4 species also were used for treatments C through G, which consisted of 4-, 8- or 12-species polycultures (the "full" assemblages) and all possible deletions of one species from each of these full assemblages (Table 1). There were 2 treatments each at the 8- and 12-species levels, and these treatments differed in their species composition. Treatment D's 8 species consisted of a single C4 grass and a single forb plus 3 species each of legumes and C3 grasses, while treatment E had a single legume, a single C3 grass, and 3 species each of C4 grasses and forbs. The two 12-species treatments differed with one having a single legume species but 3 to 5 species in the other functional groups, and the other having a single C3 grass species and 3 to 5 species in the other functional groups (Table 1). These contrasting combinations allowed determination of the effects of deleting a species from a species-rich versus a species-poor functional group. For treatments C through G, there were 5 replicates of each unique combination of species.

Experiment II assessed the impact of species richness, independent of community composition, on 2 ecosystem processes. Only the 10 most productive species from Experiment I (based on their biomass in monoculture) were used. In order of decreasing abundance in Experiment I, these were *Vicia villosa*, *Poa pratensis*, *Rudbeckia hirta*, *Lespedeza capitata*, *Elymus canadensis*, *Achillea millefolium*, *Schizachyrium scoparium*, *Koeleria pyrimidata*, *Sorghastrum nutans*, and *Lupinus perennis*. Each of the levels of diversity, from 1 to 9 species, had 10 replicates, but the identity of the species in each replicate was determined by a separate random draw of the appropriate number of species from the pool of 10 species. In addition, we planted 20 replicates of all 10 species together and maintained 10 pots of bare soil.

Methods

In both experiments, we planted the assemblages in 25.5 × 25.5 × 5.5 cm deep pots filled with a 3:1 mixture of sterilized sandy soil from Cedar Creek Natural History Area (Tilman 1987) to a commercial germination soil mixture. Soon after germination, we inoculated each pot with *Rhizobium*. Pots were watered daily, temperature was maintained between 24°C and 29°C, and natural daylight was supplemented with 450 μmol m^{-2} s^{-1} of PAR, via halogen lamps, from 0600 to 2200 to simulate a summer growing season. The pots were arranged randomly and positions were re-randomized twice a week (Experiment I) or every 10 days (Experiment II) to reduce variation in growing conditions.

In Experiment I, which was planted on 12 January 1995, each pot received 5 g of pure, live seed based on germination rates estimated from a field experiment. The total seed mass for a pot was divided equally among all the species in that pot. In Experiment II, which started on 12 December 1995, we used the germination rates of Experiment I to calculate the mass of seed needed to produce 150 plants in monoculture for each species. This mass was then divided by the number of species in a given pot so that all species should be equally abundant and each pot should have, on average, a total of 150 plants regardless of how many species it contained.

We measured the impact of species deletion on two ecosystem processes, nitrogen (N) retention and productivity. Approximately 3.5 months after the beginning of an experiment, we measured the dissolved mineral N that each assemblage lost through leaching as an estimate of N retention. The night before sampling, all pots were watered to saturation to ensure relatively consistent soil moisture across treatments. In Experiment I, we poured 500 mL of reverse osmosis and deionized water over each pot the next morning and collected the leachate in plastic tubs. Two 20-mL samples of the leachate were frozen for later analysis. In Experiment II, we used 600 mL of reverse osmosis and deionized water, recorded the volume of leachate that passed through the pot, and collected two 20-mL samples for analysis. The concentration of NO_3^- and NH_4^+ in the leachate was determined with an Alpchem RFA-1 Autoanalyzer. In Experiment I, the sum of these concentrations was our response variable. In Experiment II, the sum was weighted by the volume of the leachate to account for differences in water retention among pots.

We measured aboveground biomass as an estimate of productivity in both experiments. Four months after beginning an experiment, all biomass was cut off at ground level, dried at 40°C for one week, and weighed. In Experiment I, 2 replicates of each of the 2-, 4-, 8-, and 12-species assemblages were sorted to species before drying.

Data analysis

The relationships between species richness and ecosystem functioning were tested by simple nonlinear regression, including linear, exponential, and power functions; results of the best-fitting curve are given. This was done for each ecosystem function in each experiment for various combinations of treatments. Bare soil pots were not included in the analyses for biomass, but they were included for N leaching.

For Experiment I, we measured the impact on ecosystem functioning of losing an individual species in a treatment with the following index:

$$I_x = (X_{all} - X_{-sp})/X_{all},$$

where X is either biomass or concentration of N in the leachate. X_{all} is X averaged over the replicates of the full assemblage, and X_{-sp} is X for an individual pot in the same treatment but missing one particular species from the full assemblage. This ratio is the proportional change in the ecosystem function caused by losing that species. It is modified from the community importance index in Power et al. (1996). *t*-tests were performed on I_x to test for significant impacts of functional groups and individual species. One-way analysis of variance tested for significant differences in individual species' I_x among treatments with the same diversity, but different species composition. Significance tests were adjusted for multiple comparisons by using the sequential Bonferroni correction (Rice 1989). TableCurve 2D (AISN Software 1994) was used for regression analyses and SAS version 6.09 (SAS Institute Inc. 1989) was used for all other analyses.

Results

In both experiments, a few pots suffered severe water stress at some point; these were not included in any of the analyses.

Experiment II

Aboveground plant biomass increased significantly with species richness in the unbiased assemblages of Experiment II ($r^2 = 0.10$, $n = 101$, $P = 0.002$; Fig. 1a). N retention was also significantly, positively (amount of N leached decreased) related to species richness ($r^2 = 0.67$, $n = 106$, $P < 0.0001$; Fig. 1b), but this was driven by the bare soil pots. There was no significant relationship between N leaching and species richness when the bare soil pots were eliminated from the analysis ($r^2 = 0.02$, $n = 96$, $P = 0.20$).

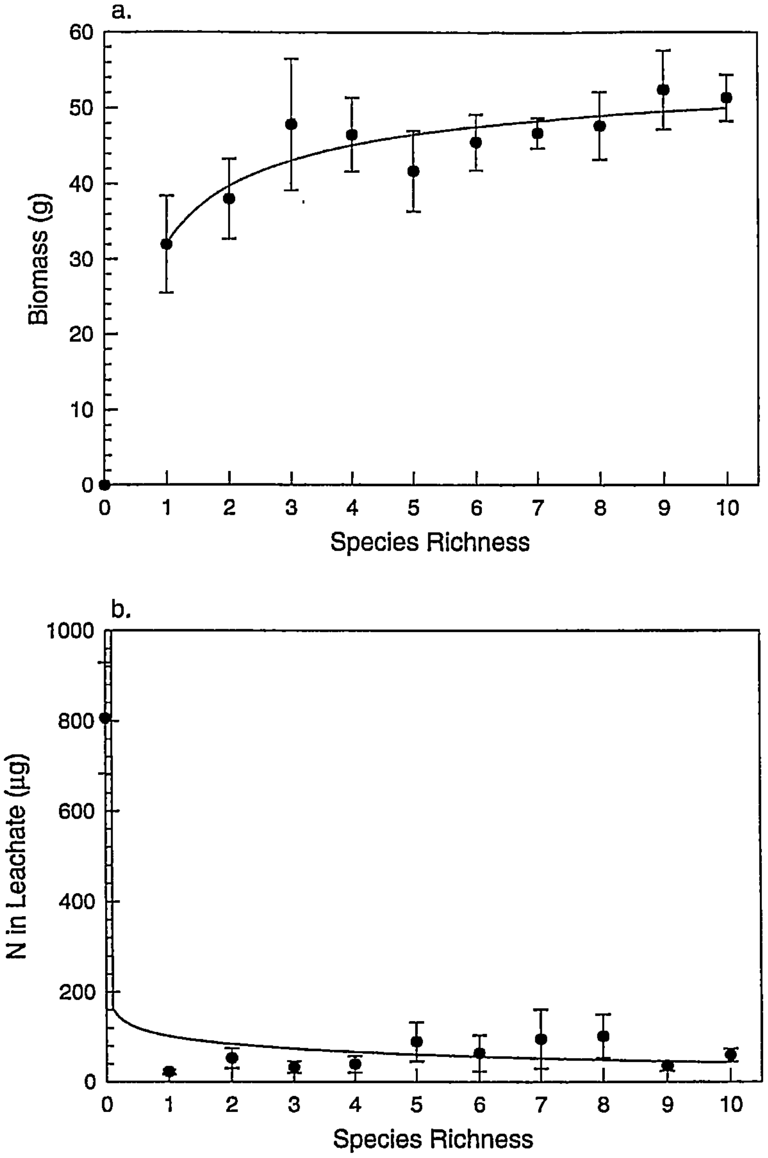


Fig. 1. Relationship between species richness and two ecosystem properties in random assemblages of ten plant species (Experiment II). Means and standard errors are shown. Curves are those that best fit the data, based on simple nonlinear regression (see text).
(a) Biomass: fitted curve is $y = 58.2 - 26.2x^{-0.5}$. (b) N in leachate: fitted curve is $y = 14546 - 14443x^{0.002}$.

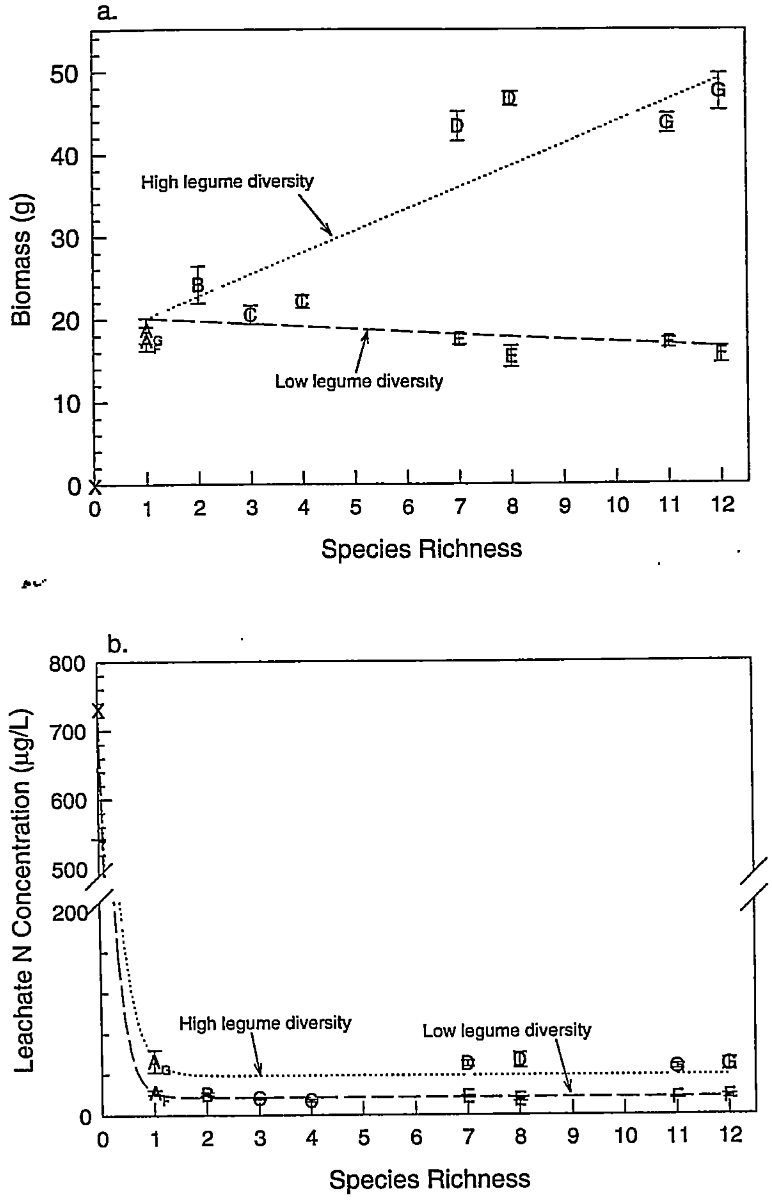
Experiment I

In Experiment I, *Stipa spartea* failed to germinate in any of the pots in which it was planted. Thus, the monoculture of *S. spartea* was treated as bare soil; species richness and productivity were both zero.

Ecosystem function depended on species composition in Experiment I. The two distinct groups of points for the 8- and 12-species treatments in Experiment I reflect the differences in composition between treatments D and G (high legume diversity) versus E and F (single legume species). In a linear regression of biomass on species richness where only treatments D and G were used for high diversity levels, biomass increased significantly with species richness ($r^2 = 0.52$, $n = 209$, $P < 0.0001$; Fig. 2a). On the other hand, when the single-legume treatments (E and F) were used for the species-rich treatmets, biomass decreased slightly with increased species richness ($r^2 = 0.03$, $n = 203$, $P = 0.009$; Fig. 2a). Thus, the effect of biased changes in the composition of a community on biomass can be as great or greater than the effect of changes in species number.

The differences in composition did not have as strong an effect on nutrient retention. The relationship between species richness and nitrogen concentration was similar whether the treatments with many legumes or the treatments with one legume were used for the high diversity treatments (Fig. 2b). However, treatments D

Fig. 2. Effect of community composition on relationships between species richness and two ecosystem properties (Experiment I). Means and standard errors for each treatment–species richness combination are shown. Letters indicate treatment code (Table 1); X indicates bare soil pots. Dotted lines (· · ·) are regressions fit to raw data from treatments A, B, C, D, and G (high legume diversity). Values for monocultures in these regressions include only the species in treatments D and G, indicated by the symbol A_G. Dashed lines (– –) are curves fit to raw data from treatments A, B, C, E, and F (low legume diversity). Values for the monocultures in these regressions include only the species in treatments E and F, indicated by the symbol A_F. (a) Biomass: curves shown are linear regressions. High legume diversity (· · ·): $y = 17.5 + 2.64x$. Low legume diversity (– –): $y = 20.4 - 0.32x$. (b) N concentration in leachate. Curves shown are best fit simple, non-linear regressions. High legume diversity (· · ·): $y = 38.4 + 695e^{-3.7x}$. Low legume diversity (– –): $y = 17.1 + 716e^{-5.0x}$.



and G, with their high legume biomass, had significantly higher mean N concentrations than did treatments E and F (contrast of means $F = 36.8$; df = 1, 312; $P < 0.0001$).

The mean value of I_{Biomass}, the impact of a species' deletion on total biomass in Experiment I, for each functional group shows that legumes were the only functional type that, on average, increased the biomass of an assemblage ($I_{\mathrm{Biomass}} > 0$; Table 2). Forbs were the only functional group that had significant impacts on N leaching. On average, the deletion of a forb species increased the amount of nitrogen leached from an assemblage (Table 2).

There was no significant difference between the impact of deleting the sole member of a functional group from an assemblage versus the impact of deleting one of many members of the same functional group. The design of Experiment I allowed us to test for this effect with four species, *L. capitata*, *P. pratensis*, *B. dactyloides*, and *R. hirta* (see Table 1). There were no significant differences in mean I_x for *L. capitata* within each species richness level for either biomass (8 species: $t = 1.58$, df = 8, $P = 0.15$; 12 species: $t = 1.89$, df = 8, $P = 0.10$; Fig 3a) or N leaching (8 species: $t = 1.25$, df = 8, $P = 0.25$; 12 species: $t = 1.09$, df = 8, $P = 0.31$; Fig 3b), although there was a tendency for I_x to be

Table 2. Impact, I, (mean ± 1 SE) of removing a species on biomass and N leaching, averaged by functional group in Experiment I. t-tested for difference of mean impact from zero. Significance (experiment-wide $\alpha \leq 0.05$) indicated by *.

Function group	Biomass		N leaching		df
	I	t	I	t	
C3 grasses	−0.103 ± 0.031	−3.39*	−0.228 ± 0.031	−2.22	72
C4 grasses	−0.099 ± 0.029	−3.37*	−0.086 ± 0.029	−1.78	76
Forbs	−0.185 ± 0.033	−5.65*	−0.284 ± 0.033	−3.43*	77
Legumes	0.283 ± 0.028	10.03*	0.035 ± 0.028	0.70	76

greater when *L. capitata* was the sole legume. This trend did not continue for *P. pratensis*, *B. dactyloides* and *R. hirta*, and these species also showed no significant differences in mean I_x when they were alone in their functional group versus when there were other species in their functional group. Thus, given our level of replication, we could not detect redundancy provided by higher diversity within a functional group.

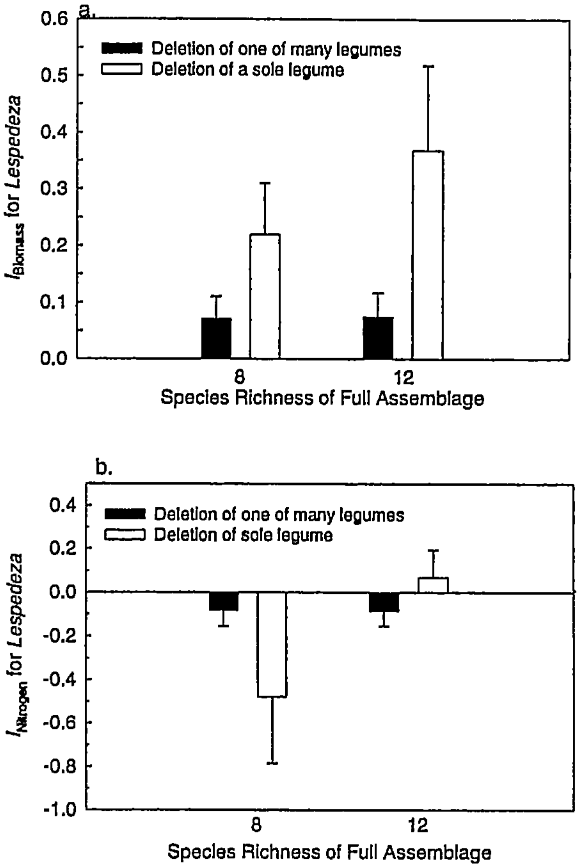


Fig. 3. Impact of removing *Lespedeza* from assemblages containing one legume species (treatments E and F) versus assemblages containing more legume species (treatment D, 3 legumes; treatment G, 5 legumes). Means and one standard error are shown. There are no significant differences between means within species richness level for either (a) Biomass (8 species: $t = 1.58$, df = 8, $P = 0.15$; 12 species: $t = 1.89$, df = 8, $P = 0.10$) or (b) Nitrogen leaching (8 species: $t = 1.25$, df = 8, $P = 0.25$; 12 species: $t = 1.09$, df = 8, $P = 0.31$).

The signs of species' impacts on biomass were consistent within functional groups. Legumes were the only species that had positive impacts on biomass, although not all legume species' impacts were statistically significant (Table 3). Species in all other functional groups had negative impacts. Alternatively, the sign of species' impacts on N retention was consistent for only C4 grasses, which had $I_{Nitrogen} < 0$. All other functional groups included species with both $I_{Nitrogen} > 0$ and $I_{Nitrogen} < 0$. Although similar analyses for species' impacts in Experiment II were complicated by differences in species composition among replicates, they supported these trends within and among functional groups. Thus, the overall impacts of individual species were consistent within functional groups for biomass but not nitrogen.

The magnitude of individual species' impacts, averaged over all treatments, varied considerably among and within functional groups. Of the 16 species in this experiment, 6 had significant impacts ($I_{Biomass} \neq 0$; experiment-wide $\alpha \leq 0.05$) on productivity: *A. millefolium*, *B. dactyloides*, *E. canadensis*, *L. capitata*, *R. hirta*, and *V. villosa* (Table 3). *V. villosa* was the only species that had a significant impact on N leaching, making it the only species that affected both ecosystem functions.

Individual species' impacts on ecosystem function were affected by the composition of an assemblage, but only at the lowest diversity level. The design of Experiment I allowed us to compare a species' I_x among assemblages with the same diversity, but different composition, for some of the species in each treatment. We could make such comparisons for 8 species in the 12-species assemblages and for 4 species in the 8-species assemblages (Table 4). Because treatments B and C included all possible combinations of 4 species taken 2 and 3 at a time, respectively, we were also able to make comparisons of these 4 species' impacts in different assemblages of 2 or 3 species (Table 4). The only significant case of community composition affecting a species' impact at high levels of diversity was for the effect of *A. millefolium* on biomass (Table 4). In the 12-species assemblage with a single legume (treatment F), deleting *A. millefolium* significantly increased assemblage biomass ($I_{Biomass} = -0.237$, $t = -7.19$, df = 4, $P < 0.01$), whereas in the 12-species assemblage with 5 legumes (treatment G), the deletion of *A. millefolium* had no effect on total biomass ($I_{Biomass} = 0.0032$, $t =$

Table 3. Impact, I, (mean ± 1 SE) of removing a species on biomass and N leaching, averaged over all treatments in Experiment I. t-tested for difference of mean impact from zero. Significance (experiment-wide $\alpha \leq 0.05$) indicated by *.

Species	Biomass		N leaching		df
	I	t	I	t	
C3 grasses					
Elymus canadensis	−0.108 ± 0.028	−3.83*	0.095 ± 0.065	1.45	9
Elytrigia smithii	−0.054 ± 0.056	−0.97	0.157 ± 0.063	2.50	9
Koeleria pyrimidata	−0.024 ± 0.051	−0.48	0.247 ± 0.051	4.82	4
Poa pratensis	−0.120 ± 0.047	−2.53	−0.465 ± 0.157	−2.97	47
Stipa spartea	−0.112 ± 0.149	−2.79	0.149 ± 0.107	1.39	4
C4 grasses					
Buchloe dactyloides	−0.118 ± 0.037	−3.17*	−0.114 ± 0.73	−1.56	47
Schizachyrium scoparium	−0.094 ± 0.057	−1.66	−0.043 ± 0.069	−0.62	14
Sorghastrum nutans	−0.039 ± 0.080	−0.48	−0.040 ± 0.067	−0.59	13
Forbs					
Achillea millefolium	−0.158 ± 0.043	−3.65*	0.011 ± 0.089	0.12	14
Anemone cylindrica	−0.083 ± 0.054	−1.55	−0.331 ± 0.130	−2.56	14
Rudbeckia hirta	−0.226 ± 0.048	−4.70*	−0.361 ± 0.123	−2.93	47
Legumes					
Amorpha canescens	0.075 ± 0.063	1.18	0.058 ± 0.094	0.62	8
Dalea purpurea	0.033 ± 0.031	1.07	0.204 ± 0.114	1.79	4
Lespedeza capitata	0.308 ± 0.032	9.60*	−0.091 ± 0.063	1.45	48
Lupinus perennis	0.068 ± 0.034	2.01	−0.062 ± 0.156	−0.40	3
Vicia villosa	0.560 ± 0.052	10.83*	0.588 ± 0.062	9.44*	9

0.09, df = 4, $P > 0.05$). *R. hirta*'s impact on biomass was the only significant case in assemblages with three species (Table 4). Deleting *R. hirta* from the 3-species assemblages with *P. pratensis* had a smaller effect on total biomass than deleting it from the 3-species assemblage without *P. pratensis* (Tukey comparison of means, experiment-wide $\alpha \leq 0.05$). In assemblages of only 2 species, however, there was a strong effect of species combination on the change in biomass and N leaching when a species was deleted. I_{Biomass} varied significantly among species combinations for 3 species (*L. capitata*, *P. pratensis*, and *R. hirta*), and I_{Nitrogen} varied significantly among combinations for all 4 species (Table 4).

Discussion

Our results emphasize three factors in the relationship between species loss and ecosystem processes. First, plant biomass decreases on average as plant species richness falls. Second, changes in plant community composition independent of diversity can have similar, significant effects on biomass. Third, decreasing the diversity of an assemblage by just one species can have a positive, negative, or negligible effect on either plant biomass or nitrogen retention, depending on the identity of the species lost and, in some cases, the composition of the community from which it was lost. The functional group to which a species belongs seems to be a good predictor for the type of impact a species has on biomass, but not on N retention.

Although factors intrinsic to greenhouse experiments (a single trophic level, small habitat size, and relatively constant environmental conditions) may limit inference from our work, other studies suggest that our results are applicable to other systems. For example, total plant cover, an estimate of biomass, increased with species richness for random assemblages in a field experiment that used many of the same species that we used in this experiment (Tilman et al. 1996). Also, although we used completely different species than Naeem et al. (1996) did in their experiment with random plant assemblages, our relationship between plant diversity and biomass was similar to theirs. Thus, random assemblages of different plant species produce the same increase in biomass with species richness that we found, as do field conditions.

The non-random assemblages in our first experiment agree with Naeem et al.'s (1995) "idiosyncratic hypothesis" and illustrate that the effects of species composition on ecosystem function can be as great, or greater, than the effects of species richness. In our study, one species, *Vicia villosa*, appears to be the major reason for the effect of composition on ecosystem functioning. This legume performed extremely well in the conditions of our experiment. In the multi-species assemblages in which it grew, it contributed 82% of the total biomass on average. Treatments D and G, which included *V. villosa*, had significantly higher total biomass and N leaching than did treatments E and F, which did not have this species (Fig. 2). Also, *V. villosa*'s values of I_{Biomass} and I_{Nitrogen} were greater than those for any other species (Table 3). Although *V. villosa* does not meet the definition of a "keystone species" in either the traditional sense (Paine 1969) or according to Power et al. (1996) because its impact on ecosystem function is not disproportionate to its biomass, our results show

Table 4. Comparison of impact, I_X, of removing a species among plant assemblages with the same diversity, but different composition. F statistics are for ANOVA's on assemblage means for each species indicated. Significant difference among treatments or assemblages (experiment-wide $\alpha \leq 0.05$) is indicated by an asterisk (*). See Table 1 for species composition of Treatments D, E, F, and G and for species abbreviations.

Species richness of full assemblage	Treatments or assemblages compared	Species deleted	df	*F*	
				Biomass	N leaching
12	Treatment F vs Treatment G	*Achillea millefolium*	1,8	2.22*	1.16
		Anemone cylindrica	1,8	1.21	0.30
		Buchloe dactyloides	1,8	1.52	1.11
		Lespedeza capitata	1,8	1.37	1.04
		Poa pratensis	1,7	1.17	0.89
		Rudbeckia hirta	1,8	1.24	1.28
		Schizachyrium scoparium	1,8	1.62	0.81
		Sorghastrum nutans	1,7	0.75	0.84
8	Treatment D vs Treatment E	*Buchloe dactyloides*	1,7	1.77	0.62
		Lespedeza capitata	1,8	1.26	1.12
		Poa pratensis	1,8	1.39	0.55
		Rudbeckia hirta	1,7	1.40	0.52
3	*Bd/Lc/Pp*; *Bd/Lc/Rh*; *Bd/Pp/Rh*	*Buchloe dactyloides*	2,9	0.09	4.04
(from Treatment C)	*Bd/Lc/Pp*; *Bd/Lc/Rh*; *Lc/Pp/Rh*	*Lespedeza capitata*	2,9	0.08	0.62
	Bd/Lc/Pp; *Bd/Pp/Rh*; *Lc/Pp/Rh*	*Poa pratensis*	2,9	2.14	3.38
	Bd/Lc/Rh; *Bd/Pp/Rh*; *Lc/Pp/Rh*	*Rudbeckia hirta*	2,9	19.98*	5.09
2	*Bd/Lc*; *Bd/Pp*; *Bd/Rh*	*Buchloe dactyloides*	2,9	0.24	5.37*
(from Treatment B)	*Bd/Lc*; *Lc/Pp*; *Lc/Rh*	*Lespedeza capitata*	2,9	10.11*	11.11*
	Bd/Pp; *Lc/Pp*; *Pp/Rh*	*Poa pratensis*	2,9	8.95*	10.60*
	Bd/Rh; *Lc/Rh*; *Pp/Rh*	*Rudbeckia hirta*	2,9	20.30*	7.66*

that, in certain conditions, the presence of one species may have major effects on ecosystem functioning (Naeem et al. 1996). These results support the prediction of Tilman et al. (1997) that diverse plant communities will, on average, have higher primary productivity than species-poor plant communities because they have a higher probability of containing the most productive species in that species pool.

Our study also demonstrates the variance in individual species' effects on ecosystem functioning. First, contrasts of species' impacts within our first experiment show that the loss of a species from one community can have significantly different effects than the loss of that same species from a community with the same number of species but different composition. This effect appears to be most important at very low levels of diversity. Thus, changes in ecosystem processes caused by an extinction in one location may not be the same in another place. Second, our work shows that the functional grouping of species need not be the same for all ecosystem processes (Vitousek and Hooper 1993, Mooney et al. 1995). In our experiment, the only species that had positive average impacts on assemblage biomass were legumes (Table 2). These results follow Vitousek (1990) and Chapin et al.'s (1996) suggestion that species that are unique (in a community) in their ability to affect soil resource pools and supply rates will probably have relatively large ecosystem-level effects. Removing a legume reduces an assemblage's access to atmospheric N, but, in our system at least, the removal of any other type of species simply released other species from competition. Sometimes, as in the case of *R. hirta*, this caused greater overall productivity. On the other hand, species' impacts on N retention varied within our predefined functional groups as much as among functional groups (Table 3). Such variability makes it difficult to predict the impact of losing a species, despite the logic behind Vitousek's (1990) and Chapin et al.'s (1996) rules.

In summary, our study shows that although decreasing the diversity of a community decreases productivity on average, the magnitude and even direction of changes in ecosystem functioning as diversity declines can depend on which species is lost and possibly on the composition of the community from which it is lost. Thus, losing a species has a certain average effect, while the effect of losing a particular species is much more variable and context-specific.

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