

# Experimental Tests of the Dependence of Arthropod Diversity on Plant Diversity

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**ABSTRACT:** Because a diversity of resources should support a diversity of consumers, most models predict that increasing plant diversity increases animal diversity. We report results of a direct experimental test of the dependence of animal diversity on plant diversity. We sampled arthropods in a well-replicated grassland experiment in which plant species richness and plant functional richness were directly manipulated. In simple regressions, both the number of species planted ( $\log_2$  transformed) and the number of functional groups planted significantly increased arthropod species richness but not arthropod abundance. However, the number of species planted was the only significant predictor of arthropod species richness when both predictor variables were included in ANOVAs or a MANOVA. Although highly significant, arthropod species richness regressions had low  $R^2$  values, high intercepts (24 arthropod species in monocultures), and shallow slopes. Analyses of relations among plants and arthropod trophic groups indicated that herbivore diversity was influenced by plant, parasite, and predator diversity. Furthermore, herbivore diversity was more strongly correlated with parasite and predator diversity than with plant diversity. Together with regression results, this suggests that, although increasing plant diversity significantly increased arthropod diversity, local herbivore diversity is also maintained by, and in turn maintains, a diversity of parasites and predators.

**Keywords:** arthropod diversity, plant diversity, grasslands, predators, parasites, herbivores.

It has been suggested that plant diversity should be important in determining animal diversity (e.g., Hutchinson 1959; Southwood 1978; Erwin 1982; Tilman 1982; May 1990; Hunter and Price 1992). Because a greater number

of resources should support a greater number of consumer species, most models predict (e.g., Lotka 1925; Volterra 1926; Gause 1934; MacArthur 1972; Whittaker 1975; Tilman 1986; Rosenzweig 1995) and some correlative studies (e.g., Murdoch et al. 1972; Nagel 1979; Southwood et al. 1979; Prendergast et al. 1993; Parmenter et al. 1995; Niemela et al. 1996) and experimental studies (e.g., Pimentel 1961; Root 1973; Altieri and Letourneau 1982; Lawton 1983; Altieri 1984; Siemann 1998) have found that increasing plant diversity increases arthropod herbivore diversity. However, these studies are confounded by changes in plant community composition that correlate with changes in plant diversity. The relationship between plant diversity and herbivore diversity may be nonlinear because herbivore loads are often lower in polycultures due to differences in the ability of herbivores to locate host plants in mixed stands, suitability of smaller patches of host plants, and/or differences in the effects of parasites and predators (reviewed in Andow 1991).

Increases in arthropod herbivore diversity could potentially cascade up to higher trophic levels, leading to a greater diversity of parasites and predators (Hunter and Price 1992; Siemann 1998). Increasing plant diversity could also increase the diversity of higher trophic levels directly by increasing the diversity of floral resources that many arthropod parasites and predators utilize or require (e.g., Sweetman 1936; Clausen 1940; Price et al. 1980; Powell 1986; Jervis et al. 1993). Changing plant diversity may also influence the interactions between herbivores and their predators and parasites, for example, by changing parasite and predator foraging efficiency (e.g., Pimentel 1961; Strong et al. 1984; Russell 1989; Andow and Prokym 1990; Coll and Bottrell 1996). These interaction modifications (*sensu* Wootton 1993, 1994) may appear as direct effects of plants on parasite and predator diversity in statistical analyses.

Because many arthropods consume or forage on certain types of plants—such as forbs versus grasses in grasslands (e.g., Hansen and Ueckert 1970; Knutson and Campbell 1974; Boutton et al. 1978; Evans 1984; Belovsky 1986; Porter and Redak 1997) or bushes versus trees

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in forests (MacArthur and MacArthur 1961; MacArthur 1965)—adding more types of plants (i.e., functional groups) may be as effective in increasing animal diversity as adding plant species per se. Correlative studies have shown that the architectural or structural diversity of plants, which is likely correlated with both plant species and functional diversity, may be an important determinant of arthropod diversity (reviewed in Lawton 1983). Because increasing plant species diversity (Naeem et al. 1995; Tilman et al. 1996) or plant functional diversity (Hooper and Vitousek 1997; Tilman et al. 1997) can increase productivity, increasing plant diversity may also increase arthropod diversity indirectly by increasing total arthropod abundance and, thus, allowing rarer species to persist locally (Hutchinson 1959; Connell and Orias 1964; MacArthur 1969; Brown 1981; Abrams 1995; Rosenzweig 1995; Siemann 1998).

Herbivore diversity may also be influenced by the diversity of higher trophic levels. If herbivores have appropriate trade-offs between predator and parasite susceptibility versus competitive ability in the absence of predation and parasitism, then predators and parasites may allow a greater diversity of herbivores to coexist (e.g., Cramer and May 1972; Roughgarden and Feldman 1975; Levin et al. 1977; Tilman 1986; Holt et al. 1994; Leibold 1996). There have been ample demonstrations that certain predators maintain herbivore diversity (e.g., Paine 1966; Connell 1972; Menge and Sutherland 1976; Power et al. 1996) and that herbivore abundance in general (e.g., Paine 1966; Connell 1972; Hairston and Hairston 1993) and arthropod herbivores in particular (e.g., Andrzejewska et al. 1967; Strong et al. 1984; Schmitz 1993; Denno et al. 1995) can be strongly limited by predators and parasites. Chain modeling (Cox and Wermuth 1993) is a tool that can be used to sort out direct and indirect responses of animal diversity to changes in plant diversity.

In order to test whether increasing plant species diversity and/or increasing plant functional diversity increases animal diversity, we directly manipulated plant species diversity and plant functional diversity in a well-replicated grassland experiment and measured arthropod diversity and abundance. In order to investigate direct and indirect responses of arthropods to plant diversity, we examined the relationships among number of species planted and the diversities of different arthropod trophic groups using chain modeling and regression.

## Material and Methods

### *Experimental Setup*

This experiment was established in a 10-ha “brome field” at Cedar Creek, Minnesota (~50 km north of Minneapolis/St. Paul), primarily to study the effects of plant

diversity on ecosystem functioning (Tilman et al. 1997). The experimental design and setup are reported in detail elsewhere (Tilman et al. 1994).

In August 1993, the field was sprayed with a general herbicide (Round-Up, Monsanto, St. Louis) and burned after the vegetation was dead and dry. The upper 6–8 cm of sod and soil were then removed to reduce the seed bank. The remaining soil was plowed and repeatedly disked. In spring 1994, the field was disked again and smoothed. The field was divided into 342 plots (13 m × 13 m with only the inner 11 m × 11 m sampled) separated by walkways and roadways that were kept bare. In May 1994, plots were seeded with a constant mass of seeds added to each plot (divided equally among the species). Plots were reseeded in May 1995. As plants grew, some plots were sprayed with suitable herbicides to eliminate weeds. All plots were hand weeded two to four times every year of the experiment, and some plots were also spot sprayed with herbicides in the first and second years of the experiment. The experiment was composed of three subexperiments. Two of these subexperiments were described elsewhere (Tilman et al. 1997) and were used in this study.

In order to test for the effects of plant taxonomic diversity on arthropod diversity, the plant species composition of each of 163 13 × 13-m plots was determined by random draws of one, two, four, eight, or 16 perennial plant species drawn from a core pool of 18 species (four species each of four functional groups—C<sub>3</sub> grasses, C<sub>4</sub> grasses, legumes, and nonlegume forbs—and two species from the woody functional group). There were 34, 35, 29, 30, and 35 replicates, respectively, at each level of diversity. In this subexperiment, plant diversity and plant composition are uncorrelated.

To better distinguish between the responses of arthropod diversity to plant taxonomic and functional diversity, 79 additional plots were assigned combinations of one, two, or three functional groups and two, four, or eight species. Species compositions of these plots were chosen by random draws of functional groups followed by random draws of species within these functional groups. When needed, we used a pool of 16 additional species (four species in each of the four nonwoody functional groups). Another 46 plots were created with 32 of these 34 species. The 288 plots (from pooling these two types of plots with the random species draw subexperiment) uncouple species diversity, functional diversity, and functional composition but have a weak correlation between these and species composition. In order to estimate the number of arthropods that might be present as aerial plankton, an additional two plots were kept bare. A complete list of the plant species used in the experiment is given in appendix A, and the number of plots of each treatment is given in appendix B.

Plant and ecosystem results have been reported elsewhere (Tilman et al. 1997). These plant productivity data (peak aboveground living plant standing crop from four  $0.1 \times 3.0$ -m strips per plot in July 1996) and plant cover data (number of plant species in four  $1.0 \times 0.5$ -m areas in July 1996) are also used here.

#### *Arthropod Sampling*

On August 16, 1996, we sampled arthropods in the plots using sweep nets. Each sample consisted of all the arthropods caught in a 38-cm diameter muslin net swung 25 times while walking a line 3 m in from the edge of each plot. Samples were manually sorted under magnification, specimens identified to species or morphospecies within known families or genera, and enumerated. Field observations and a literature review (see Siemann 1997) were used to assign each species to one of four trophic categories. The parasite category included all species that were either parasitic in the adult stage or parasitic as larvae regardless of adult diet (mainly nectar, pollen, and/or host fluids; Sweetman 1936; Clausen 1940). Nonparasites were classified into three other categories—herbivore, predator, or detritivore—based on whether the adults fed primarily on plants, animals, or dead matter or fungi.

Sweep net sampling is a good measure of relative abundance and relative species richness for all but the smallest vegetation-dwelling arthropods for areas with similar vegetation structure (Turnbull and Nicholls 1966; Evans et al. 1983). Our conclusions require only that measures of abundance and diversity be relative. Our plots were all sparsely vegetated (on average  $37\% \pm 14\%$  vegetation cover), and woody plants were small. Studies at Cedar Creek that employed multiple sampling methods have never found conflicting patterns of arthropod diversity or community structure in either descriptive studies (Siemann et al. 1997: sweep nets, pitfall traps, light traps, and visual surveys) or experimental studies (Siemann 1998: sweep nets and vacuum samplers).

#### *Analyses*

Using data from all 288 plots (all except bare ground plots), we used simple ordinary least squares (OLS) regression to test whether total observed arthropod species richness increased with the number of species planted ( $\log_2$  transformed to achieve linearity, giving values of 0, 1, 2, 3, 4, and 5 corresponding to one, two, four, eight, 16, and 32 species planted) or increased with the number of functional groups planted. In order to test whether the slight correlation of taxonomic diversity and species composition could be responsible for the effects of taxonomic diversity, we repeated the analysis using only plots

from the random species draw subexperiment. In order to test whether rare arthropod species were causing these responses, we repeated these analyses using total effective arthropod species richness ( $e^{H'}$  where  $H'$  = Shannon's index) as the response variable. We repeated analyses using observed plant species richness in place of number of species planted.

In order to see how changing plant species diversity impacted different types of arthropods, we tested whether the species richness of arthropod trophic groups depended on  $\log_2$ (number of species planted) or number of functional groups planted in one-way MANOVAs. In all MANOVAs in this study, Wilk's  $\lambda$ , Pillai's trace, Hotelling-Lawley trace, and Roy's greatest root all gave identical  $F$  values with identical degrees of freedom. We used simple regression to investigate the dependence of individual arthropod trophic group species richness on  $\log_2$ (number of species planted) or number of functional groups planted. In order to see how different types of plants impacted arthropod diversity, we used regression to determine how adding each functional group affected herbivore species richness.

We used a two-way ANOVA to test whether total arthropod species richness depended on  $\log_2$ (number of species planted) or number of functional groups planted. We repeated this analysis with one- and 32-species plots excluded in order to see whether the results of this analysis depended on the strong correlation of the predictors in these plots (app. B). We used a two-way MANOVA to test whether arthropod species richness (four variables, one for each trophic group) depended on  $\log_2$ (number of species planted) or number of functional groups planted.

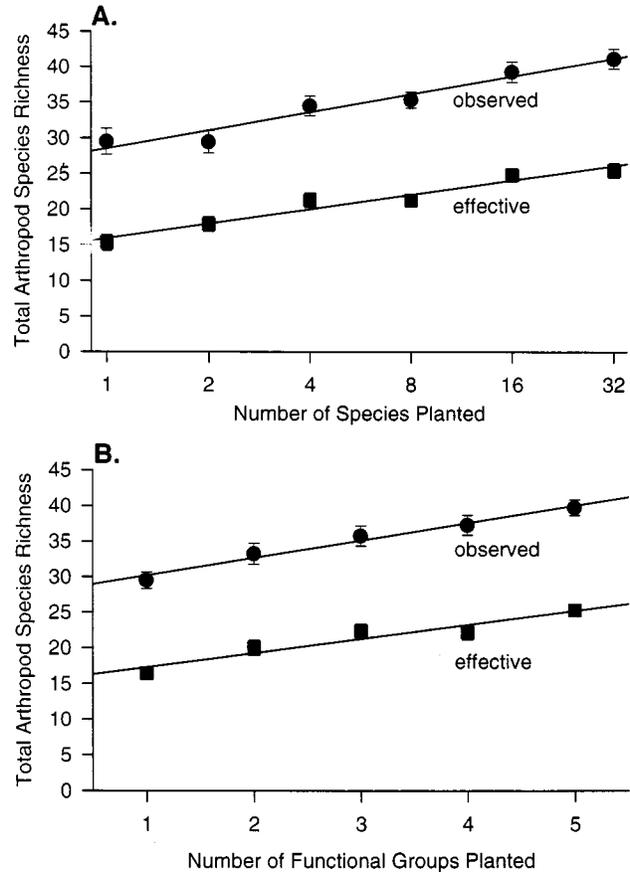
We wanted to determine both whether changing plant diversity changed arthropod diversity and how plant diversity might be causing these changes. We used the marginal and conditional dependencies (i.e., simple and partial correlations) of plant and arthropod trophic group diversities to examine their relationships and to suggest chain models, using the general approach described in detail by Cox and Wermuth (1993). Path analysis and chain modeling in expert systems both belong to this more general method of analysis (Cox and Wermuth 1993). For example, if response variable  $X$  and predictor variable  $W$  are significantly marginally correlated but are conditionally independent when another variable  $V$  is included ( $X \perp\!\!\!\perp W|V$ ), this is consistent with a path of causation  $W$  to  $V$  to  $X$ . In order to examine whether changes in plant productivity may have been responsible for plant diversity effects on arthropod diversity, we repeated these analyses with plant productivity included as a variable.

We used MANOVA to test whether the proportions of individuals in different arthropod trophic groups in plots (three response variables: parasite abundance/total abun-

dance, herbivore abundance/total abundance, and predator abundance/total abundance) depended on  $\log_2$ (number of species planted). A significant result was taken as evidence that the arthropods present in plots were not simply random subsamples of the individuals in the field (see Morin 1983 for a full discussion of this method of analysis). We used the number of specimens in bare plots as an estimate of the number of specimens in vegetated plots likely present as aerial plankton. Because there may have been patterns of arthropod diversity at spatial scales larger than plots, we tested whether a plot's arthropod species richness depended on both its absolute location within the experiment and on its distance from edge of experiment. For the 218 plots that were not on the edge of the experiment, we used regression to test how total arthropod species richness depended on  $\log_2$ (number of species planted) and the average number of species planted in the plot and the eight adjacent plots. Because Homoptera are thought to be both more host specific and more sedentary than most herbivores (Strong et al. 1984), we used simple regression to test the dependence of Homoptera species richness on  $\log_2$ (number of species planted).

**Results**

In total, arthropod sampling caught 36,857 individuals of 491 species in 16 orders (app. C). Both plant species diversity and plant functional diversity influenced total arthropod diversity and arthropod trophic group diversity. In simple regressions,  $\log_2$ (number of species planted) (fig. 1A, table 1) and the number of functional groups planted (fig. 1B, table 2) significantly increased both total observed and effective ( $e^H$ ) arthropod species richness but not total arthropod abundance. The effect of number of species planted on total arthropod species richness (allsr) was similar in the random species draw subexperiment (allsr =  $29.7 + 2.35 \log_2$ [number of species planted],  $F = 37.3$ ,  $df = 1, 161$ ,  $P < .0001$ ,  $R^2 = 0.15$ ). The species richness of arthropod trophic groups depended significantly on  $\log_2$ (number of species planted) ( $F = 13.07$ ,  $df = 5, 282$ ,  $P < .0001$ ) and the number of functional groups planted ( $F = 11.80$ ,  $df = 4, 283$ ,  $P < .0001$ ) in one-way MANOVAs. In simple regressions,  $\log_2$ (number of species planted) (fig. 2A, table 1) and the number of functional groups planted (fig. 2B, table 2) significantly increased herbivore, parasite, and predator species richness but not detritivore species richness. Observed plant species richness (plsr) significantly increased total, herbivore (herbsr), parasite (parsr), and predator (predsr) species richness (allsr =  $23.3 + 1.0 \text{ plsr}$ ,  $F = 43.2$ ,  $df = 1, 286$ ,  $P < .0001$ ,  $R^2 = 0.13$ ; herbsr =  $15.1 + 0.58 \text{ plsr}$ ,  $F = 35.7$ ,  $df = 1, 286$ ,  $P < .0001$ ,  $R^2 = 0.11$ ;



**Figure 1:** The dependence of total arthropod observed and effective ( $e^H$ ) species richness on (A) number of species planted ( $\log_2$  axis scaling) and (B) number of functional groups planted. Lines are from OLS regressions (see tables 1, 2). (circles = observed species richness; squares = effective species richness).

**Table 1:** Dependence of arthropod species richness and abundance on the number of species planted

Variable	Intercept	$\text{Log}_2(\text{species planted})$	$R^2$
Total observed species richness	23.36***	2.54***	.14
Total effective species richness	15.96***	1.97***	.17
Total abundance	117.80***	1.08 NS	<.01
Detritivore species richness	.84***	.05 NS	<.01
Herbivore species richness	18.17***	1.32***	.16
Parasite species richness	5.01***	.56***	.07
Predator species richness	4.35***	.48***	.11

Note: Intercepts, parameters, and  $R^2$  values are from regressions.  $N = 288$ ,  $df = 287$ . NS means  $P \geq .05$ .

\*\*\*  $P < .001$  for significance test of parameter value from 0.

**Table 2:** Dependence of arthropod species richness and abundance on the number of functional groups planted

Variable	Intercept	Number of functional groups	R <sup>2</sup>
Total observed species richness	27.60***	2.48***	.13
Total effective species richness	15.02***	2.05***	.18
Total abundance	122.86***	-.77 NS	<.01
Detritivore species richness	.89***	.03 NS	<.01
Herbivore species richness	17.44***	1.40***	.11
Parasite species richness	4.73***	.58***	.08
Predator species richness	4.32***	.43***	.09

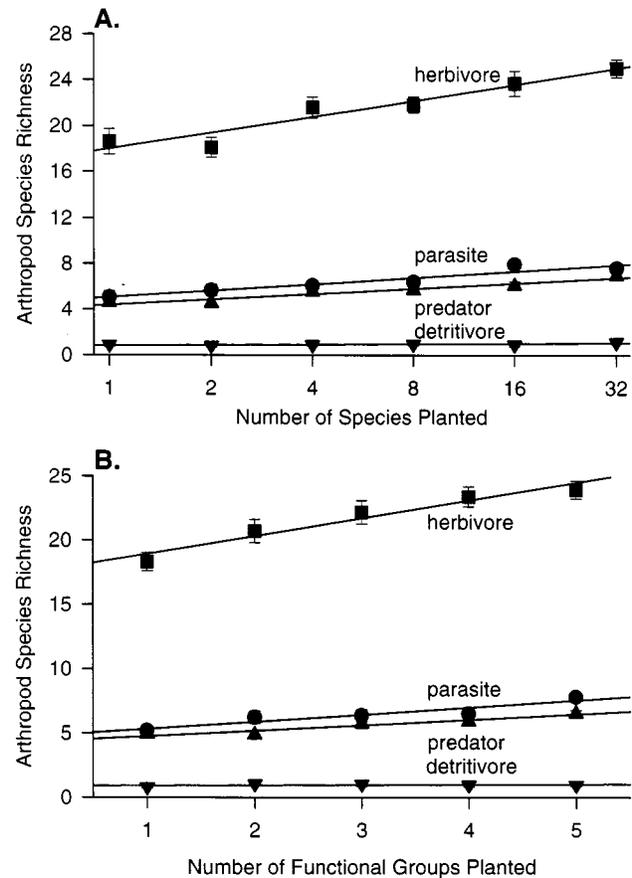
Note: Intercepts, parameters, and R<sup>2</sup> values are from regressions. N = 288, df = 287. NS means  $P \geq .05$ .

\*\*\*  $P < .001$  for significance test of parameter value from 0.

$\text{parsr} = 4.3 + 0.20 \text{ plsr}$ ,  $F = 15.8$ ,  $df = 1, 286$ ,  $P < .0001$ ,  $R^2 = 0.05$ ;  $\text{predsr} = 3.2 + 0.21 \text{ plsr}$ ,  $F = 41.0$ ,  $df = 1, 286$ ,  $P < .0001$ ,  $R^2 = 0.13$ ). The presence of C<sub>3</sub> grasses or legumes in a plot allowed an additional 3.5 ( $t = 4.3$ ,  $df = 282$ ,  $P < .0001$ ) or 3.7 ( $t = 4.5$ ,  $df = 282$ ,  $P < .0001$ ) arthropod herbivores to be present. The presence of C<sub>4</sub> grasses tended to increase herbivore species richness ( $t = 1.8$ ,  $df = 282$ ,  $P = .08$ ), and the presence of forbs ( $t = -1.7$ ,  $df = 282$ ,  $P = .09$ ) or woody plants ( $t = -0.4$ ,  $df = 282$ ,  $P = .69$ ) tended to decrease herbivore species richness. Herbivore species richness in monocultures of C<sub>3</sub> grasses, C<sub>4</sub> grasses, forbs, legumes, and woody plants were 19.3, 19.9, 14.6, 21.1, and 18.0, respectively.

Plant species diversity was a better predictor of arthropod diversity than was plant functional diversity. In a two-way ANOVA, total arthropod species richness depended significantly on  $\log_2(\text{number of species planted})$  ( $F = 2.56$ ,  $df = 5, 278$ ,  $P < .05$ ) but not the number of functional groups planted ( $F = 1.84$ ,  $df = 4, 278$ ,  $P = .12$ ). Results were similar when plots with one or 32 species were excluded from the analysis ( $\log_2[\text{number of species planted}]$ :  $F = 3.49$ ,  $df = 3, 200$ ,  $P < .05$ ; number of functional groups planted:  $F = 1.91$ ,  $df = 4, 200$ ,  $P = .11$ ). In a two-way MANOVA, the species richness of trophic groups depended significantly on  $\log_2(\text{number of species planted})$  ( $F = 2.56$ ,  $df = 4, 282$ ,  $P < .05$ ) but not the number of functional groups planted ( $F = 1.45$ ,  $df = 4, 282$ ,  $P = .22$ ).

Plant diversity had both direct and indirect effects on arthropod trophic groups. Consistent with the results above,  $\log_2(\text{number of species planted})$  was significantly correlated with herbivore, parasite, and predator species richness (table 3). Additionally, herbivore, parasite, and predator species richness were all themselves significantly



**Figure 2:** The dependence of species richness of arthropod trophic groups on (A) number of species planted ( $\log_2$  axis scaling) and (B) number of functional groups planted. Lines are from OLS regressions (see tables 1, 2). (Squares = herbivore; circles = parasite; triangles pointing up = predator; triangles pointing down = detritivore.)

correlated. Partial correlations indicated the conditional independence of  $\log_2(\text{number of species planted})$  and parasite species richness and of predator and parasite species richness (table 3). Including plant productivity as a variable did not change the sign or significance levels of any partial correlations, and there were no significant partial correlations between plant productivity and any of these arthropod variables (herbivore:  $r = 0.11$ ,  $P = .06$ ; parasite:  $r = 0.07$ ,  $P = .27$ ; predator:  $r = 0.07$ ,  $P = .23$ ) despite significant simple correlations between plant productivity and all of these arthropod variables (herbivore:  $r = 0.36$ ,  $P < .001$ ; parasite:  $r = 0.28$ ,  $P < .001$ ; predator:  $r = 0.27$ ,  $P < .001$ ). Together, these results suggested that changing plant diversity directly influenced herbivore and predator species richness (which are themselves highly correlated even after controlling for correlations with plant and parasite diversity), that plant diversity influenced parasite species richness only indirectly via changes in herbivore species richness, and that

**Table 3:** Simple and partial correlations among number of species planted and arthropod herbivore, parasite, and predator species richness

Variable	$\log_2(\text{number of species planted})$	Herbivore species richness	Parasite species richness	Predator species richness
$\log_2(\text{number of species planted})$	1.00	.35***	.27***	.34***
Herbivore species richness	.13*	1.00	.66***	.54***
Parasite species richness	.07NS	.58***	1.00	.36***
Predator species richness	.19***	.39***	-.01NS	1.00

Note: Numbers to the right of 1.00 are simple correlations; numbers to the left of 1.00 are partial correlations.  $N = 288$ ; NS means  $P \geq .05$ .

\*  $.01 \leq P < .05$ .

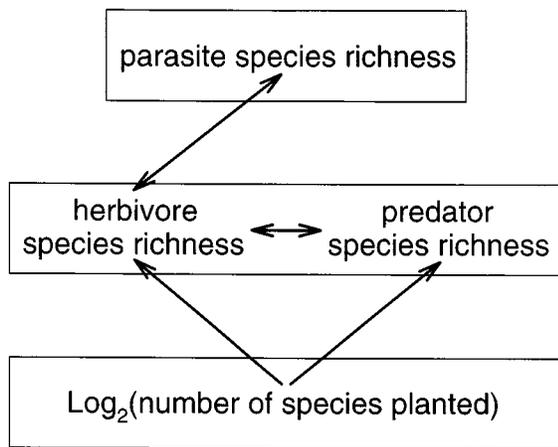
\*\*\*  $P < .001$  for significance test from 0 correlations.

herbivore species richness was highly correlated with all three other variables even in a multivariate analysis. The chain model shown in figure 3 is consistent with all of this information. Multiple regressions for each of the arthropod variables based on this chain model were as follows:  $\text{herbsr} = 8.58 + 0.40 \times \log_2(\text{plsr}) + 1.05 \text{ parsr} + 0.93 \text{ predsrs}$ ,  $R^2 = 0.57$ ,  $F = 113.9$ ,  $df = 3, 284$ ,  $P < .001$ ;  $\text{predsr} = 1.41 + 0.25 \times \log_2(\text{plsr}) + 0.16 \times \text{herbsr}$ ,  $R^2 = 0.31$ ,  $F = 65.4$ ,  $df = 2, 285$ ,  $P < .001$ ;  $\text{parsr} = -0.54 + 0.32 \times \text{herbsr}$ ,  $R^2 = 0.43$ ,  $F = 219.4$ ,  $df = 1, 286$ ,  $P < .001$ . Regressions using measured plant species richness gave similar results:  $\text{herbsr} = 7.63 + 0.18 \text{ plant species}$

$\text{richness} + 1.06 \text{ parsr} + 0.90 \text{ predsrs}$ ,  $R^2 = 0.55$ ,  $F = 114.4$ ,  $df = 3, 284$ ,  $P < .001$ ;  $\text{predsr} = 0.76 + 0.12 \text{ plsr} + 0.16 \text{ herbsr}$ ,  $R^2 = 0.32$ ,  $F = 68.0$ ,  $df = 3, 284$ ,  $P < .001$ .

The arthropod assemblages of plots were not random subsets of the field community. In a MANOVA, the proportion of individuals in trophic groups within plots depended significantly on  $\log_2(\text{number of species planted})$  ( $F = 5.06$ ,  $df = 3, 284$ ,  $P < .01$ ). Total arthropod species richness depended on  $\log_2(\text{number of species planted})$  ( $\beta = 1.9$ ,  $t = 4.1$ ,  $df = 215$ ,  $P < .0001$ ) but not on the average species richness of the plot and the eight adjacent plots ( $\beta = 0.3$ ,  $t = 1.3$ ,  $df = 215$ ,  $P = .19$ ). The bare plots each had 11 individuals compared to an average of  $120.9 \pm 57.4$  in vegetated plots. Homoptera species richness depended significantly on  $\log_2(\text{number of species planted})$  (Homoptera species richness =  $5.4 + 0.17 \log_2[\text{plsr}]$ ,  $F = 6.2$ ,  $df = 1, 286$ ,  $P = .01$ ,  $R^2 = 0.03$ , range 0–11).

However, processes at scales larger than single plots also influenced arthropod diversity because there was a gradient of arthropod diversity across the experiment. Arthropod species richness was significantly higher at the southeast end of the experiment ( $\text{allsr} = 28.74 + 0.03 \times [\text{number of plots south (range 1–18) from the northwest corner of experiment}] + 0.03 \times [\text{number of plots east (range 1–19) from the northwest corner of the experiment}]$ ,  $P$  for each term  $< .01$ ,  $F = 7.62$ ,  $df = 2, 285$ ,  $P < .001$ ,  $R^2 = 0.05$ ). However, there was no effect on arthropod diversity of a plot being near the edge of the experiment. A plot's distance from the closest edge of the experiment had no effect on its total arthropod species richness ( $F = 1.99$ ,  $df = 1, 286$ ,  $P = .16$ ).



**Figure 3:** Model consistent with a correlation structure (table 3) with simple correlations between all four variables and conditional independence of parasite species richness and predator species richness and parasite species richness and  $\log_2(\text{number of species planted})$ . Following the guidelines of Cox and Wermuth (1993), arrows point from explanatory variables to response variables, lines with two heads represent correlations among response variables, and boxes surround the predictor variable (plant diversity), response variables that respond directly to changes in plant diversity (herbivore and predator diversity), and response variables that respond only indirectly to changes in plant diversity (parasite diversity).

## Discussion

In this direct experimental test of the dependence of animal diversity on plant diversity, we found that total arthropod species richness (fig. 1A) and arthropod herbi-

vore, parasite, and predator, but not detritivore, species richness (fig. 2A) increased significantly with the number of species planted in a plot (table 1). Arthropod species richness also depended significantly on the number of species planted in the random species draw subexperiment, in which plant species composition and plant diversity were uncorrelated. This suggests that the slight correlation between plant diversity and plant species composition in the 288-plot experiment was not responsible for the effects of plant diversity on arthropod diversity. Total arthropod (fig. 1B) and arthropod herbivore, parasite, and predator, but not detritivore, species richness (fig. 2B) also increased significantly with the number of functional groups planted (table 2).

When the effects of the number of species planted and the number of functional groups planted were considered together in an ANOVA and a MANOVA, total arthropod species richness and species richness of arthropod trophic groups, respectively, depended significantly on only the number of species planted. However, the number of species planted and the number of functional groups planted are unavoidably correlated in any experimental gradient that includes monocultures. This correlation between treatments was not likely responsible for this result because plant species diversity was still the only significant predictor of arthropod diversity when we excluded one- and 32-species plots in which the treatments were most strongly correlated (app. B). These results suggest that plant taxonomic diversity is a more important determinant of local arthropod diversity than is plant functional diversity. This is consistent with the fact that some arthropod herbivores feed on only a single species of plant, rejecting even closely related species (e.g., Wilcox 1979; Price 1984; Dixon 1985; Tabashnik and Slansky 1987). It contrasts with the finding that local ecosystem processes depend more on plant functional diversity than plant species diversity (Hooper and Vitousek 1997; Tilman et al. 1997). However, because changes in herbivore species richness in response to the addition of different plant functional groups differed in both magnitude and sign, this functional perspective (Lawton and Brown 1993; Vitousek and Hooper 1993) may have some relevance for predicting arthropod diversity as well.

#### *Direct versus Indirect Responses*

Were these significant increases in herbivore diversity direct responses to a greater diversity of resources or indirect responses mediated through effects of plant diversity on higher trophic levels? Chain modeling results suggested that both mechanisms might be responsible. In these analyses (table 3), there was indeed a significant chain of direct effects cascading up from plant diversity to herbivore diversity to parasite diversity (fig. 3), as pre-

dicted by consumer resource models (e.g., MacArthur 1972; Whittaker 1975; Tilman 1986; Rosenzweig 1995). In fact, the conditional independence of plant diversity and parasite diversity when herbivore diversity was included suggests that the entire effect of plant diversity on parasite diversity was mediated through increases in herbivore diversity (table 3, fig. 3).

Chain modeling also indicated direct effects of plant diversity on herbivore and predator diversity, which were themselves highly correlated (table 3, fig. 3). There are several potential explanations for a direct response of predator diversity, none of which can be eliminated from consideration, though some may be more likely than others. First, many predaceous arthropods are to some extent omnivorous, feeding on nectar (Hagen 1987). Therefore, changes in the diversity or amount of nectar available in these plots may have influenced predator diversity. Even though this nectar may only meet a small amount of their energy needs and most predators require prey to complete development (Hagen 1987), if there are trade-offs such that a species that requires a greater density of prey to survive without nectar is better able to substitute nectar calories for prey calories, two predator species can survive on a single prey species rather than just one (Tilman 1982). Second, rather than specializing on the arthropods on a single plant, arthropod predators may have evolved habitat specialization, much like birds (MacArthur and MacArthur 1961; MacArthur 1964) or lizards (Pianka 1967) apparently have. This could decouple herbivore diversity and predator diversity in local habitats. Studies of tropical spiders (Greenstone 1984) and the lack of a similar response by parasites both support this hypothesis. Third, rather than indicating a direct response, this apparent direct effect of plant diversity on predator diversity may actually represent a modification of the interactions between herbivores and predators (Wootton 1993). For instance, studies have shown that foraging efficiency depends on environmental complexity (Andow and Risch 1985; Andow and Prokym 1990; Coll and Bottrell 1996).

#### *Interactions within the Arthropod Community*

It must be noted that, even though chain modeling offers advantages over conventional multiple regression in inferring complex mechanisms of response to manipulation of a single trophic level (Cox and Wermuth 1993; Mitchell 1993; Wootton 1993), it still can only reveal patterns of correlation (Smith et al. 1997). Nonetheless, partial correlations indicate that herbivore diversity is more strongly correlated with predator and parasite diversity than with plant diversity (table 3, fig. 3). Furthermore, although the effects of plant species richness on arthropod species richness variables were highly significant,  $R^2$

values were generally low (maximum = 0.16, table 1), regression slopes were very shallow (only 2.5 additional arthropod species for each doubling of number of plant species added; table 1, fig. 1A), and the intercepts were high (24 arthropod species in monocultures; table 1, fig. 1A). Although plant diversity is thought to be overwhelmingly influential in determining regional and global arthropod diversity (Southwood 1978; Erwin 1982; May 1990), these results suggest it is not the only, or perhaps not even the most, important factor influencing local arthropod diversity. Rather, for our terrestrial arthropod communities, predator-prey and parasite-host interactions may be more important than usually believed.

Two prey or host species can coexist on a single resource if predators or parasites switch to feed on more abundant prey or host species (Murdoch 1969), predators and parasites are not selective but prey or host species are spatially aggregated (May 1978; Holt 1993; Holt et al. 1994), or predators or parasites preferentially feed on vulnerable species (Paine 1966; Vance 1974; Levin et al. 1977; Tilman 1986). With appropriate trade-offs between competitive ability and predator and parasite susceptibility, each additional parasite or predator species can allow one additional consumer (herbivore) species to coexist (Levin et al. 1977; Tilman 1986). This prediction agrees closely with the fitted values of 1.05 and 0.93 additional herbivore species per parasite and predator species, respectively, that we found. In contrast to this close agreement with predictions, each additional herbivore species allowed far fewer than one additional parasite and predator species to persist (0.32 and 0.16, respectively), and each additional plant species allowed, on average, only 0.18 additional herbivore species to persist. This suggests that local predator and parasite diversity may be more important than plant diversity in determining local herbivore diversity.

#### *Plant Diversity*

Potential explanations for the weak response of arthropod diversity to manipulations of plant diversity include the following. First, because herbivores are better able to locate larger patches of plants and/or larger patches are more likely to sustain viable herbivore populations (reviewed in Andow 1991), each plant species may support fewer herbivore species when it occurs in a diverse planting. So, only a small proportion of consumer species that theoretically could be present given the local diversity of resources may actually be present in the local area. These effects may be stronger for plants with secondary compound defenses (i.e., "qualitative defenses") and more specialized herbivores (Strong et al. 1984). The tendency of adding forbs or woody plants to decrease herbivore species richness supports this explanation. Second, with

such a large experiment, monocultures could not be completely free of weeds and plant species did not establish equally well in all plots. This could have caused regressions using number of species planted to underestimate the true slope of the relationship between arthropod and plant diversity in the plots. In fact, the slope of the herbivore species richness and observed plant species richness relationship was steeper (0.58) than that obtained with the treatment variable (table 1, equivalent to 0.20). However, the high number of herbivore species for monocultures (14) in this regression together with its lower  $R^2$  value suggests that this is not a sufficient explanation. Third, plots may have been too small to accurately test the dependence of arthropod diversity on plant diversity. Several results suggest that the relationship we found in these plots may indeed be representative of patterns at larger scales.

The dependence of arthropod species richness on the number of species planted in the plot but not on the average number of species planted in the plot and the eight adjacent plots suggests that increasing the sizes of plots by an order of magnitude would not have produced a stronger relationship between arthropod and plant diversity. However, the position of a plot within the experiment explained about 5% of the total variance in arthropod diversity. This suggests that other factors, perhaps such as prevailing winds or surrounding habitat type, also may influence local arthropod diversity (e.g., Robinson et al. 1992; Kruess and Tschardtke 1994; Roland and Taylor 1997) independent of local plant diversity. The very low numbers of arthropods in bare ground plots suggest that the arthropods present in plots were not simply aerial plankton. The similar responses of herbivore species richness and the species richness of Homoptera, which are more sessile and specialized than most herbivores (Strong et al. 1984), to increases in plant species richness also suggest that the plots were large enough to accurately assess relationships among arthropod and plant diversity. Extremely high herbivore diversity in large agricultural monocultures (e.g., Turpinseed and Kogan 1976; Chiang 1978; Strong et al. 1984; Luttrell et al. 1994) is further evidence suggesting that factors other than plant diversity may be important in determining local herbivore diversity.

#### *Artifacts*

There is also the possibility that the correlations among arthropod variables are sampling artifacts. The parameter values of one additional herbivore species for each parasite or predator species that we found would also be predicted if local assemblages were simply random subsamples of individuals from the larger field community. Multiple pieces of evidence suggest this is not the case. In

a MANOVA, the proportion of individual arthropods in different trophic groups depended significantly on the number of species planted. Each additional herbivore species allowed far fewer than one additional parasite and predator species to persist. The partial correlation between parasite and predator species richness was not significant (table 3).

Plant diversity treatments could also influence sweep net sampling efficiency. However, the significant increase of total effective arthropod species richness ( $e^{H'}$ ) with the number of plant species added and with the number of plant functional groups added (figs. 1 and 2, tables 1 and 2), together with the lack of a significant response of total arthropod abundance to the number of plant species added (tables 1 and 2), suggest that the increase in total arthropod species richness we found was not simply the result of differences in sampling efficiency. The insensitivity of the results to the inclusion of plant productivity as a covariate implies that the relationship between plant diversity and plant productivity at Cedar Creek (Tilman et al. 1996; Tilman et al. 1997) was not responsible for these results. Also, the functional groups of plants that are crucial to the diversity and productivity relationship ( $C_4$  grasses and legumes, Tilman et al. 1997) are not those that most strongly increased arthropod diversity ( $C_3$  grasses and legumes). These results suggest that changing plant diversity concurrently changed plant productivity and arthropod diversity, which may explain both the significant simple correlations between productivity and arthropod diversity in this experiment and the insignificant partial correlations when plant diversity was included as a variable.

### Conclusions

We have found that increasing plant diversity significantly increases arthropod diversity mainly via effects of plant diversity on herbivores and predators. Although the statistical significance of this increase is beyond question, the low  $R^2$  values and shallow slopes of regressions, the high arthropod diversity in monocultures, and the generally weak associations between plant diversity and arthropod diversity suggest a cautious interpretation of the importance of plant diversity in determining local arthropod diversity. Rather, our results suggest that local arthropod herbivore diversity may also be maintained by and, in turn, maintain a diversity of parasites and predators that prevent competitive exclusion, allowing a high diversity of herbivores to coexist on even a single plant species.

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## APPENDIX A

Table A1: Plant species used in the experiment

<i>Species</i>	<i>Group</i>
<i>Achillea millefolium</i>	Forb
<i>Agropyron repens</i>	$C_3$ grass
<i>Agropyron smithii</i>	$C_3$ grass
<i>Amorpha canescens</i>	Legume
<i>Andropogon gerardi</i>	$C_4$ grass
<i>Asclepias tuberosa</i>	Forb
<i>Astragalus canadensis</i>	Legume
<i>Baptista leucantha</i>	Legume
<i>Bouteloua curtipendula</i>	$C_4$ grass
<i>Bouteloua gracilis</i>	$C_4$ grass
<i>Bromus inermis</i>	$C_3$ grass
<i>Buchloe dactyloides</i>	$C_4$ grass
<i>Calamagrostis canadensis</i>	$C_3$ grass
<i>Coreopsis palmata</i>	Forb
<i>Elymus canadensis</i>	$C_3$ grass
<i>Koeleria cristata</i>	$C_3$ grass
<i>Leersia oryzoides</i>	$C_3$ grass
<i>Lespedeza capitata</i>	Legume
<i>Liatris aspersa</i>	Forb
<i>Lupinus perennis</i>	Legume
<i>Monarda fistulosa</i>	Forb
<i>Panicum virgatum</i>	$C_4$ grass
<i>Petalostemum candidum</i>	Legume
<i>Petalostemum purpureum</i>	Legume
<i>Poa pratensis</i>	$C_3$ grass
<i>Quercus ellipsoidalis</i>	Woody
<i>Quercus macrocarpa</i>	Woody
<i>Rudbeckia hirta</i>	Forb
<i>Schizachyrium scoparium</i>	$C_4$ grass
<i>Solidago nemoralis</i>	Forb
<i>Sorghastrum nutans</i>	$C_4$ grass
<i>Sporobolus cryptandrus</i>	$C_4$ grass
<i>Stipa comata</i>	$C_3$ grass
<i>Vicia villosa</i>	Legume
<i>Zizia aurea</i>	Forb

## APPENDIX B

**Table B1:** The number of plots of each treatment (after Tilman et al. 1997)

Functional groups per plot	Species per plot						
	0	1	2	4	8	16	32
0	2	0	0	0	0	0	0
1	0	34	12	12	15	0	0
2	0	0	33	14	15	0	0
3	0	0	0	20	13	0	0
4	0	0	0	10	18	1	16
5	0	0	0	0	11	34	30

## APPENDIX C

**Table C1:** The number of arthropod species and individuals within taxonomic orders and trophic groups

Group	Species	Individuals
Taxonomic orders:		
Acarina (mites)	2	13
Araneida (spiders)	29	1,052
Coleoptera (beetles)	49	1,211
Collembola (springtails)	1	92
Diptera (flies)	105	8,423
Ephemeroptera (mayflies)	1	4
Hemiptera (bugs)	36	4,442
Homoptera (leafhoppers, aphids)	38	11,613
Hymenoptera (wasps, bees, ants)	143	5,197
Lepidoptera (moths, butterflies)	48	1,312
Neuroptera (lacewings)	3	36
Odonata (dragonflies, damselflies)	2	4
Opiliones (harvestmen)	1	3
Orthoptera (grasshoppers, crickets)	24	1,251
Psocoptera (barklice)	4	116
Thysanoptera (thrips)	5	2,088
Total	491	36,857
Trophic orders:		
Detritivores	15	664
Herbivores	257	26,611
Parasites	142	5,419
Predators	73	3,981
Nonfeeding	4	182
Total	491	36,857

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