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An experimental test of the effect of plant functional group diversity on arthropod diversity

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Characteristics used to categorize plant species into functional groups for their effects on ecosystem functioning may also be relevant to higher trophic levels. In addition, plant and consumer diversity should be positively related because more diverse plant communities offer a greater variety of resources for the consumers. Thus, the functional group composition and richness of a plant community may affect the composition and diversity of the herbivores and even higher trophic levels associated with that community. We tested this hypothesis by sampling arthropods with a vacuum sampler (34531 individuals of 494 species) from an experiment in which we manipulated plant functional group richness and composition. Plant manipulations included all combinations of three functional groups (forbs, C_3 graminoids, and C_4 graminoids) removed zero, one, or two at a time from grassland plots at Cedar Creek Natural History Area, MN. Although total arthropod species richness was unrelated to plant functional group richness or composition, the species richness of some arthropod orders was affected by plant functional group composition.
Two plant characteristics explained most of the effects of plant functional groups on arthropod species richness. Nutritional quality, a characteristic related to ecosystem functioning, and taxonomic diversity, a characteristic not used to designate plant functional groups, seemed to affect arthropod species richness both directly and indirectly. Thus, plant functional groups designated for their effects on ecosystem processes will only be partially relevant to consumer diversity and abundance.

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Concerns about the effects of the widespread loss of biodiversity have prompted many recent studies investigating the relationship between biodiversity and ecosystem functioning. These studies have focused on the effects of plant diversity on such ecosystem properties as primary productivity and nutrient retention (Ewel et al. 1991, Vitousek and Hooper 1993, Naeem et al. 1994, 1995, Tilman et al. 1996, 1997a, b, Hooper and Vitousek 1997, 1998, Hooper 1998, Symstad et al. 1998). Few of these studies, however, have considered the relationships between plant diversity and the diversity and structure of higher trophic levels. Early studies of the relationships between plant and insect communities revealed the great diversity of insects that utilized just a single plant species (e.g. Southwood 1961, Claridge and Wilson 1981, Southwood et al. 1982). This work suggests and many models predict that, because a greater variety of resources may support a greater diversity of consumers, plant diversity and arthropod herbivore diversity should be positively related (e.g. Lotka 1925, Volterra 1926, Gause 1934, MacArthur 1972, Lawton 1978, Tilman 1986, Rosenzweig 1995). Some observational and experimental studies support this prediction (Murdoch et al. 1972, Nagel 1979, Southwood et al. 1979, Crisp et al. 1998, Siemann 1998, Siemann et al. 1998). Because consumer community structure may re-

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spond to aspects of plant diversity not considered in plant-ecosystem studies, it is important to understand the relationship between the concepts relevant to the effects of plant diversity on ecosystem functioning and concepts related to plant-consumer interactions.

One of the tools used for predicting the effects of plant diversity on ecosystem properties is that of functional groups – plant species grouped together based on characteristics relevant to one or more ecosystem properties (e.g. Körner 1993, Vitousek and Hooper 1993, Smith et al. 1997). Many of the characteristics used to categorize plants into functional groups, such as nitrogen use efficiency, morphology, and phenology, may also be relevant to the animals living in and consuming the plants through their effects on nutritional quality (e.g. Caswell et al. 1973, Mattson 1980), habitat structure (Lawton 1983, Strong et al. 1984), and hunting efficiency (e g. Strong et al. 1984, Russell 1989, Andow and Prokym 1990, Coll and Bottrell 1994). In a small step toward understanding the intricate web of interactions between plant diversity, consumers, and ecosystem functioning, we investigated the effect of plant functional group richness and composition on arthropod community structure in an experimental grassland study. Specifically, we tested two hypotheses. First, we predicted that a greater diversity of resources in more diverse plant communities would cause arthropod species richness to be positively related to plant functional group richness. Second, we predicted that plant functional group composition would affect arthropod community composition because of differences in morphology, nutritional quality, etc., among the plant functional groups.

Methods

Field site

This experiment was conducted at Cedar Creek Natural History Area, which lies on a glacial outwash sand plain in east-central Minnesota (Tilman 1987), about 50 km north of Minneapolis, MN, USA. The experimental plots were in an old field (Field C, Tilman 1987, Inouye et al. 1987, Siemann 1998) last cultivated in 1934 and now dominated by the following plant species: *Schizachyrium scoparium* (25% of plant cover), *Ambrosia psilostachya* (15%), *Poa pratensis* (12%), *Helianthus pauciflorus* (7%), *Solidago nemoralis* (7%), and *Artemisia ludoviciana* (5%). [Nomenclature follows Gleason and Cronquist (1991).]

Experimental design

The three plant functional groups used in this experiment, C_3 graminoids, C_4 graminoids, and forbs, comprised >99.9% of the biomass in this field. The functional classifications were operationally based on photosynthetic pathway, phenology and morphology. C_3 graminoids, mainly *Poa pratensis*, *Panicum oligosanthes*, and *Elytrigia repens* in this experiment, grow primarily during the cool part of the growing season (spring thaw to mid-June and September to snow cover), set seed by early summer, and, as a group, have higher tissue nitrogen content than C_4 graminoids (Brown 1985, Wedin and Tilman 1990, Marschner 1995, Symstad 1998). C_4 graminoids, dominated by *Schizachyrium scoparium* and *Sorghastrum nutans* in this experiment, are warm-season plants, growing from June through August, and are generally nitrogen-poor (Brown 1985, Wedin and Tilman 1990, Marschner 1995, Symstad 1998). Although all forbs in this experiment have the C_3 photosynthetic pathway, they tend to differ in their growth form and herbivore defense methods (Feeny 1976, Levin 1976, Rhoades and Cates 1976, Crawley 1983, Strong et al. 1984) from the graminoids, and in this experiment had on average the highest tissue nitrogen content of all three functional groups (Symstad 1998). The three functional groups also differed in their species richness prior to manipulations. As in native prairie (Turner et al. 1995), the most diverse functional group in this experiment was the forbs, which included 47 of the 68 species observed. The diversities of the graminoid functional groups were low and approximately equal, with 6 C_3 species and 9 C_4 species.

During the summer of 1993, 12 treatments were established in 50 4 m × 8 m plots in a completely randomized design. Seven of these treatments were used for this study. These treatments consisted of all possible combinations of zero, one, or two plant functional groups removed at a time, producing the following combinations of functional groups: C_4 graminoids only, C_3 graminoids only, forbs only, C_3 and C_4 graminoids, forbs and C_4 graminoids, forbs and C_3 graminoids, and all three functional groups (the control). Each treatment had four replicates except for the control, which had six. Initially (1993), biomass was "removed", or killed, by hand-painting a non-selective herbicide (Roundup®, Monsanto Co., St. Louis, MO) on leaves of individual plants to kill only C_3 or only C_4 graminoids or by spraying the appropriate selective herbicide (AMINE 4, Platte Chemical Co., Fremont, NE, to remove forbs; Poast Plus®, BASF Corp., Research Triangle Park, NC, to remove all graminoids). Roundup®, AMINE 4, and Poast Plus® are all nontoxic to insects (Kidd and James 1991, Anonymous 1994).

After some herbicide use early in 1994, all treatments were maintained by hand weeding from elevated platforms to minimize herbicide and trampling effects. All plots were burned in early May, 1994. Burning at Cedar Creek does not significantly change insect diversity (Siemann et al. 1997).

Sampling

Aboveground biomass of the vegetation was sampled in late August, 1995. Two 0.1 m × 3 m strips were clipped from each plot, sorted to species or litter (dead biomass), dried, and weighed. From these samples, plant species richness, total live biomass, and percentage of nitrogen (N) of the live biomass were calculated for each plot. Plant species richness was calculated by pooling the species from the two subsamples. Biomass values were summed for the two subsamples, then converted to mass per unit area. To assess tissue nitrogen, species from both clip samples in each plot were combined by functional group, ground, and analyzed for total carbon and N with a Carlo-Erba NA1500 Analyzer (Milan, Italy). Live tissue N for the plot was calculated by summing the functional group values weighted by their proportional biomass.

Arthropods were sampled on 30 June, 26 July, and 4 September, 1995. Each plot was sampled by collecting the arthropods from eight 20-cm-diameter areas (0.251 m^2 total) located in the central 2 m × 6 m area of the plot with a D-vac vacuum sampler. All specimens in the samples were sorted under a microscope to species or morphospecies within known genus or family and enumerated.

Analyses

We used simple linear regressions to test for the effects of plant functional group richness on plant characteristics (total live biomass, tissue N concentration, and species richness). To test for effects of specific plant functional groups on plant characteristics, we used three-way ANOVAs in which three categorical variables indicating the presence or absence of each plant functional group were the independent variables. A separate regression and ANOVA was performed for each plant characteristic.

All analyses relating arthropod diversity to plant community characteristics used the full season arthropod data. This corresponds to the plant data, which, because we collected it at the peak of aboveground biomass, is an average for the entire growing season. We used three types of response variables for arthropod diversity in this study: total arthropod species richness, species richness of individual arthropod orders, and species richness of trophic or taxonomic divisions of orders. For the final set of variables, we divided orders based on taxonomy or feeding characteristics. Diptera were divided into suborders, Hymenoptera into superfamilies, and Coleoptera and Hemiptera by trophic group. Trophic categories were based on personal observation and a literature review (Siemann 1997) of the species' primary food source as adults and were used for orders in which identification was secure (>99% identified to species). We did not divide the other orders due to difficulties in identification (Acari and Collembola) or trophic classification (Thysanoptera), low species richness (Orthoptera), or because their feeding characteristics are relatively uniform within the order (Araneida = predators, Homoptera = xylem/phloem-feeding herbivores, and Lepidoptera = pollen/nectar-feeding adults and foliage-chewing larvae). Although these divisions are somewhat arbitrary, they were the most reasonable to us based on our confidence in identification and the distribution of species and individuals among and within orders.

The topic of this paper is just one component of an experiment designed to test the effects of plant functional group diversity on community and ecosystem properties (Symstad 1998). Differences among the seven treatments in one of these properties, aboveground plant biomass (see Fig. 1), was apparently an artefact of the *method* of establishing this experiment (biomass removal), and not necessarily an effect of plant functional group diversity per se. Because of this artefact and because plant biomass could be important to arthropod community structure, we used total live plant biomass as a covariate in all analyses of variance. Thus, our analyses testing for the effects of plant functional group richness and composition on arthropod species richness and community composition consisted of the following. First, we used one-way analysis of covariance (ANCOVA) to test for differences in total arthropod species richness among the seven experimental treatments. Second, we used three-way ANCOVAs to test for the effects of individual plant functional groups and their two-way interactions

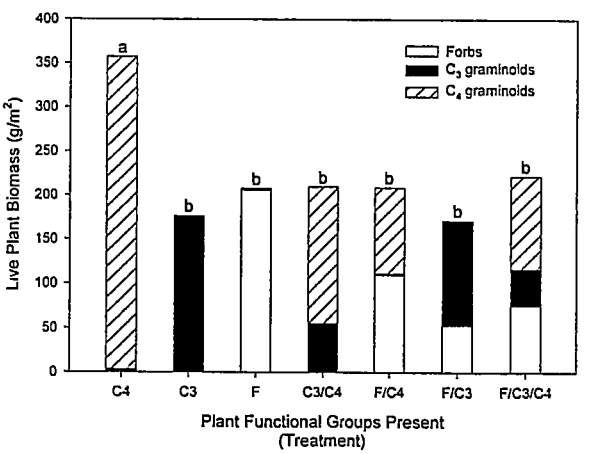

Fig. 1. Mean aboveground plant biomass, by functional group, for each of the seven experimental treatments. Labels under each bar indicate the plant functional group(s) present in the treatment, where C4 = C_4 graminoids, C3 = C_3 graminoids, and F = forbs. Letters above the bars indicate significant differences ($p < 0:05$) in total aboveground plant biomass among treatments according to a one-way ANOVA on treatment ($F = 4.34$, df = 6, 23, $p = 0.004$) and Tukey comparison of means.

on total arthropod species richness and on species richness of the arthropod groups. Because none of the interaction terms were significant for any arthropod groups, we then used three-way ANCOVAs without the interactions to increase the power of the analysis to detect effects of individual plant functional groups. In addition to these ANCOVAs, we also used stepwise multiple regressions to test for the relationship between arthropod diversity and the measured plant characteristics (live aboveground biomass, species richness, and tissue N concentration) in order to more thoroughly understand any significant effects of specific plant functional groups. Although stepwise regression can change experiment-wide error, it has the advantage of being both exploratory and confirmatory.

Because interactions among arthropods may also affect their community structure, we looked for gross relationships in species richness between all possible pairs of taxonomic orders using Pearson correlation coefficients. Finally, we used ANCOVAs and multiple regressions of parasitoid species richness on plant community characteristics and the species richness of the parasitoids' probable hosts to explore for possible indirect effects of plants on higher trophic levels through the herbivore trophic level.

Two aspects of the experimental design, small plot size and spatial characteristics of the field, may also have contributed to the results we observed. First, because of the small area in which this experiment was performed, it is possible that the arthropods present in a plot were simply random subsamples of the individuals in the field (Siemann et al. 1998). To test for this possibility, we used a multivariate analysis of variance (MANOVA) with ten response variables (Acari abundance/total abundance, Coleoptera abundance/total abundance, etc.) to test whether the proportion of arthropod individuals in different taxonomic orders differed among treatments as they might if our treatments influenced community structure. A significant result of this MANOVA indicated that the arthropods in a plot were not random subsamples of individuals from the whole field community (Morin 1983, Siemann et al. 1998). Second, because the arthropod species in plots may have been spatially autocorrelated, we tested whether the difference in total arthropod species richness and the similarity of arthropod species composition (Jaccard index of similarity) between two plots was related to the distance between the centers of the plots (Siemann et al. 1998). In addition, because there may have been patterns of arthropod diversity at scales larger than the experimental plots, we tested whether a plot's arthropod species richness depended on its location within the experiment.

All statistical analyses were done with SAS version 6.09 (SAS Institute 1989). ANOVAs and analyses of covariance were done with the GLM procedure and least-squares regressions were performed with the REG procedure. Multiple regression models were checked for multicollinearity using the following two criteria: variance inflation factor $< 1/(1 - r^2)$, where r^2 is the squared correlation coefficient of the whole model; and condition index < 30 (Freund and Littell 1991). Models discussed in this paper included only variables that met these criteria. When applicable, significance tests from ANOVAs and correlation analyses were adjusted for multiple comparisons by using the sequential Bonferroni correction, which controls experiment-wide error (Rice 1989).

Results

Plant characteristics

As expected, the experimental manipulations resulted in changes in plant community composition among the treatments (Fig. 1). However, plant functional group richness and composition affected only some of the three plant characteristics measured for this study. Only plant species richness was significantly related to plant functional group richness (species richness $= 12.14 + 3.14 \times$ functional group richness; $n = 30$, $r^2 = 0.13$, $p = 0.049$). Aboveground plant biomass and tissue nitrogen content of the live biomass were not related to plant functional group richness ($p > 0.05$). Three-way ANOVAs on the presence or absence of each plant functional group showed significant effects of specific functional groups on two of the three vegetation characteristics. The presence of forbs increased plant species richness ($F = 16.38$, df $= 1, 26$, $p = 0.0004$) and tissue N concentration ($F = 14.71$, df $= 1, 26$, $p = 0.0007$), and the presence of C_4 graminoids decreased tissue N concentration ($F = 108.92$, df $= 1, 26$, $p < 0.0001$). Aboveground biomass was not related to the presence or absence of a single plant functional group, but the treatment with just C_4 graminoids did have significantly higher biomass than the other treatments (Fig. 1).

Total arthropod species richness

In total, arthropod sampling caught 34531 individuals of 494 species in 15 orders (Table 1). A simple linear regression of total arthropod species richness on plant functional group richness showed that the two were unrelated in this experiment ($r^2 = 0.0001$, $n = 30$, $p = 0.96$). Functional group composition also did not affect total arthropod species richness; there were no significant differences among treatments (one-way ANCOVA with live biomass as the covariate: $F = 2.00$, df $= 6, 23$, $p = 0.11$) and no significant effects of specific functional groups ($p > 0.05$ for all three functional groups in three-way ANCOVA; Fig. 2A). Total arthropod species richness also was not related to any of the measured

Table 1. The number of arthropod species and individuals within taxonomic orders and divisions of orders in this study.

Order	Species	Individuals
*Acari (mites and ticks)	7	571
Araneida (spiders)	31	1977
Coleoptera (beetles)	69	849
herbivorous	45	524
non-herbivorous	24	325
*Collembola (springtails)	6	3952
Diptera (flies)	94	6867
Nematocera	22	3455
Brachycera	72	3412
Hemiptera (bugs)	52	1679
herbivorous	42	1277
predaceous	10	402
Homoptera (leafhoppers, aphids)	65	7851
Hymenoptera (wasps, bees, ants)	105	9196
Ichneumonoidea	25	113
Chalcidoidea	30	1193
Proctotrupoidea	22	533
Formicoidea	13	7288
≠ miscellaneous	14	66
Lepidoptera (moths, butterflies)	31	336
*Neuroptera (lacewings)	3	60
*Odonata (dragonflies, damselflies)	2	2
Orthoptera (grasshoppers, crickets)	19	600
*Pseudoscorpiones	1	50
*Psocoptera (barklice)	3	42
*Thysanoptera (thrips)	6	499
Total	494	34531

* These orders were not included in analyses by order because of low species richness.
≠ This group was not included in statistical analyses because of low abundance and wide variety of feeding habits.

plant characteristics (live biomass, tissue N concentration, and plant species richness; $p > 0.05$ for all parameters).

Species richness of arthropod groups

Orders with low species richness (< 2% of the total) were not included in the analyses for arthropod groups (Table 1). Those orders included in the analyses, therefore, were the Araneida, Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, and Orthoptera.

As with total arthropod diversity, species richness of individual orders was generally not related to the number of plant functional groups in the community. Only the Homoptera were affected by plant functional group richness [Homoptera species richness = 14.61 + 1.61 × (functional group richness); $r^2 = 0.14$, $F = 4.50$, df = 1, 28, $p = 0.04$]. Plant functional group composition affected more orders, however. When effects of live biomass were accounted for, Coleoptera and Homoptera species richness increased in the presence of forbs, and Hemiptera and Hymenoptera species richness decreased in the presence of C_4 graminoids (Fig. 2, Table 2). Significant relationships between the diversity of arthropod orders and the measured plant characteristics were generally consistent with the plant functional group effects. Coleoptera and Homoptera species richness were positively related to plant species richness, (Fig. 3A, B, Table 2) and Hemiptera species richness was positively related to tissue N concentration (Table 2). Hymenoptera diversity was positively related to both tissue N concentration and live plant biomass (Table 2).

Dividing orders into smaller groups increased the resolution of plant functional group composition effects on arthropod diversity in two ways. First, for Coleoptera, Hemiptera, and Hymenoptera, it suggested which part of an order may have caused the significant effect of a plant functional group on the order as a whole. The species richness of herbivorous Coleoptera increased significantly in the presence of forbs, whereas the diversity of Chalcidoidea (Hymenoptera) and herbivorous Hemiptera was lower in the presence of C_4 graminoids (Table 3). Second, dividing orders into smaller groups also brought out a significant effect of plant functional group composition on arthropod diversity that was hidden by the whole-order analysis. This was true for the Ichneumonoidea (Hymenoptera), for which species richness was negatively related to the presence of C_3 graminoids (Table 3).

Plant functional group effects and relationships between the diversity of these arthropod groups and plant characteristics were again generally consistent (Table 3). The species richnesses of herbivorous Coleoptera and Ichneumonoidea (Hymenoptera) were positively related to plant species richness (Fig. 3C, D). Diversity of the herbivorous Hemiptera and of Chalcidoidea (Hymenoptera) were positively related to tissue N concentration. Chalcidoid species richness was also positively related to live biomass. Although there was no significant effect of plant functional group composition on either of the divisions of Diptera, nematoceran species richness was positively related to live biomass.

Only two of the 28 pairs of taxonomic orders showed significant correlations in species richness. Both Diptera and Hymenoptera species richness were significantly, positively related to the species richness of Lepidoptera ($r^2 = 0.36$ and 0.33, $p = 0.0005$ and 0.0008, respectively; $n = 30$.) Some of the correlation between Hymenoptera and Lepidoptera species richness is explained by significant, positive relationships between the two most diverse superfamilies of Hymenoptera (Chalcidoidea and Ichneumonoidea) and Lepidoptera [Chalc SR = 5.02 + 0.35 × Lep SR; $r^2 = 0.13$, $n = 30$, $p = 0.0495$; Ichneum SR = 0.49 × Lep SR (intercept not significant); $r^2 = 0.29$, $n = 30$, $p = 0.002$]. Both the Chalcidoidea and the Ichneumonoidea frequently parasitize Lepidoptera lar-

vae. However, the diversity of these two superfamilies seemed to be influenced differently by host diversity and plant community characteristics. For the Ichneumonoidea, accounting for potential host species richness eliminated the significance of either plant species richness ($F = 3.38$, df = 1, 27, $p = 0.08$) or the presence of C_3 graminoids ($F = 3.92$, df = 1, 27, $p = 0.06$; separate models). In contrast, live plant biomass and C_4 graminoid presence remained significant predictors of Chalcidoid diversity when host species richness was accounted for (biomass: $F = 18.41$, $p < 0.001$; C_4 presence: $F = 10.60$, $p = 0.003$; Lepidoptera species richness: $F = 9.16$, $p < 0.006$; df = 1, 26 for each variable).

Tests for artefacts

The arthropod assemblages of plots were not random subsets of the total field community. In a MANOVA, the proportion of individuals or species in taxonomic orders differed significantly among treatments (proportion of individuals: Hotelling-Lawley Trace $F = 5.57$, df = 60, 74, $p < 0.0001$, proportion of species: Hotelling-Lawley Trace $F = 3.17$, df = 60, 74, $p < 0.0001$).

Processes at larger scales than single plots may have influenced arthropod community composition. The similarity in species composition between pairs of plots, measured by the Jaccard index (J), decreased as the distance between centers of plots increased ($J =$

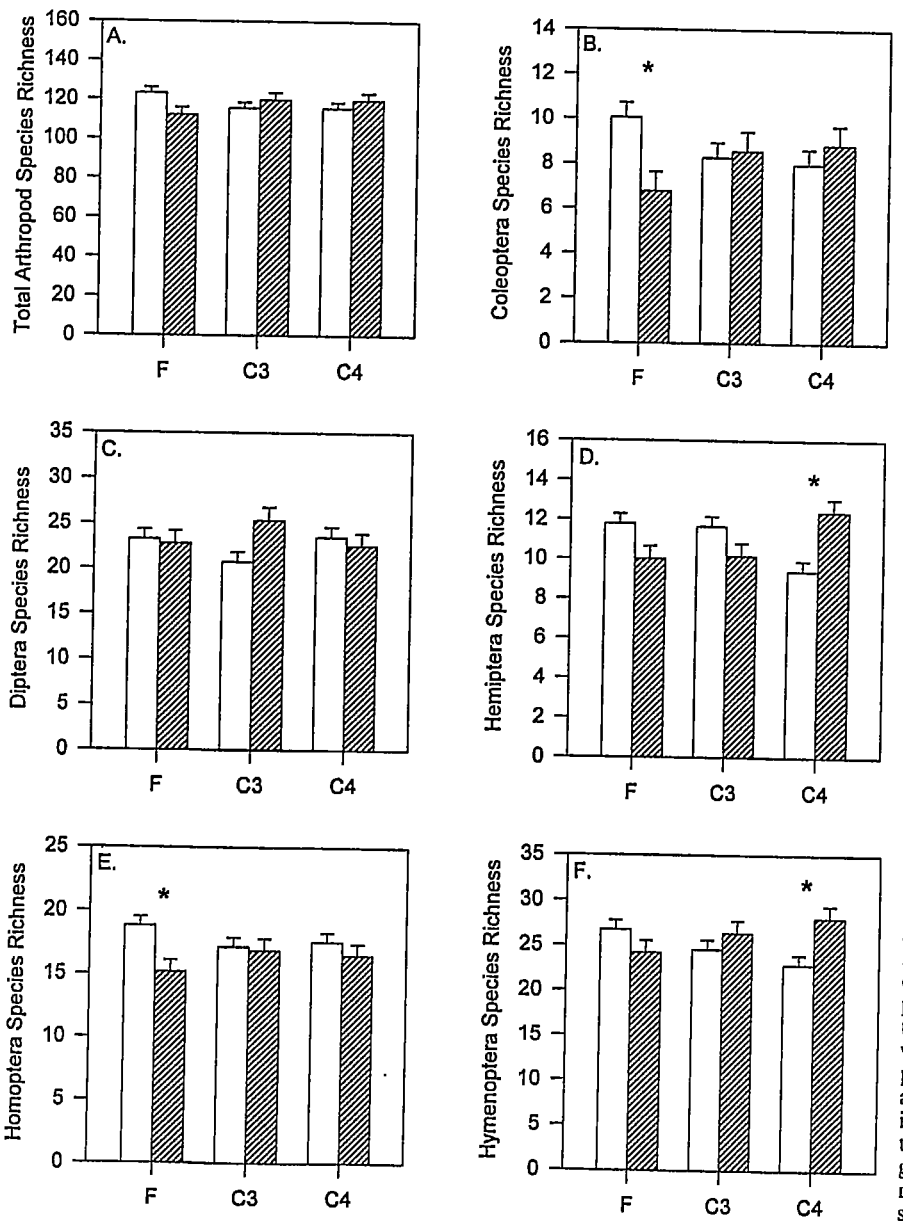

Fig. 2. Three-way ANCOVAs of plant functional group effects on total arthropod species richness and the species richness of the five most diverse orders. Least squares means plus 1 se are shown for treatments with (open bars) or without (hatched bars) each plant functional group. An asterisk above a pair of bars indicates a significant effect of the presence of that functional group on arthropod species richness. See Table 2 for statistics.

Table 2. Significant relationships between plant functional groups or plant characteristics and species richness of arthropod orders. Plant functional group effects were determined using three-way ANCOVAs with live plant biomass as a covariate. Relationships between arthropod diversity and plant characteristics were determined using stepwise multiple regressions in which plant species richness, live plant biomass, and tissue N concentration were the possible predictor variables. For both the ANCOVAs and regressions, only the variable(s) with significant effects are shown [$p<0.012$ for ANCOVAs (sequential Bonferroni correction), $p<0.05$ for regressions].

Order	Three-way ANCOVA			Multiple regression			
	Functional group	F	p	Characteristic	Parameter	r^2	F
Araneida	none	–	–	none	–	–	–
Coleoptera	+Forbs	9.13	0.006	plant species richness	0.22	0.24	8.66**
Diptera	none	–	–	none	–	–	–
Hemiptera	$-C_4$ graminoids	13.24	0.001	tissue N concentration	6.10	0.35	15.16***
Homoptera	+Forbs	9.25	0.006	plant species richness	0.18	0.14	4.38*
Hymenoptera	$-C_4$ graminoids	8.80	0.006	live plant biomass‡	0.04	0.27	9.75**
				tissue N concentration‡	11.63	0.25	8.94**
Lepidoptera	none	–	–	none	–	–	–
Orthoptera	none	–	–	none	–	–	–

+/− sign in front of a plant functional group indicates a positive/negative effect of that functional group on the order's species richness. df = 1, 25 for F-values in the ANCOVAs and 1, 28 for the multiple regressions. * $0.05>p\geq0.01$; ** $0.01>p\geq0.001$; *** $p<0.001$. ‡r^2 are partial correlation coefficients; for full model, $F=6.09$, df = 2, 27, $p=0.007$.

$0.376-0.00091$ distance (m), $F=18.5$, df = 1, 433, $p<0.0001$, $r^2=0.04$). The difference in total arthropod species richness between two plots was also related to the distance between the plots ($\Delta SR = 10.4+0.184$ distance (m), $F=17.8$, df = 1, 433, $p<0.0001$, $r^2=0.04$). There was no significant effect of plot location on total arthropod diversity ($p>0.5$ for both east-west and north-south variables in regression).

Discussion

Although many ecological theories predict that increasing plant diversity should increase the diversity of higher trophic levels (e.g. Lotka 1925, Volterra 1926, Gause 1934, MacArthur 1972, Whittaker 1975, Tilman 1986, Rosenzweig 1995), total arthropod species richness was insensitive to the number and types of plant functional groups present in the community in this experiment. The species richness of most individual arthropod orders was also unrelated to plant functional group richness, but was affected by plant functional group composition. Characteristics associated with the plant functional groups generally explained the associations between certain plant and arthropod groups, but the significant characteristics were not always those on which the plant functional group classifications were based.

Total arthropod species richness

The lack of a relationship between plant functional group richness and total arthropod species richness in this experiment at first glance seems contrary to the results of a related experiment in the same ecosystem (Tilman et al. 1997b), which found a significant, positive relationship between total arthropod species richness and plant functional group richness (Siemann et al. 1998). They suggested, however, that this relationship may have been caused by a confounding relationship between plant functional group richness and plant species richness because plant species richness, but not functional group richness, was a significant predictor of total arthropod species richness when both were included in the same analyses.

The lack of an effect of plant functional group diversity that was found in both of these experiments suggests that the categorizations of plant species into functional groups used in their experiment (C_3 grasses, C_4 grasses, legumes, non-legume forbs, and woody plants-see Tilman et al. 1997b for details) and ours are less relevant to the arthropods living on the plants than to ecosystem processes. For example, many herbivorous insects feed on only one or a few species of plants, rejecting even those in the same genus or family (e.g. Wilcox 1979, Price 1984, Strong et al. 1984, Dixon 1985, Tabashnik and Slansky 1987). For many herbivore species, and in turn herbivore species richness, the presence or absence of particular suitable host plants may be poorly predicted by the presence or absence of functional groups. In both experiments, however, functional group composition or richness did affect some ecosystem properties (Tilman et al. 1997b, Symstad 1998).

Plant and arthropod community composition

Although the species richnesses of some individual insect orders were related to plant functional group composition (Table 2, Fig. 1), the effects seemed to be relatively subtle because there were no gross shifts in species richness from one order to another across the

whole experiment (no significant negative correlations between pairs of orders). Instead, certain groups of insects responded to individual plant functional groups, either directly through the plant resources or perhaps indirectly through plant effects on the species richness of their hosts.

Both the species richness of the Homoptera and of the Coleoptera (likely driven by their herbivorous components) responded positively to the presence of forbs (Table 2, Fig. 1). This was not surprising for the Coleoptera, since all of the species for which we could identify host plants are forb-feeders. The positive effect of forbs on homopteran species richness is less easy to explain because, of the ten most abundant species in our experiment, eight are grass feeders. However, we could not reliably identify host plants for 61% of the homopteran species that we collected. Thus, the increased species richness of the Homoptera in the presence of forbs may be due to these rarer species. It is also difficult to know what characteristic of the forbs the Homoptera were responding to, since forbs differ from grasses in many ways. The positive response of Homoptera species richness to plant species richness (Fig. 3B, Table 2) suggests that the forbs' taxonomic diversity was more important to homopteran diversity than was higher plant N concentration, which also was positively related to forb presence. "Top-down" effects (e.g., Cramer and May 1972, Roughgarden and Feldman 1975, Levin et al. 1977, Tilman 1986, Holt et al. 1994, Leibold 1996, Siemann 1998, Siemann et al. 1998) of predators and parasites may also have been a factor influencing homopteran species richness. Although species richness of the predaceous or parasitic groups were unrelated to forb presence or Homoptera species richness, their foraging efficiencies and/or patch selection by Homoptera may have been impacted by the presence of forbs (e g., Strong et al. 1984, Russell 1989, Andow and Prokym 1990, Coll and Bottrell 1994).

The negative effect of C_4 graminoids on herbivorous Hemiptera species richness, and therefore on the diversity of Hemiptera as a whole, seems partially due to the C_4 graminoids' low nutritional quality. Not only do the C_4's have low tissue nitrogen compared to the forbs and C_3 graminoids, but their specialized anatomy may prevent many species from feeding on them (Caswell et al. 1973, Mattson 1980). The positive response of herbivorous hemipteran species richness to plant tissue N concentration (Table 3) supports this explanation. However, since only 13 of the 30 herbivorous hemiptera species for which we could identify host plants feed on graminoids, other factors must have also been important in determining hemipteran species richness.

The significant effects of plant functional group composition on two groups of parasitic Hymenoptera, the Ichneumonoidea and the Chalcidoidea (Table 3), seem to have been caused at least partly by plant effects on their host species. The majority of species that we collected in both of these superfamilies parasitize Lepidoptera (Sweetman 1936, Clausen 1940, Askew 1971), thus potentially producing the positive correlation between Hymenoptera and Lepidoptera species richness. For ichneumonoid diversity, this relationship between host and parasite species richness eliminated the predictive power of any plant characteristics we measured. This suggests that the plants affected parasite diversity through the herbivore trophic level. On the other hand, plant biomass and the presence of C_4 graminoids still explained a significant portion of chalcidoid species

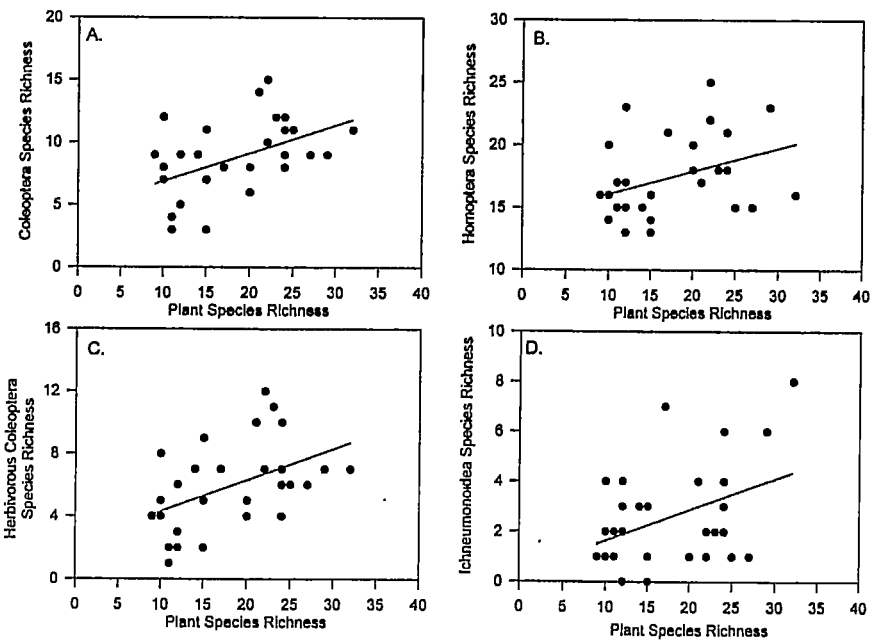

Fig. 3. Effects of plant species richness on species richness of some arthropod groups. Lines represent least-squares regressions, and all are significant. See Tables 2 and 3 for statistics.

Table 3. Significant relationships between plant functional groups or plant characteristics and species richness of arthropod order divisions. Plant functional group effects were determined using three-way ANCOVAs with live, aboveground plant biomass as a covariate. Relationships between arthropod diversity and plant characteristics were determined using stepwise multiple regressions in which plant species richness, live plant biomass, litter biomass, and tissue N concentration were the possible predictor variables. For both the ANCOVAs and regressions, only the variable(s) with significant effects are shown ($p<0.012$ for ANCOVAs (sequential Bonferroni correction), $p<0.05$ for regressions].

Division	Three-way ANCOVA			Multiple regression			
	Functional group	F	p	Characteristic	Parameter	r^2	F
Coleoptera							
herbivorous	+ Forbs	11.35	0.002	plant species richness	0.20	0.23	8.19**
non-herbivorous	none	–	–	none	–	–	–
Diptera							
Nematocera	none	–	–	plant biomass	0.012	0.23	8.46**
Brachycera	none	–	–	none	–	–	–
Hemiptera							
herbivorous	− C_4 graminoids	13.10	0.001	tissue N concentration	5.12	0.30	11.84**
predaceous	none	–	–	none	–	–	–
Hymenoptera							
Ichneumonoidea	− C_3 graminoids	8.15	0.008	plant species richness	0.12	0.16	5.31*
Chalcidoidea	− C_4 graminoids†	8.35	0.008	tissue N concentration‡	4.80	0.23	10.57***
				plant biomass‡	0.020	0.18	6.29***
Proctotrupoidea	none	–	–	none	–	–	–
Formicoidea	none	–	–	none	–	–	–

+/− sign in front of plant functional group indicates a positive/negative effect of that functional group on the order's species richness. df = 1, 25 for F-values in the ANCOVAs and 1, 28 for the multiple regressions. * $0.01 \leq p < 0.05$; ** $0.001 \leq p < 0.01$; *** $p < 0.001$. †Plant biomass was a significant factor in this ANCOVA: $F = 16.66$, $P = 0.0004$. ‡r^2 are partial correlation coefficients; for full model, $F = 9.51$, df = 2, 27, $P = 0.0007$.

richness even when host diversity was accounted for. Thus, these plant characteristics may have had a direct effect on the chalcidoids. The group's species richness may have been negatively affected by the presence of C_4 graminoids through a reduction in forb biomass, which is an index of floral resources for the adult chalcidoids (e.g. Sweetman 1936, Clausen 1940, Price et al. 1980, Powell 1986, Jervis et al. 1993). Although we cannot be sure of the exact mechanisms for any of the patterns in parasitoid species richness we found, the results of our experiment suggest that plant functional group composition affected higher trophic levels through both direct and indirect effects.

Artefacts

Although the absolute location of a plot within the experiment did not affect total arthropod species richness, plots near each other were more similar in arthropod species composition (as measured by the Jaccard Index) and species richness than were plots far from each other. This similarity in species composition may be explained by a gradient in plant species composition across the experiment (A. Symstad pers. obs.). The low r^2 values for these spatial effects (0.04 for both) suggest that the importance of spatial autocorrelation for explaining our results is low.

Categorizing plants for higher trophic levels vs ecosystem functioning

The lack of a relationship between plant functional group richness and arthropod diversity in this direct experimental test seems to suggest a less than perfect concordance between the characteristics that higher trophic levels respond to and the characteristics commonly used to designate plant functional groups for their effects on ecosystem functioning. Significant effects of the presence or absence of particular plant functional groups on the diversity of taxonomic and trophic groups of arthropods, however, imply that for some groups the similarity may be substantial. Tissue nitrogen concentration, a characteristic used to designate functional groups because of its effects on ecosystem processes, was significantly correlated with arthropod diversity of some groups. Caution should be used in generalizing this relationship, however, because total tissue N of a plant does not indicate nutritional quality for all herbivorous insects, since different guilds (e.g. sucking insects, leaf miners, chewing insects) feed on different parts of a plant. On the other hand, the forb functional group apparently affected the diversity of some arthropod groups simply because a disproportionate number of species in some arthropod groups fed on forbs, or perhaps because of the forbs' high taxonomic diversity. Neither was a characteristic used to designate functional groups. Thus, because plant func-

tional groups designated for their effects on ecosystem functioning will only be partially relevant to consumer diversity and abundance, there is still considerable work to be done in relating plant-ecosystem functioning concepts to plant-consumer diversity interactions.

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