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Contrasting Effects of Plant Richness and Composition on Insect Communities: A Field Experiment

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abstract: We experimentally separated the effects of two components of plant diversity—plant species richness and plant functional group richness—on insect communities. Plant species richness and plant functional group richness had contrasting effects on insect abundances, a result we attributed to three factors. First, lower insect abundances at higher plant functional group richness were explained by a sampling effect, which was caused by the increasing likelihood that one low-quality group, C_4 grasses, would be present and reduce average insect abundances by 25%. Second, plant biomass, which was positively related to plant functional group richness, had a strong, positive effect on insect abundances. Third, a positive effect of plant species richness on insect abundances may have been caused by greater availability of alternate plant resources or greater vegetational structure. In addition, a greater diversity of insect species, whose individual abundances were often unaffected by changes in plant species richness, may have generated higher total community abundances. After controlling for the strong, positive influence of insect abundance on insect diversity through rarefaction, insect species richness increased as plant species richness and plant functional group richness increased. Although these variables did not explain a high proportion of variation individually, plant species richness and plant functional group richness had similar effects on insect diversity and opposing effects on insect abundances, and both factors may explain how the loss of plant diversity influences higher trophic levels.

Keywords: abundance, composition, diversity, functional groups, insects, species richness.

The loss of plant diversity has been reported to cause higher insect abundances, particularly abundances of specialist insect pests (Elton 1958; Pimentel 1961; Root 1973; Kareiva 1983; Risch et al. 1983; Strong et al. 1984; Andow 1991), and to lower insect species richness (Murdoch et al. 1972; Southwood et al. 1979; Strong et al. 1984; Siemann et al. 1998; Knops et al. 1999). Herbivore abundances are thought to be higher in plant monocultures, where specialist herbivores are more likely to find and to remain on their hosts and/or generalist predators are less abundant (Root 1973). Empirical studies have shown that specialist herbivores have higher reproductive rates and higher immigration into but lower emigration from monocultures than polycultures (Bach 1980*a*, 1980*b*, 1984; Risch 1981; Kareiva 1985; Elmstrom et al. 1988). Insect species richness, especially the richness of specialist herbivores, is thought to increase with increasing plant species richness because a greater diversity of plants provides a greater diversity of resources for insects (Murdoch et al. 1972; Southwood et al. 1979; Strong et al. 1984; Siemann et al. 1998; Knops et al. 1999). Higher diversity of herbivorous insects may then support a higher diversity of insect predators and parasitoids (Hunter and Price 1992; Knops et al. 1999).

Despite this previous work, it remains unclear whether these changes in insect communities are driven more by changes in the number of plant species or changes in plant community composition that are usually associated with changes in plant diversity. Interest in this question has emerged from recent studies of effects of plant biodiversity, which have shown that plant community composition can strongly affect ecosystem processes (e.g., Tilman et al. 1997*b*; Hooper and Vitousek 1998; Symstad et al. 1998). Plant composition is often determined by separating plants into functional groups, that is, groups of species that differ in physiology, phenology, and morphology—and thus also in their effects on ecosystem processes (Chapin et al. 1996). One important conclusion of recent studies is that the effects of diversity on ecosystem properties may result from both changes in the number of species and changes in plant functional group composition (Hooper and Vitousek

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1997, 1998; Tilman et al. 1997*b*; Symstad et al. 1998; Hector et al. 1999).

Although plant functional groups in these studies were not chosen specifically for their effects on insects, insects might be expected to respond to changes in plant functional group composition for two reasons. First, plants within the same functional group, which are often determined with respect to plant resource use, have some similarities in tissue quality. For example, legumes are typically separated from other forbs because they fix nitrogen. Their high tissue nitrogen would then provide a higher-quality resource for herbivores (e.g., Mattson 1980; Strong et al. 1984). Likewise, grasses are often divided by their photosynthetic pathway (which also corresponds to differences in growing season). Warm-season grasses that photosynthesize via the C_4 pathway generally have low tissue nitrogen, higher toughness, and structural characteristics that protect starches and nutrients from herbivores (Caswell et al. 1973). Thus, they are poorer-quality food resources for herbivores (Boutton et al. 1978; Kroh 1978; Pinder and Kroh 1987). The second reason insect communities might respond to plant composition is that functional groups separate plants into species that are more similar taxonomically. Insects are often specialists within a plant genus or family, and functional groups encompass the food plants of these herbivores.

We tested two primary hypotheses regarding the effects of plant species richness, plant functional group richness, and plant functional group composition on insect communities in a grassland experiment. First, we tested the hypothesis that higher plant diversity causes lower total insect abundances and that the negative effects of plant diversity are best explained by higher plant functional group richness rather than by higher plant species richness. This hypothesis arises from work in agroecosystems, where monocultures have higher insect abundances (measured either for individual species or for the entire insect community) than polycultures composed of very different plant functional groups, such as corn (grass), beans (legume), and squash (forb; Bach 1980*a*; Risch 1981; Andow 1990), or agricultural crops and weeds (Pimentel 1961; Tahvanainen and Root 1972; Root 1973). If, as we hypothesized, higher plant functional group richness causes lower total insect abundances and explains the negative relationship between plant diversity and insect abundances, then changes in plant species richness within functional groups would have no effect on insect abundances. An alternative hypothesis is that plant species richness has an opposite, positive effect on total insect abundances. This hypothesis has some support from evidence of associational susceptibility, whereby a less preferred host attracts more herbivores in polyculture because it is planted with a more preferred host (Bach 1980*b*; Brown and Ewel 1987; Wahl and Hay 1995) and from evidence of polycultures increasing abundances of generalist herbivores that can exploit alternative hosts (Risch 1981).

Our second primary hypothesis was that higher plant species richness, rather than higher plant functional group richness, best explains higher insect species richness. In other experiments, insect species richness has been shown to be positively related to plant species richness (Knops et al. 1999) and to plant functional group richness (Siemann et al. 1998; Symstad et al. 2000). We did not replicate the results of previous studies. Here, we separated the effects of plant species richness, plant functional group richness, and plant functional group composition on insect diversity. Our hypothesis that plant species richness has the strongest positive effect on insect species richness was based on the observation that the diversity of insects is often correlated with the diversity of resources (e.g., Murdoch et al. 1972; Strong et al. 1984; Siemann et al. 1998; Knops et al. 1999), regardless of plant functional types. In addition to studies of the entire insect community, we also analyzed the responses of the abundance and diversity of each insect trophic group and herbivore feeding guild.

The two community attributes that are the focus of this article, insect species richness and insect abundance, may each help to inform the response of the other factor. Insect species richness is often positively correlated with total insect abundance because sampling more individuals leads to higher counts of species. In our analyses of total insect species richness, we used rarefaction to estimate insect species richness before testing for effects of plant species richness, plant functional group richness, or plant composition. Knowledge of the number of species may in turn help to interpret responses of insect abundances in the entire community. Most previous studies of insect responses to plant diversity have focused on one insect species (Tahvanainen and Root 1972; Bach 1980*a*; Risch 1981; Andow 1991; but see Root 1973). We examined the responses of several of the most abundant individual herbivore species to plant species richness and plant functional group richness, as well as responses of the entire insect community. The total insect community integrates the individual responses of many insect species, and the mean response of insects per species provides a standard to compare effects of plant diversity on total community abundance to the numerical responses of individual species.

Material and Methods

Plant Species Richness × Plant Functional Group Richness Experiment

To separate the effects of plant diversity on insects, we studied insect communities in a well-replicated, randomized experiment where both plant species richness and plant functional group richness were manipulated (described in Tilman et al. 1997*b*; Siemann et al. 1998; Knops et al. 1999). The experiment was developed to test for effects of plant biodiversity on a host of community and ecosystem properties, including responses of insects. The experiment was conducted at Cedar Creek Natural History Area in east-central Minnesota and consisted of 342 experimental plots, each 169 m^2, that formed an 18 × 19-plot grid. The experiment was created in 1994 when plots were planted with either zero, one, two, four, eight, 16, or 32 perennial, savannah grassland species representing zero to five functional groups (table 1; Tilman et al. 1997*b*). Insects were sampled in 285 of the 342 plots that were designed to separate the effects of plant species richness and plant functional group richness. Plots were created in three ways. First, we created 163 plots by randomly drawing one, two, four, eight, or 16 species from a pool of 18 species that represented five functional groups. Second, to balance the design with a similar number of plots containing each combination of plant species richness and plant functional group richness, we created 76 additional plots by first randomly drawing one to three functional groups (from the pool of five functional groups) and then randomly drawing two, four, or eight species in those functional groups that were contained in a larger pool of 34 species. The expanded pool of species was needed to create, for example, plots with eight species from one functional group, which was not possible in random draws from the pool of 16 species. Third, we created 46 additional plots with the highest level of plant species richness and plant functional group richness by planting 32 species chosen from the pool of 34 species. We attempted to maintain treatment levels by periodic removal of weeds and application of herbicides, and four species with poor germination success were replaced in 1995. However, because all species did not germinate in all plots where they were planted and because weeding did not eradicate all unwanted species, imposed levels of plant species richness were approximate. All plots were burned in May 1997 to prevent litter accumulation, which could affect plant species composition. We recognize that burning could influence insect communities. Siemann et al. (1997) found individualistic responses of many species to fire at Cedar Creek; however, they found little effect of fire frequency on total insect species richness or abundance. In addition, in a review of the history of fire at Cedar Creek, Tilman et al. (2000) found evidence for annual to biennial burn frequency.

Table 1: Plant species and their functional group designations in the experiment

Plant species	Plant functional group
Achillea millefolium	Forb
Agropyron repens	C_3 grass
Agropyron smithii	C_3 grass
Amorpha canescens	Legume
Andropogon gerardii	C_4 grass
Asclepias tuberosa	Forb
Astragalus canadensis	Legume
Baptisia leucantha	Legume
Bouteloua curtipendula	C_4 grass
Bouteloua gracilis	C_4 grass
Bromus inermis	C_3 grass
Buchloe dactyloides	C_4 grass
Calamagrostis canadensis	C_3 grass
Coreopsis palmata	Forb
Elymus canadensis	C_3 grass
Koeleria cristata	C_3 grass
Leersia oryzoides	C_3 grass
Lespedeza capitata	Legume
Liatris aspera	Forb
Lupinus perennis	Legume
Monarda fistulosa	Forb
Panicum virgatum	C_4 grass
Petalostemum candidum	Legume
Petalostemum purpureum	Legume
Petalostemum villosum	Legume
Poa pratensis	C_3 grass
Quercus ellipsoidalis	Woody
Quercus macrocarpa	Woody
Rudbeckia hirta	Forb
Schizachyrium scoparium	C_4 grass
Solidago nemoralis	Forb
Solidago rigida	Forb
Sorghastrum nutans	C_4 grass
Sporobolus cryptandrus	C_4 grass
Stipa spartea	C_3 grass
Vicia villosa	Legume
Zizea aurea	Forb

Plant species were classified into five functional groups based on their physiological, phenological, and morphological characteristics, which included their resource requirements, seasonality of growth, and life history. Functional groups were chosen based on plant attributes within ecosystems and not with respect to their impacts on insects. However, the classification organized plants in ways that have relevance to insects, particularly in their taxonomic relatedness and in their relative tissue quality. Cool-season grasses that photosynthesize via the C_3 pathway have higher tissue nitrogen than do warm-season grasses that photosynthesize via the C_4 pathway. Forbs are herbaceous dicots. Legumes are forbs that fix nitrogen, the limiting nutrient at Cedar Creek (Tilman 1987). Woody plants produce a perennial stem.

Plant community and nutrient responses to the manipulations were described in Tilman et al. (1997*b*). In each plot, we estimated actual plant species richness and percentage cover by each plant species in four 0.5 × 1-m subplots and then took the average values from the four subplots to generate one estimate per plot. We measured peak aboveground living plant biomass (a strong correlate of aboveground plant productivity because there was little overwintering aboveground production) by clipping four 0.1 × 3.0-m strips per plot that were then combined, dried to a constant dry weight at 55°C, and weighed. To measure plant tissue nitrogen and carbon, plant samples were ground and analyzed on a Carlo Erba NA 1500 elemental analyzer (Carlo Erba Instruments, Milan).

Insect Samples

Insects and terrestrial arthropods were collected three times during the season of greatest plant production, on June 20, July 28, and August 22, 1997. We swept each of the 285 plots with a 38-cm-diameter muslin net, which we swung 25 times while walking in a line 3 m from the plot edge. We swept plots rather than sampling by another method (like suction sampling) because we decided to cover a larger area that would better represent plot level characteristics of the plant and insect community and because previous work at Cedar Creek has demonstrated that insect community responses to changes in diversity were similar when insects were collected by sweeping or by a D-vac (Siemann 1998; N. M. Haddad, unpublished data). One bias of sweep sampling is against some leaf minors and galling insects, which are often specialized and would thus respond to changes in plant species richness and resource concentration. Specimens were identified to species or morphospecies within known genera or families and counted.

Insect abundance was quantified as the total number of individuals. A second analysis that is not presented here quantified insect abundance as insect biovolume, an approximation of biomass, which was calculated as the average product of the maximum length, width, and thickness of each species (Siemann et al. 1996; Haddad et al. 2000). The number of individual insects and insect biovolume were highly correlated (Pearson correlation coefficient = 0.608; $P = .001$), and results were qualitatively similar to the results of analyses of total number of individuals.

To determine the effects of plant species richness, plant functional group richness, and plant functional group composition on insect trophic structure, insect species were classified into one of five trophic categories based on field observations and literature review. Herbivores, parasitoids, predators, detritivores, and omnivores were classified by whether they fed, respectively, on live plant tissue, within other animals, on insects that they killed, on dead plant or animal tissues or by-products, or on combinations of food sources. Herbivores were further divided into one of four feeding guilds: chewing, sucking, boring, or seed/pollen feeding. Insects occupying different trophic levels in different stages of their life cycles were classified based on their larval stage unless we could identify a species' adult food resources within the experiment. A small number of individuals with aquatic larval stages were difficult to classify using the above criteria and were excluded from trophic analyses.

Analysis

We used backward elimination multiple regression to separate the effects of plant species richness, plant functional group richness, and plant functional group composition on insect abundance and diversity. The effects of plant species richness and plant functional group richness are necessarily correlated (i.e., a plot with one species must have one functional group). However, well-replicated and randomized experiments where the levels of plant species richness and plant functional group richness are specifically manipulated can be used to distinguish the effects of each variable through multiple regression. In most of our analyses, several measures indicated that these variables were not markedly collinear and that their effects could be legitimately separated.

The experimental design included many replicates at each combination of one to eight species and one to five functional groups. At higher levels of diversity, however, the design was incomplete. Because plant species composition was constrained by fixed pools of 18 or 34 species, plots with 16 or 32 species always had four or five functional groups (see description of experiment; Tilman et al. 1997*b*; Siemann et al. 1998). When we conducted separate analyses that included only plots containing up to eight species, our results did not differ qualitatively from those using all plots. Because of this, we decided to retain plots at all levels of plant species richness.

Although there was a strong relationship between planned levels of plant species richness and actual plant species richness (Pearson correlation coefficient = 0.66; $P = .001$), the two values differed because plant cover plots were small, weedy species were not completely eradicated, and some species failed to establish, especially in high-diversity plots. Because actual plant species richness explained more variation in every analysis of insect species richness and abundance (see also Knops et al. 1999), we used it as our independent variable in analyses. We analyzed the effects of plant composition by including a dummy variable indicating the presence or absence of each plant functional group. To account for the effect of the number of individual insects within a plot on insect species richness, we rarefied our total community data to estimate species richness based on the plot with lowest total abundance using EcoSim software (Gotelli and Entsminger 2000).

We included three other variables that may affect insect communities in our analyses: plant biomass, plant C : N, and a spatial index. Although other variables, like soluble N, amino acid concentration, or soluble carbohydrates, are also important measures of plant tissue quality to insects (e.g., Mattson 1980; Prestidge 1982; Prestidge and McNeill 1983; Strong et al. 1984; Brodbeck and Strong 1987; Nordin et al. 1998), we assumed that plant tissue C : N was correlated with these other measures and that it was a representative indicator of plant quality in the experiment. Plots were located on a grid, and each plot was typically bordered by three other plots and separated from a fourth plot by a 2-m-wide road. To control for spatial influences of adjacent plots, our analyses included a neighborhood index that quantified the average insect abundance or insect species richness in the four (or fewer) neighboring plots that bordered the edges of each plot. Neighborhood indices quantifying spatial effects at larger distances (i.e., including the four neighboring plots and the four diagonal plots) were also computed but were never significant.

Backward elimination multiple regressions were also conducted on each trophic level and herbivore feeding guild. In trophic analyses, the total abundance or species richness of herbivores (or predators and parasitoids) was included in multiple regression analyses of predator and parasitoid (or herbivore) abundance or species richness. Finally, we analyzed individually the responses of the 18 most abundant insect herbivore species to plant species richness and plant functional group richness, including only plots with plant functional groups that contained each herbivore's food plants. Assumptions of linearity, normality, and homogeneity of variances were evaluated through examination of residuals, and data were log transformed when appropriate. For all analyses, independent variables were evaluated for collinearity, and one was dropped if its variance inflation factor was $>1/(1-R^2)$, its eigenvalue was near 0, and/or its condition index was >24 (Freund and Littell 1991).

Results

Plant standing crop biomass responded to plant species richness and plant functional group richness in 1997 as it has in previous years (Tilman et al. 1997*b*). In multiple regression analyses, plant biomass increased significantly as functional group richness increased but was not related to plant species richness ($F = 9.70$, $\mathrm{df} = 2, 282$, $R^2 = 0.06$, $P < .001$). Plant tissue C : N was not related to either plant species richness or plant functional group richness. Because plant tissue C : N was measured for each plot, we could not determine how tissue C : N varied among functional groups within each plot. However, we analyzed plant tissue C : N in plots with one functional group and found that it was lowest in plots with legumes ($\overline{X} \pm$ SE; 28.41 ± 1.78), higher in forbs (45.91 ± 3.45) and C_3 grasses (46.00 ± 1.97), and highest in C_4 grasses (61.22 ± 1.51; ANOVA: $F = 38.79$, $\mathrm{df} = 3, 62$, $P = .001$).

In the three insect sampling periods, we collected and identified 46,485 individual insects and other terrestrial arthropods comprising 608 species (table 2). Insect samples collected in June in 24 plots rotted after inadvertently being removed from the freezer. Our conclusions remained unchanged whether we analyzed data using sweeps from all months for the 261 complete samples, sweeps from July and August for all 285 plots, or sweeps from each month analyzed independently. In multiple regressions performed separately for each month, insect abundance significantly increased as plant species richness and plant biomass increased and significantly decreased as plant functional group richness increased (June: $F = 5.33$, $\mathrm{df} = 4, 256$, $R^2 = 0.08$, $P = .001$; July: $F = 25.38$, $\mathrm{df} = 4, 280$, $R^2 = 0.27$, $P = .001$; August: $F = 8.89$, $\mathrm{df} = 4, 280$, $R^2 = 0.11$, $P = .001$). Also in each month, insect species richness significantly increased as plant species richness, insect abundance, and plant biomass increased (June: $F = 152.81$, $\mathrm{df} = 5, 255$, $R^2 = 0.75$, $P = .001$; July: $F = 170.23$, $\mathrm{df} = 5, 279$, $R^2 = 0.75$, $P = .001$; August: $F = 57.33$, $\mathrm{df} = 5, 279$, $R^2 = 0.51$, $P = .001$). There were two differences in responses of insect species richness in the three months, including a significant, positive relationship between insect species richness and plant tissue C : N in July ($t = 3.19$, $P = .002$) and a significant, positive relationship between insect species richness and plant functional group

Table 2: Composition of arthropods pooled from all plots and sampling dates

Order	Number of families	Number of species	Number of individuals
Aràneae	10	34	2,090
Opiliònes	1	1	5
Àcari	2	3	94
Collembola	2	2	154
Ephemeroptera	1	1	2
Odonata	4	7	52
Orthoptera	3	29	3,512
Psocoptera	1	4	170
Hemiptera	13	52	2,976
Homoptera	7	55	11,760
Thysanoptera	1	5	1,147
Neuroptera	3	5	104
Coleoptera	22	70	3,716
Diptera	40	126	14,698
Trichoptera	2	2	4
Lepidoptera	12	56	674
Hymenoptera	34	156	5,327

richness in August ($t = 2.07$, $P = .04$). In the analyses that follow, we report community level results from the pooled July and August data for all 285 plots. However, because abundances of individual species varied throughout the season, we used data from all three months in analyses of individual species.

Effects of Plant Richness and Composition on Insect Abundance

In simple regressions ($N = 285$), total insect abundance was significantly and positively related to plant species richness (fig. 1*A*) and standing crop plant biomass (fig. 1*B*). Insect abundance was not associated with plant functional group richness, but after controlling for plant species richness, residual insect abundance was significantly and negatively related to plant functional group richness (fig. 1*C*). Insect abundance was also significantly and positively related to mean insect abundance in the four neighboring plots (fig. 1*D*) and significantly and negatively related to plant tissue C : N (fig. 1*E*). Mean insect abundance per insect species was significantly and negatively related to plant functional group richness (fig. 1*F*) but was not related to plant species richness.

We included plant species richness, plant functional group richness, standing crop biomass, plant tissue C : N, and the neighborhood index in multiple regression analyses. As in the simple regressions, insect abundance was significantly and positively related to plant species richness, plant biomass, and the neighborhood index (table 3) and was also significantly and negatively related to plant functional group richness and plant tissue C : N.

To determine the effects of plant functional group composition on insect abundance, we conducted a multiple regression analysis like the one described above, except that we replaced plant functional group richness with five variables that coded for the presence or absence of each plant functional group. Responses to the other independent variables were the same as above (table 3), except that insect abundance was significantly and negatively related to the presence of C_4 grasses and not related to plant tissue C : N. When the effect of plant functional group richness was assessed along with variables representing the presence or absence of each functional group, the presence or absence of C_4 grasses replaced functional group richness as a significant variable (full multiple regression model: $F = 20.64$, $\mathrm{df} = 9, 275$, $R^2 = 0.40$, $P = .001$; functional group richness: $t = -1.85$, $P = .06$; C_4 grasses: $t = 3.58$, $P = .001$). Because of the strong, negative influence of C_4 grasses on insect abundance, we analyzed differences in insect abundances in plots with and without C_4 grasses. The presence of C_4 grasses caused a 25% reduction in total insect abundances (fig. 2*A*). In plots without C_4 grasses, plant biomass explained 55% of the variation in insect abundance (fig. 2*B*). This contrasted with plots containing C_4 grasses, where plant biomass explained a much smaller amount of variation in insect abundances (fig. 2*C*).

To determine whether the effects of plant species richness or functional group richness could be ascribed to dominant species in the experiment (a concern raised by Aarssen [1997] and Huston [1997]), we conducted an additional multiple regression analysis that included plant species richness, plant functional group richness, plant biomass, plant tissue C : N, neighborhood abundance, and the presence or absence of the five most abundant plant species. These species included two legumes, *Lupinus perennis* and *Lespedeza capitata*, and three C_4 grasses, *Schizachyrium scoparium*, *Andropogon gerardii*, and *Sorghastrum nutans*. Insect abundance was significantly and positively related to the presence of *L. capitata* ($t = 3.18$, $P = .002$) and significantly and negatively related to the presence of *S. scoparium* ($t = -2.99$, $P = .003$) and *S. nutans* ($t = -2.90$, $P = .004$). Even after accounting for the effects of dominant species, however, insect abundances were significantly and positively related to plant species richness ($t = 4.34$, $P = .001$) and significantly and negatively related to plant functional group richness ($t = -2.93$, $P = .004$; full model: $F = 19.15$, $R^2 = 0.41$, $P = .001$).

Effects of Plant Richness and Composition on Abundances of Insect Trophic Groups and Feeding Guilds

We conducted more detailed analyses on insect abundances by trophic groups. Herbivorous insects, the most abundant trophic group, responded to plant species richness and plant functional group richness much as did the entire insect community. Herbivore abundance increased significantly as plant species richness, plant biomass, and predator and parasitoid abundance increased but decreased significantly as plant functional group richness and plant tissue C : N increased (fig. 3*A*, 3*B*; full multiple regression model: $F = 28.42$, $R^2 = 0.34$, $P = .001$). Herbivore feeding guilds responded differently to experimental treatments (table 4). The abundance of sucking herbivores was significantly and positively related to plant species richness but significantly and negatively related to plant functional group richness and plant tissue C : N. The abundance of chewing herbivores was significantly and positively related to plant species richness and plant biomass but not to plant functional group richness and plant tissue C : N. The abundance of boring herbivores was significantly and positively related to plant species richness and plant biomass and significantly and negatively related to plant functional group richness and plant tissue C : N.

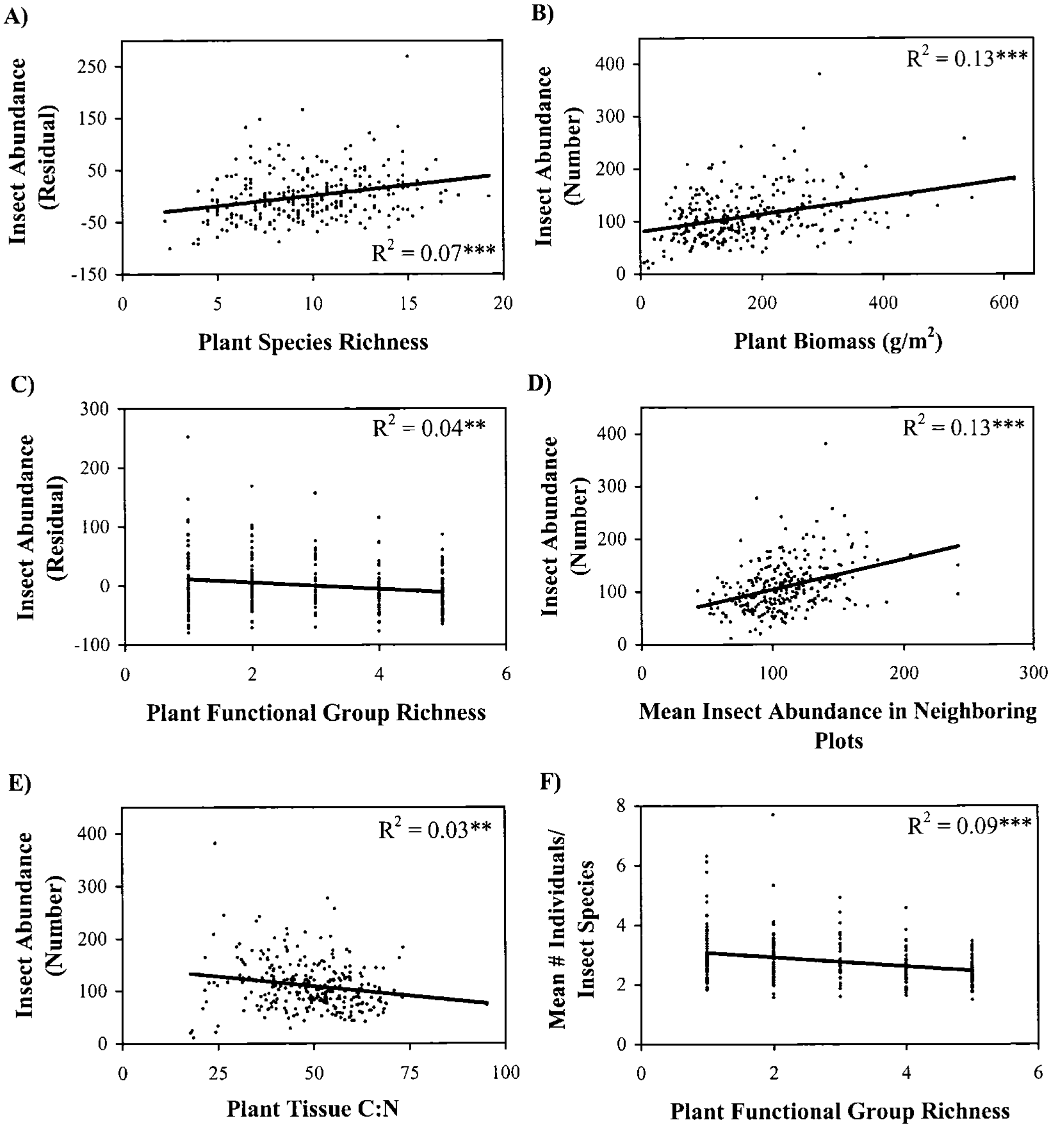

Figure 1: Simple regressions of insect abundance against manipulated and other measured variables, which include (*A*) plant species richness (dependent variable is the residual insect abundance after controlling for plant functional group richness; $y = 4.0157x - 39.254$), (*B*) plant biomass (g/m^2; $y = 0.1654x + 80.229$), (*C*) plant functional group richness (dependent variable is the residual insect abundance after controlling for plant species richness; $y = -5.4617x + 16.251$), (*D*) mean insect abundance in four neighboring plots ($y = 0.575x + 46.95$), and (*E*) plant tissue C : N ($y = -0.7316x + 145.41$); (*F*) shows the relationship between plant functional group richness and the mean number individual insects/insect species (the relationship with plant species richness was not significant; $y = -0.1511x + 3.2131$). $^{**}P = .01$; $^{***}P = .001$.

The abundance of seed and pollen-feeding herbivores was significantly and positively related to plant biomass and significantly and negatively related to plant functional group richness (table 4).

We analyzed the responses of individual insect species to plant species richness and plant functional group richness by analyzing responses of the 18 most abundant herbivore species (with mean abundances >0.75 individuals/plot). We used field observations, literature reports, and abundances in this study from plots containing only one functional group (table 5) to determine food preferences of these species at the level of plant functional groups. We note that the preferred plant was not always a host plant. For example, the grass-feeding dipteran leafminers *Oscinella* sp1. and *Olcella* sp. were most abundant in plots with legumes and/or forbs, which may have provided nectar resources for adults. We then conducted a multiple regression analysis with plots that contained only the pre-

Table 3: Effects of plant species richness and plant functional group richness or composition on insect abundance

Variable	Parameter estimate	Squared partial correlation	P
Functional group richness:			
Intercept	27.76	…	.081
Plant species richness	4.79	.092	.001
Plant functional group richness	−8.24	.066	.001
Total plant biomass	.16	.141	.001
Plant tissue C : N	−.40	.014	.047
Neighborhood index	.47	.115	.001
Functional group composition:			
Intercept	29.19	…	.011
Plant species richness	3.37	.071	.001
C_3 grasses present	…	…	NS
C_4 grasses present	−33.91	.148	.001
Forbs present	…	…	NS
Legumes present	…	…	NS
Woody plants present	−8.24	.011	.076
Total plant biomass	.16	.159	.001
Plant tissue C : N	…	…	NS
Neighborhood index	.42	.101	.001

Note: Statistical results from the final regression models: plant functional group richness ($F = 29.02$, df $= 5, 279$, $R^2 = 0.34$, $P = .001$) and plant functional group composition ($F = 36.50$, df $= 5, 279$, $R^2 = 0.40$, $P = .001$). NS = not significant.

ferred plant functional group. Of the 18 most abundant herbivore species, the abundances of 13 showed a significant, negative relationship to plant functional group richness (table 5). Five species showed a significant, positive relationship to plant species richness. Six species showed a significant, positive relationship to plant biomass, and two showed a significant, negative relationship to plant biomass. Five species showed a significant, negative relationship to plant tissue C : N.

Finally, we analyzed the responses of nonherbivorous insects in multiple regression analyses. Predator abundance was significantly and positively related to plant species richness, plant biomass, and herbivore and detritivore abundance but not to plant functional group richness (fig. 3*C*, 3*D*; full multiple regression model: $F = 68.44$, $R^2 = 0.42$, $P = .001$). Parasitoid abundance was significantly and positively related to plant functional group richness, plant biomass, and herbivore and detritivore abundance but not to plant species richness (fig. 3*E*, 3*F*; full multiple regression model: $F = 7.09$, $R^2 = 0.07$, $P = .001$). Detritivore abundance was significantly and positively related to plant functional group richness, plant biomass, and predator and parasitoid abundance but not to plant species richness or plant tissue C : N (fig. 3*G*, 3*H*; full multiple regression model: $F = 19.82$, $R^2 = 0.17$, $P = .001$; note that the results of

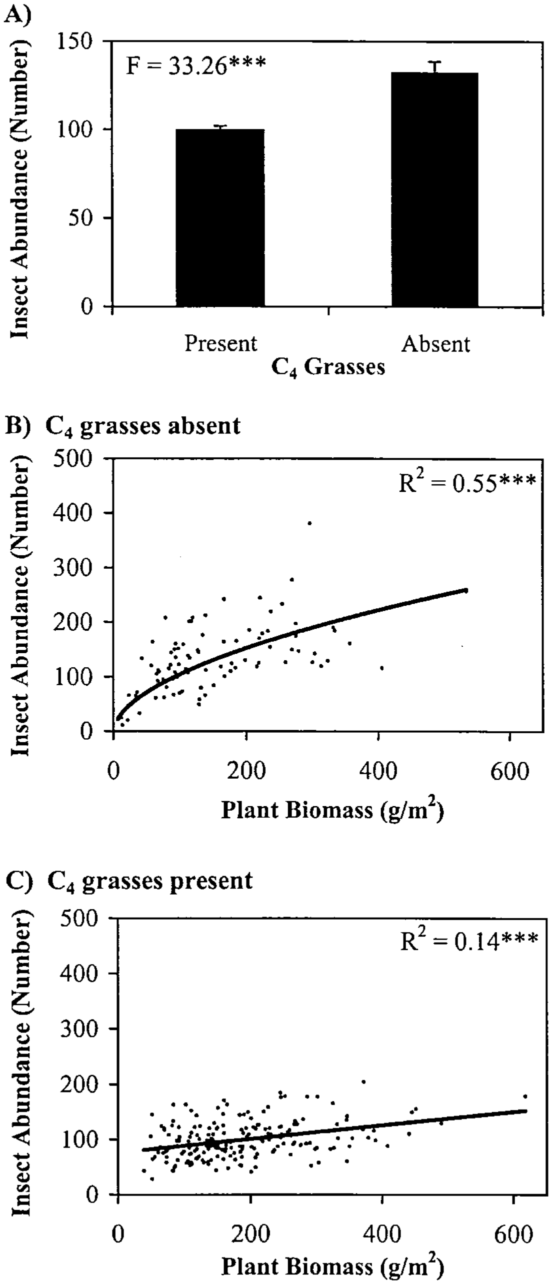

Figure 2: The effects of C_4 grasses on insect abundance. Graphs compare (*A*) insect abundances in plots with and without C_4 grasses (F statistics and P values are the results of a general linear model analysis on the two classes of plots), (*B*) the relationship between plant biomass and insect abundance in plots with no C_4 grasses ($y = 8.5371 \times x^{0.544}$), and (*C*) the relationship between plant biomass and insect abundance in plots that contain C_4 grasses ($y = 0.1239x + 76.057$). $^{***}P = .001$.

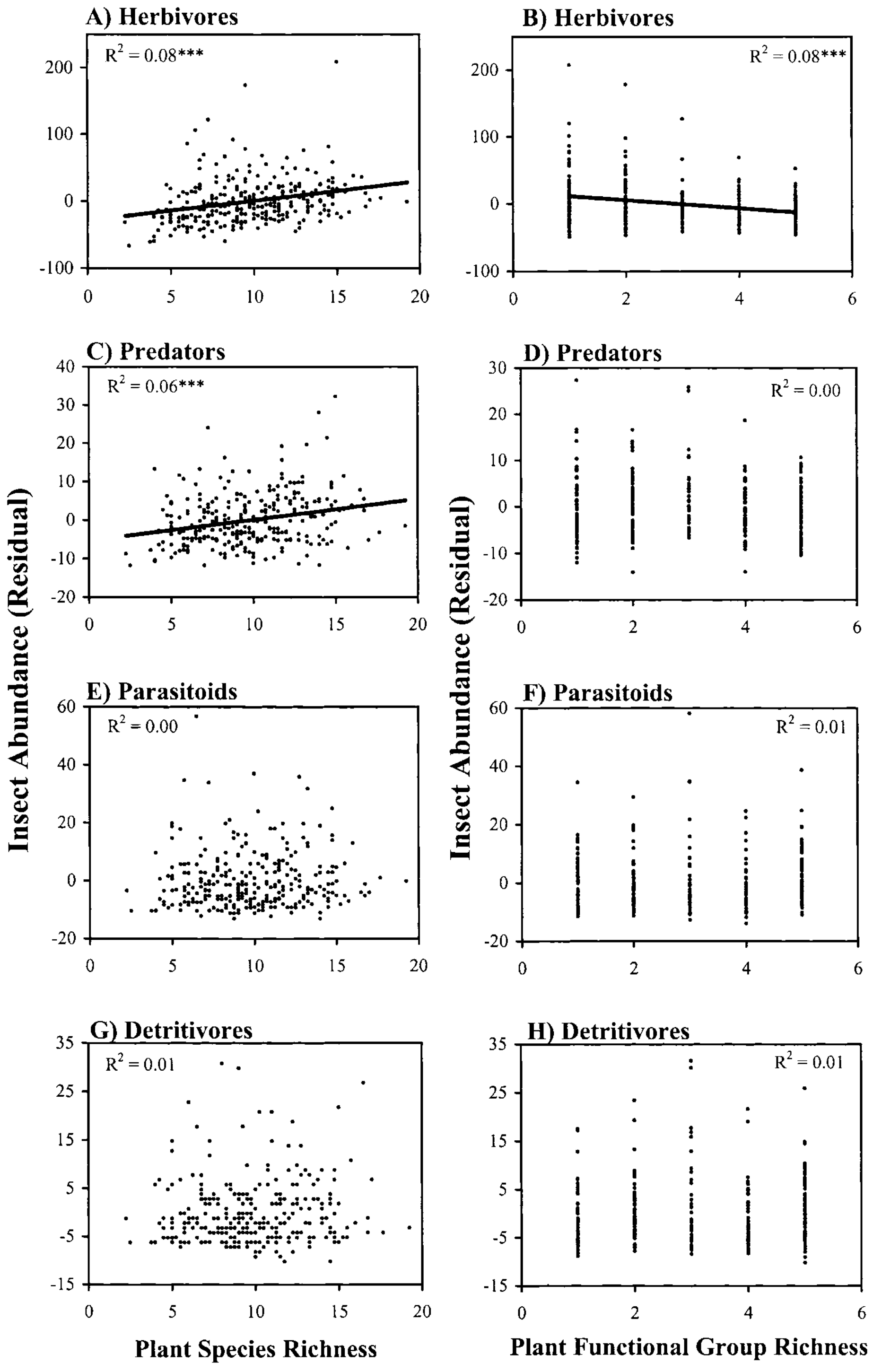

Figure 3: Relationship between plant species richness or plant functional group richness and the number of herbivores (*A*, *B*; *A*: $y = 2.9478x - 28.815$; *B*: $y = -6.0317x + 17.947$), predators (*C*, *D*; *C*: $y = 0.5391x - 5.2696$), parasitoids (*E*, *F*), or detritivores (*G*, *H*). The dependent variables are the residual abundances after controlling for plant species richness or plant functional group richness. $^{***}P = .001$.

Table 4: Effects of plant species richness and plant functional group richness on the abundance of herbivore functional feeding groups

Variable	Parameter estimate	Squared partial correlation	*P*
Sucking herbivore abundance:			
Intercept	48.62	…	.001
Plant species richness	1.52	.045	.001
Plant functional group richness	−4.49	.092	.001
Total plant biomass	…	…	NS
Plant tissue C : N	−.28	.032	.003
Chewing herbivore abundance:			
Intercept	−1.86	…	.148
Plant species richness	.28	.020	.017
Plant functional group richness	…	…	NS
Total plant biomass	.04	.309	.001
Plant tissue C : N	…	…	NS
Boring herbivore abundance:			
Intercept	18.15	…	.001
Plant species richness	1.11	.058	.001
Plant functional group richness	−2.06	.049	.001
Total plant biomass	.03	.057	.001
Plant tissue C : N	−.21	.044	.001
Seed/pollen-feeding herbivore abundance:			
Intercept	7.32	…	.005
Plant species richness	…	…	NS
Plant functional group richness	−1.64	.020	.017
Total plant biomass	.03	.020	.018
Plant tissue C : N	…	…	NS

Note: Statistical results from the full regression model: sucking herbivores ($F = 16.02$, df = 3, 281, $R^2 = 0.15$, $P = .001$), chewing herbivores ($F = 72.62$, df = 2, 282, $R^2 = 0.34$, $P = .001$), boring herbivores ($F = 14.88$, df = 4, 280, $R^2 = 0.18$, $P = .001$), and seed- or pollen-feeding herbivores ($F = 4.62$, df = 2, 282, $R^2 = 0.03$, $P = .011$). NS = not significant.

multiple regressions differed from simple regressions). Omnivore abundance was significantly positively related to plant species richness (full multiple regression model: $F = 5.74$, $R^2 = 0.02$, $P = .02$).

Effects of Plant Richness and Composition on Insect Diversity

Insect species richness was strongly related to insect abundance (fig. 4*C*). Rarefied insect species richness (based on the lowest number of individuals [11] from any one plot) was significantly and positively dependent on both plant species richness and plant functional group richness (table 6; fig. 4*A*, 4*B*). However, in backward elimination multiple regression, insect species richness was not related to plant biomass (fig. 4*D*), plant tissue C : N, and insect species richness in neighboring plots (fig. 4*E*). When plant functional group richness was replaced by the presence or absence of each of the five plant functional groups, rarefied insect species richness was significantly and positively related to plant species richness, the presence of C_3 and C_4 grasses and legumes and significantly and negatively related to the presence of forbs (table 6).

Herbivores, the most diverse insect trophic group, responded to treatments much as did all insects. Herbivore diversity increased significantly as plant species richness, herbivore abundance, plant biomass, and predator and parasitoid species richness increased (fig. 5*A*–5*C*; full multiple regression model: $F = 62.40$, $R^2 = 0.53$, $P = .001$), but after controlling for these variables in a multiple regression analysis, herbivore species richness was only marginally positively related to plant functional group richness ($t = 1.87$, $P = .06$). Rarefaction was not used on insect subgroups because it eliminates information by reducing abundance to the lowest in any plot, which was often 0 or 1. Sucking herbivore diversity was significantly and positively related to plant species richness, plant functional group richness, sucking herbivore abundance, and plant biomass (table 7). Chewing herbivore diversity was significantly and positively related to ln(chewing herbivore abundance). Boring herbivore diversity was significantly and positively related to plant functional group richness, ln(boring herbivore abundance), and plant tissue C : N and significantly and negatively related to plant biomass. Seed and pollen-feeding herbivore diversity was significantly and positively related to plant species richness and to ln(seed and pollen-feeding herbivore abundance). (See table 7.)

Predators were the only other insect trophic group besides herbivores to show a positive response to plant species richness in multiple regressions. Predator species richness was significantly and positively related to plant species richness, plant functional group richness, and predator abundance but not to herbivore and detritivore species richness or to plant biomass (fig. 5*D*–5*F*; full multiple regression model: $F = 203.49$, $R^2 = 0.68$, $P = .001$). Parasitoid species richness was significantly and positively related to herbivore and detritivore species richness and to ln(parasitoid abundance) but not to plant species richness, plant functional group richness, or plant biomass (fig. 5*G*–5*I*; full multiple regression model: $F = 159.06$, $R^2 = 0.54$, $P = .001$; please note differences between simple and multiple regressions). Detritivore species richness was significantly and positively related to predator and parasitoid species richness, detritivore abundance, and plant biomass, significantly and negatively related to plant tissue C : N, and not related to plant species richness or plant functional group richness (fig.

Table 5: Effects of plant species richness and plant functional group richness on the 18 most abundant herbivore species

			Abundance in plots with one plant functional group (mean number/plot)				Estimates				
Species	Order	Total abundance	C_3 grasses	C_4 grasses	Forbs	Legumes	Plant species richness	Plant functional group richness	Plant biomass (g/m^2)	Plant tissue C : N	Model R^2
Philygria sp.	Diptera	2,616	7.29	**19.75**	6.57	5.75	−.55	−.69	−.01	.12	.14***
Empoasca fabae	Homoptera	2,318	.00	.04	4.57	**40.00**	.65	−3.64***	.03***	−.52***	.38***
Oscinella sp1.	Diptera	2,107	7.00	2.58	10.64	**20.92**	.77**	−1.83***	.02**	−.15*	.21***
Melanoplus femurrubrum	Orthoptera	2,009	5.50	4.17	4.57	**13.08**	.35	−1.04*	.04***	−.03	.30***
Olcella sp.	Diptera	1,663	5.71	1.83	**17.79**	**18.25**	.45*	−2.53***	.00	−.15**	.26***
Macrosteles fascifrons	Homoptera	1,301	3.36	2.88	**12.71**	**14.67**	−.07	−1.55***	−.02***	−.14***	.39***
Chauliognathus pennsylvanicus	Coleoptera	1,148	.00	.00	**21.64**	1.33	−.13	−5.67***	.03*	.08	.19***
Notoxus bifasciata	Coleoptera	1,040	**12.00**	1.71	3.43	3.75	.63**	−1.44**	−.01	.00	.08**
Delphacodes campestris	Homoptera	802	**5.50**	4.58	.43	.83	.03	−.61***	−.00	.02	.10**
Trigonotylus coelestialium	Hemiptera	735	**6.71**	**4.12**	.29	.25	.12	−.35*	−.01***	.03	.14***
Thrip sp.	Thysanoptera	661	3.36	1.71	3.71	3.25	.25**	−.40	.00	.01	.06*
Oscinella sp2.	Diptera	588	**3.43**	**2.92**	.64	.50	.09	−.31*	−.00	.02	.03
Phoetaliotes nebrascenis	Orthoptera	546	1.43	**3.08**	.07	.17	.04	−.24	.01***	.04	.09**
Nesosteles neglectus	Homoptera	508	**6.93**	.88	.43	.17	.22	−1.57***	.00	.00	.16***
Delphacodes sp.	Homoptera	322	.71	**2.83**	.00	.08	−.05	−.21	−.00	.02	.10***
Nysius niger	Hemiptera	316	1.86	.29	**6.79**	3.50	.02	−1.01**	−.00	−.05	.07*
Melanoplus augustipennis	Orthoptera	288	.43	.38	**1.00**	**1.58**	.02	−.02	.00	−.02	.03
Adelphocoris lineolatus	Hemiptera	227	.07	.04	.64	**3.92**	.10*	−.33**	.004***	−.04*	.23***

Note: Preferred functional groups, in bold font, were determined from field observations, the literature, and from abundances of each species sampled in plots with one functional group (sample sizes: C_3 grasses [$n = 14$], C_4 grasses [$n = 24$], forbs [$n = 14$], legumes [$n = 12$]). Parameter estimates are from the multiple regression model that included only those plots with the species' preferred plant functional group (or, for generalist species, all plots in the experiment).

* $P < .05$.

** $P < .01$.

*** $P < .001$.

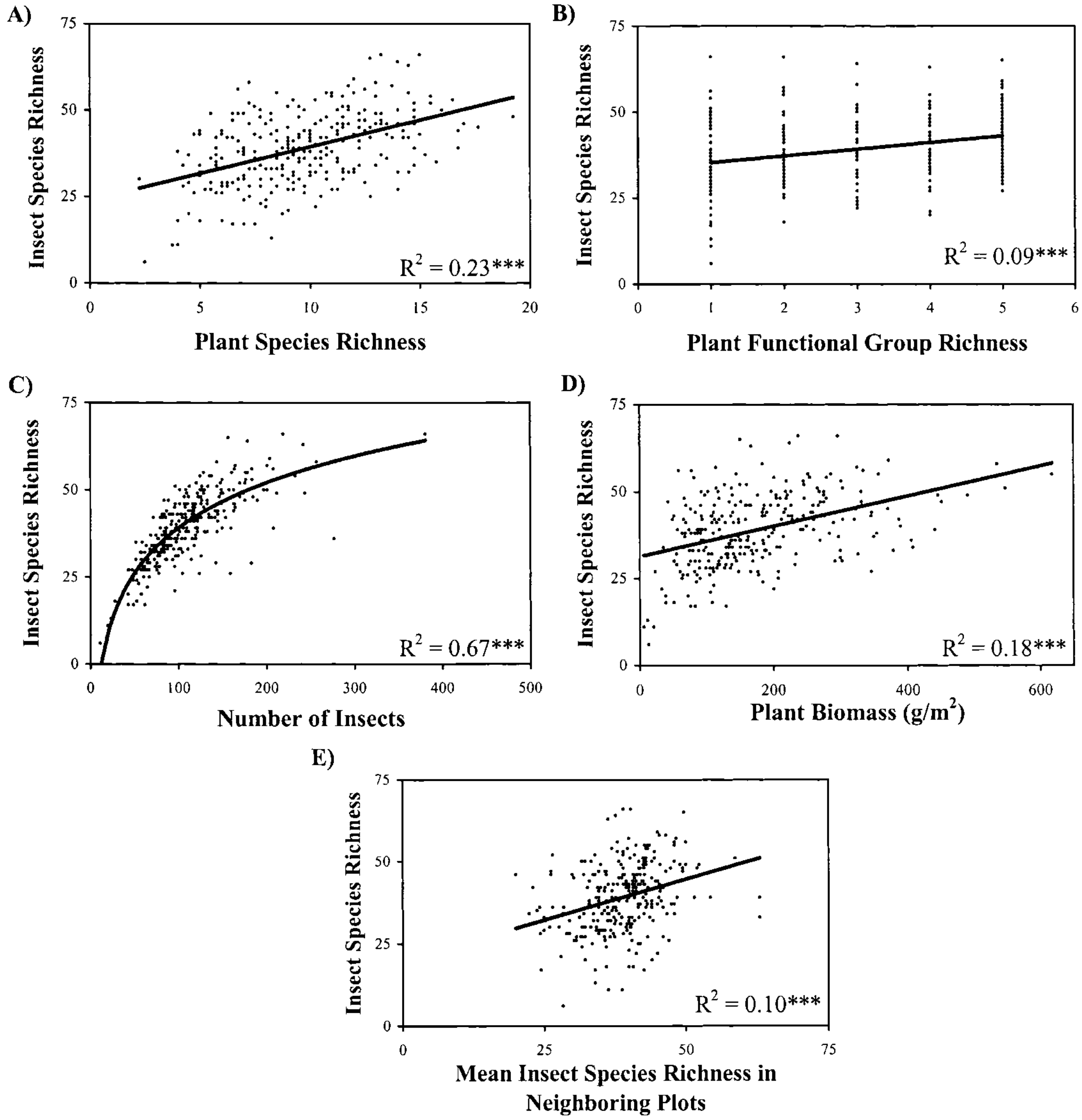

Figure 4: Simple regressions of insect species richness against manipulated and other measured variables, which included (*A*) plant species richness ($y = 1.5447x + 23.971$), (*B*) plant functional group richness ($y = 1.9371x + 33.306$), (*C*) insect abundance ($y = 18.821 \times \ln(x) - 47.623$), (*D*) plant biomass (g/m^2; $y = 0.0435x + 31.32$), and (*E*) mean insect species richness in four neighboring plots ($y = 0.4983x + 19.705$). ***$P = .001$.

5*J*–5*L*; full multiple regression model: $F = 52.62$, $R^2 = 0.43$, $P = .001$). Omnivore species richness was significantly and positively related to omnivore abundance and to plant biomass but not to plant species richness, plant functional group richness, or plant tissue C : N (full multiple regression model: $F = 68.71$, $R^2 = 0.33$, $P = .001$).

Discussion

We found that plant species richness, plant functional group richness, and plant functional group composition could have similar or opposing effects on insect communities. Both plant species richness and plant functional group richness had significant, positive effects on total insect species richness. This supports the results of other studies that have shown a positive relationship between insect species richness and plant diversity (Murdoch et al. 1972; Southwood et al. 1979; Strong et al. 1984), such as in recent experiments that vary plant species richness (Knops et al. 1999) and plant functional group richness (Siemann et al. 1998; Symstad et al. 2000).

Our results with respect to insect abundance were more

Table 6: Effects of plant species richness and plant functional group richness or composition on insect species richness, which was estimated through rarefaction for a sample size of 11 insect individuals

Variable	Parameter estimate	Squared partial correlation	*P*
Functional group richness:			
Intercept	7.50	…	.001
Plant species richness	.05	.026	.007
Plant functional group richness	.21	.109	.001
Total plant biomass	…	…	NS
Plant tissue C : N	…	…	NS
Neighborhood index	…	…	NS
Functional group composition:			
Intercept	7.18	…	.001
Plant species richness	.08	.057	.001
C_3 grasses present	.25	.020	.019
C_4 grasses present	.62	.121	.001
Forbs present	−.23	.016	.032
Legumes present	.37	.040	.001
Woody plants present	…	…	NS
Total plant biomass	…	…	NS
Plant tissue C : N	…	…	NS
Neighborhood index	…	…	NS

Note: Statistical results from the full regression models: plant functional group richness ($F = 44.08$, df = 2, 282, $R^2 = 0.24$, $P = .001$) and plant functional group composition ($F = 27.35$, df = 5, 279, $R^2 = 0.33$, $P = .001$). NS = not significant.

complex. Multiple regression analyses (tables 3–5) show that higher plant functional group richness caused lower insect abundance, which supports our hypothesis that was based on numerous studies of insects in agroecosystems (reviewed in Risch et al. 1983 and Andow 1991). Although previous studies did not manipulate plant diversity as we did in this study (monocultures were typically compared with polycultures), they have found lower insect abundances in diverse plant communities (i.e., Pimentel 1961; Tahvanainen and Root 1972; Root 1973; Bach 1980*a*; Risch 1981). These agroecosystem studies often included cultivated plant species that were of different functional types. Perhaps these earlier patterns were caused by plant compositional effects rather than by the effects of diversity measured as the number of plant species. We were surprised to find that after controlling for the effects of plant functional group richness, higher plant species richness increased insect abundances. We identified three mechanisms that appear to explain the contrasting effects of plant species richness and plant functional group richness on insect abundances: a sampling effect (Aarssen 1997; Huston 1997; Tilman et al. 1997*c*), a plant productivity effect, and positive effects of plant species richness on insect abundances.

The Sampling Effect of Plant Diversity on Insect Abundances

The negative effect of plant functional group richness on insect abundance may have been an effect of plant functional group composition, which was caused by the significant, negative impact of C_4 grasses on insect abundance. The presence of C_4 grasses led to insect abundances 25% lower than those found when C_4 grasses were absent (table 3; fig. 2). The C_4 grasses are low-quality food plants for herbivores: they had the highest tissue C : N of the functional groups considered in this study (see "Results") and are defended by structural characteristics, like higher leaf toughness (Caswell et al. 1973). When C_4 grasses were not present, insect abundances were best explained by plant biomass, which alone accounted for 55% of the variation in insect abundances (fig. 2*B*), or by plant species richness. The presence of other functional groups did not explain any additional variance. In contrast to the other functional groups, C_4 grasses were among the most productive but poorest-quality plant species, which caused a particularly dramatic effect. Relative to biomass, the insect community on C_4 grasses was impoverished.

The result that C_4 grasses depress insect abundances emphasizes one critical effect of diversity—the "sampling effect" (Aarssen 1997; Huston 1997; Tilman et al. 1997*c*). As functional group richness increased within a plot, it became more likely that C_4 grasses would be part of the plant community composition and decrease total insect abundances. The importance of C_4 grasses in affecting insect abundances was shown in analyses where its presence or absence replaced functional group richness as the significant variable predicting insect abundances. Our results were not caused by a single dominant species, a concern that has been raised in debate over the mechanisms underlying responses in diversity experiments (Aarssen 1997; Huston 1997; Tilman 1997; Tilman et al. 1997*c*; Hector 1998; Loreau 1998; Tilman 1999). Of the five most productive species in the experiment, three were C_4 grasses. Two of the dominant C_4 grass species did have negative effects on insect abundances, just as one dominant legume had positive effects on insect abundances. We interpret this result as a response by herbivores to plant quality—legumes and C_4 grasses have, respectively, the lowest and highest plant tissue C : N. Although there was a positive effect of one legume species, it did not remove the significant effects of plant species richness and plant functional group richness. In addition, all legumes combined had no significant effect on total insect abundances, probably because variation was best explained by other correlated factors, like legume biomass. However, our multiple regression analyses that also included the effects of dominant species showed that the effects of plant species

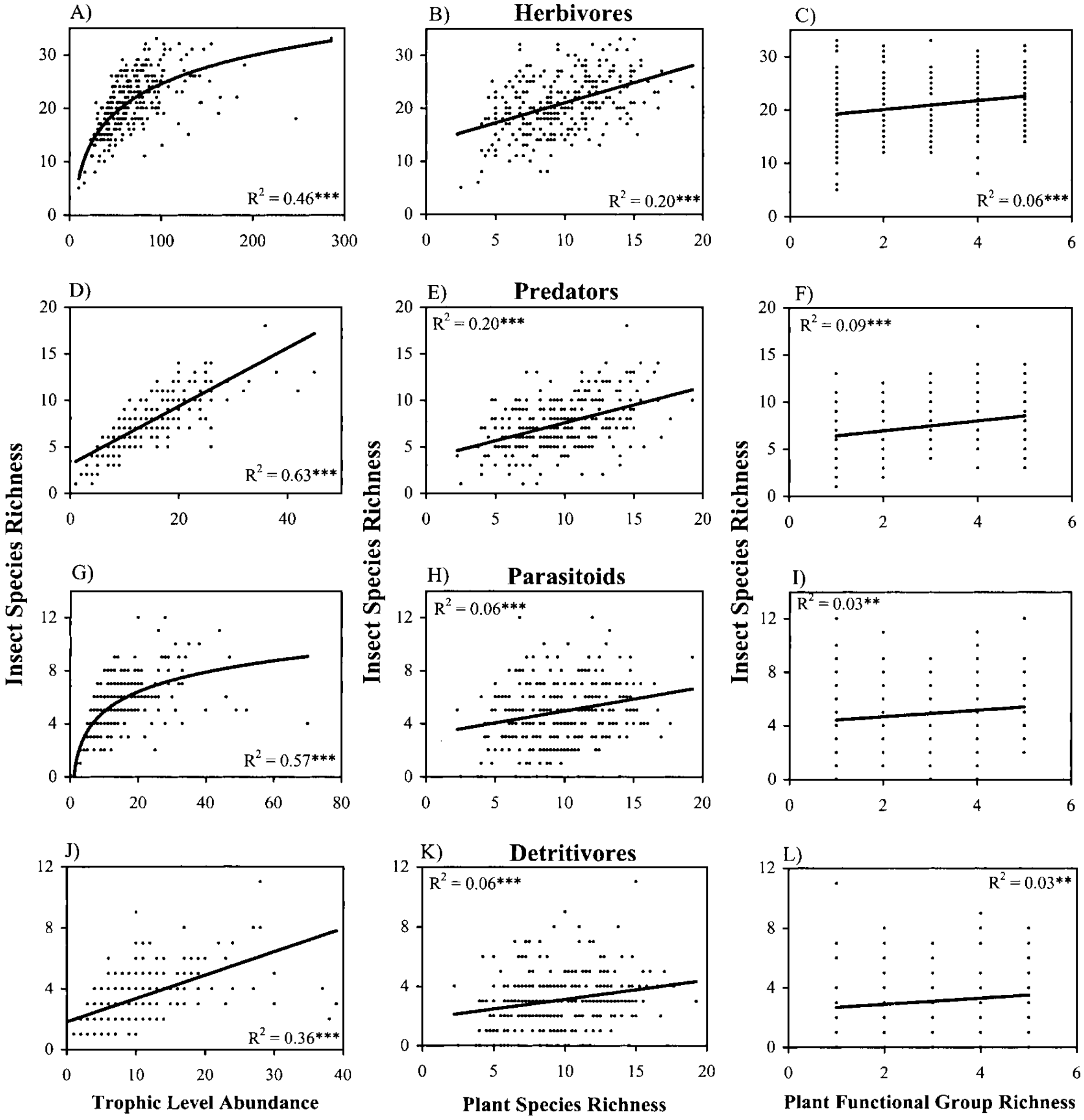

Figure 5: Relationship between trophic level abundance, plant species richness, or plant functional group richness and the species richness of herbivores (*A*: $y = 7.6791 \times \ln(x) - 10.837$; *B*: $y = 0.7586x + 13.452$; *C*: $y = 0.8421x + 18.361$), predators (*D*: $y = 0.3119x + 3.1152$; *E*: $0.3859x + 3.6975$; *F*: $y = 0.5303x + 5.8923$), parasitoids (*G*: $y = 2.1322 \times \ln(x) + 0.0099$; *H*: $y = 0.18x + 3.1424$; *I*: $y = 0.2458x + 4.1704$), or detritivores (*J*: $y = 0.1536x + 1.831$; *K*: $y = 0.1317x + 1.8035$; *L*: $y = 0.2085x + 2.4708$). $^{**}P = .01$; $^{***}P = .001$.

richness and plant functional group richness were still significant and were not attributable only to the impact of a dominant C_4 grass species.

The Productivity Effect on Insect Abundances

Aboveground plant biomass was consistently the most important variable in explaining insect abundances. Aboveground plant biomass is a good index of plant productivity in these plots because most aboveground vegetation dies each year and because plots were burned in the spring. In plots without C_4 grasses, plant biomass explained approximately 55% of the variation in insect abundances (fig. 2*B*). Higher herbivore abundances then led to higher predator and parasitoid abundances. These results support those of other studies that have also demonstrated the importance of plant productivity for insect abundances (e.g., Brown and Southwood 1983; Hunter and Price 1992; Power 1992; Rit-

Table 7: Effects of plant species richness and plant functional group richness on the diversity of each herbivore functional feeding group

Variable	Parameter estimate	Squared partial correlation	*P*
Sucking herbivore diversity:			
Intercept	−2.85	…	.002
Plant species richness	.12	.023	.011
Plant functional group richness	.20	.015	.043
ln(sucking herbivore abundance)	2.75	.311	.001
Total plant biomass	.00	.030	.004
Plant tissue C : N	…	…	NS
Chewing herbivore diversity:			
Intercept	−.67	…	.001
Plant species richness	…	…	NS
Plant functional group richness	…	…	NS
ln(chewing herbivore abundance)	2.49	.754	.001
Total plant biomass	…	…	NS
Plant tissue C : N	…	…	NS
Boring herbivore diversity:			
Intercept	−.88	…	.112
Plant species richness	…	…	NS
Plant functional group richness	.14	.025	.008
ln(boring herbivore abundance)	2.02	.438	.001
Total plant biomass	−.00	.020	.017
Plant tissue C : N	.01	.017	.027
Seed/pollen-feeding herbivore diversity:			
Intercept	−.31	…	.088
Plant species richness	.09	.081	.001
Plant functional group richness	…	…	NS
ln(seed/pollen herbivore abundance)	1.14	.586	.001
Total plant biomass	…	…	NS
Plant tissue C : N	…	…	NS

Note: Statistical results from the full regression model: sucking herbivores ($F = 46.94$, df = 4, 280, $R^2 = 0.40$, $P = .001$), chewing herbivores ($F = 867.15$, df = 1, 283, $R^2 = 0.75$, $P = .001$), boring herbivores ($F = 57.96$, df = 4, 280, $R^2 = 0.45$, $P = .001$), and seed- or pollen-feeding herbivores ($F = 253.66$, df = 2, 282, $R^2 = 0.64$, $P = .001$). NS = not significant.

chie 2000). As discussed by Ritchie (2000), the strong effect of plant biomass on insect abundances may be particularly important in nitrogen limited, unproductive systems like those at Cedar Creek. Aboveground living plant biomass in many of the experimental plots was <100 g/m^2. These plots had sparse vegetation that may not support the quantity of resources required by many insects. Low-biomass plots also had simpler spatial structure and less total volume of space for use as habitat, potentially limiting insect abundances (Ritchie and Olff 1999). Because plant productivity was generally low, the experiment was not prone to insect outbreaks as are common in agricultural systems and in fertilized natural systems (Haddad et al. 2000).

The effects of plant biomass on insect abundances also suggest a second, indirect effect of plant diversity. Several studies have shown that higher plant diversity can lead to higher plant productivity (Naeem et al. 1994; Tilman et al. 1996; Tilman et al. 1997*b*; Hector et al. 1999). Although these results have generated great debate (Aarssen 1997; Huston 1997; Tilman et al. 1997*a*; Wardle et al. 1997; Hodgson et al. 1998; Lawton et al. 1998), the positive relationship between plant functional group richness and plant biomass did hold in this study. Higher plant diversity may then have increased insect abundances indirectly by increasing plant biomass and thus the quantity of resources for insects. Because we control for plant biomass in our study, the effects of plant diversity on insect abundances through changes in biomass are controlled. In addition, many factors control plant productivity, not only (or even most importantly) plant diversity. Nonetheless, increasing plant productivity may be an important way that higher plant diversity influences insect abundances.

We cannot separate the effects of plant biomass in this study with another, correlated factor, plant density, which might also influence insect abundances. Plant density has been shown to be an important factor explaining plant diversity along fertility gradients (Stevens and Carson 1999). Higher plant density would increase resource concentration, potentially attracting a greater number or diversity of insects. More work is needed to separate the effects of plant biomass from plant density on insect communities.

Other Effects of Plant Diversity on Insect Abundances

Even after controlling for other factors, including the sampling effect caused by C_4 grasses, the plant productivity effect, as well as significant effects of neighboring plots and of plant tissue C : N, insect abundance was still significantly and positively related to plant species richness. This consistent relationship in our data differs from results reported in most agroecosystem studies. We generated three hypotheses that might explain the positive relationship between plant species richness and insect abundance. First, although the abundances of individual species may not be related to plant species richness, total community insect abundances may be positively related to plant species richness due to larger numbers of insect species in more diverse plots. This follows from the result that as the number of plant species increased, the number of insect species increased but the mean number of insects per insect species did not change. Individual insect species often responded in a way that was consistent with our initial hypothesis: 72% (and 11 of 12 specialists) of herbivores considered showed a significant, negative response to plant functional group richness, but only 28% showed a significant, positive response to plant species richness. Second, higher plant diversity may increase the availability of alternate resources, including alternate hosts within a functional group for herbivores (within and among seasons), as well as vegetative and floral resources for species that require both (Price et al. 1980; Powell 1986). Third, diverse plots may have been more structurally complex, providing suitable habitat or greater space for more insects (Southwood et al. 1979; Lawton 1983; Ritchie and Olff 1999), independent of the amount of food available. Any one of these three hypotheses or a combination may explain why insect abundances were positively related to plant species richness, and more work is needed to determine which combination of these factors may cause the positive effect of plant species richness on insect abundances in natural ecosystems.

We note that the effects of manipulated variables and other factors on insect abundances were generally small (but significant) when considered in simple regressions (fig. 1). Because of correlations among variables, some variables that were significant in simple regressions were not significant when considered in multiple regressions. High variability in insect responses may have been caused by the scale of the experiment, differences between the imposed and actual levels of plant diversity in experimental plots, and the individualistic responses of hundreds of insect species.

Trophic and Feeding Guild Responses

Herbivores, the most abundant and diverse trophic group, responded much as did the entire insect community. Because plant tissue C : N is a measure of plant quality to insects, the negative relationship between plant tissue C : N and herbivore abundance is unsurprising. Unlike sucking and boring herbivores, which showed the same pattern as all herbivores, the abundance of chewing insects, primarily generalist grasshoppers, was most strongly and positively related to plant biomass. Other trophic groups responded positively to plant species richness or plant functional group richness, possibly due to the greater diversity of habitats (or resources for generalist species) at higher levels of plant diversity. Although our results regarding higher trophic levels are limited because we did not manipulate insects, we found no evidence that herbivore or detritivore abundances were limited by predator and parasitoid abundances.

Effects of Plant Diversity and Composition on Insect Diversity

Our results support other studies that have shown that higher plant diversity leads to higher insect diversity (e.g., Murdoch et al. 1972; Southwood et al. 1979; Strong et al. 1984; Siemann et al. 1998; Knops et al. 1999). This study makes three novel contributions in this area. First, our study shows that contrary to our initial hypothesis, both plant species richness and plant functional group richness have significant, positive effects on insect species richness. Second, as explained above, our results regarding insect diversity shed light on the effects of plant species richness on insect abundance.

Third, although insect diversity is strongly and positively related to insect abundance, the effects of plant species richness and functional group richness were still significant even when the effects of insect abundance on insect diversity were controlled through rarefaction. At each trophic level, the most important determinant of insect species richness was the abundance of insects. Insect abundance explained 31%–75% of variation in species richness. Again, the experimental plots were relatively unproductive, and the availability of food resources limited insect abundances and thus species richness. After controlling for the effects of insect abundance, herbivores and predators were the only trophic groups whose species richness showed a significant, positive relationship to plant species richness. There was some evidence that higher predator and parasitoid diversity may have increased herbivore diversity, as would be predicted if predators and parasitoids limit the abundance of otherwise dominant herbivores (Paine 1966; Tilman and Pacala 1993; Siemann et al. 1998). Predator species richness was significantly and positively related to plant functional group richness, perhaps because of their use of alternate resources, like nectar at flowering plants.

Plant Species Richness versus Functional Group Composition

The results of this study demonstrate that two aspects of plant diversity, plant species richness and plant functional group richness, have similar effects on insect species richness but contrasting effects on insect abundances. These results are more complex than those of recent studies that have found that plant functional group richness, plant functional group composition, or both have similar effects on ecosystem responses to changes in plant diversity (Hooper and Vitousek 1997; Tilman et al. 1997*b*; Symstad et al. 1998; Hector et al. 1999). The contrasting response of insects to changes in each component of plant diversity reinforces the need to consider each factor in evaluating how loss of biodiversity affects community or ecosystem properties.

Our study supports previous results showing that the diversity of insects is related to the diversity of their resources (e.g., Murdoch et al. 1972; Southwood et al. 1979; Strong et al. 1984; Siemann et al. 1998; Knops et al. 1999). Our results are also consistent with previous studies of insect abundances in monoculture and polyculture, but they differ in emphasis. In previous studies, diverse treatments contained a small number of functionally disparate plant species. Herbivore abundances in agricultural monocultures were typically compared with diverse plant communities that included weeds or hedgerows, or intercropping systems that combined species as functionally diverse as corn, squash, and beans (Risch 1981). In such systems, changes in plant functional group composition may have been the most important factor causing lower insect abundances at higher plant diversity. In natural ecosystems, much diversity is attributable to the presence of many functionally redundant species (e.g., Naeem and Li 1997; Naeem 1998). At Cedar Creek, for instance, the diversity of prairies and savannas is determined to a great extent by the diversity of forbs. Our results that plant species richness and plant composition influence insect abundances extend findings from previous studies and demonstrate that plant diversity influences insect communities in ways that were not previously detected in agricultural systems.

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