EXPERIMENTAL TESTS OF EFFECTS OF PLANT PRODUCTIVITY AND DIVERSITY ON GRASSLAND ARTHROPOD DIVERSITY

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Abstract. Because the quantity, quality, and heterogeneity of resources should affect the diversity of consumers, plant productivity, plant composition, and plant diversity may influence the diversity of trophic levels higher up the food chain (''bottom-up'' control of diversity). Increasing plant productivity may increase herbivore diversity by: increasing the abundance of rare resources (''resource rarity hypothesis''), increasing herbivore abundance and local persistence (''consumer rarity hypothesis'') or increasing intraspecific density dependence (''density dependence hypothesis''). Increasing plant diversity may increase the diversity of herbivores because herbivores specialized on these new plant species can persist locally. Increasing the diversity of herbivores could likewise increase the diversity of predators and parasites, although parasite and predator diversity may also respond directly to changes in vegetation. Here I use data from a well-replicated grassland experiment at Cedar Creek, Minnesota, to analyze the responses of arthropod diversity to independent manipulations of (1) plant productivity and (2) plant diversity and composition. Long-term nitrogen addition (''historical treatment'') decreased plant diversity and favored C_3 grasses. Short-term nitrogen addition (''modern treatment'') increased plant productivity without appreciably changing plant diversity or plant composition. Arthropods were sampled using both sweep nets and vacuum samplers.

Total arthropod species richness and abundance, as well as species richness and abundance of every trophic group (detritivores, herbivores, parasites, and predators), were significantly greater in plots with higher levels of modern fertilization and greater plant productivity. Path analysis supported the consumer rarity hypothesis, because modern fertilization increased herbivore species richness only indirectly by increasing herbivore abundance. Surprisingly, higher levels of historical fertilization that lowered plant species richness (but did not change plant productivity) significantly increased total arthropod species richness, did not affect detritivore or herbivore species richness, and significantly increased parasite and predator species richness. Direct and indirect effects of historical fertilization on the species richness of trophic groups were separated statistically using block regression chain modeling. Herbivore species richness was decreased through the direct pathway, but this was offset through indirect effects so that there was no overall response to historical fertilization. In plots with low plant diversity, similar numbers of herbivore species supported a greater diversity of parasites and predators. These results suggest that the diversity and composition of plants control the diversity of consumers not only directly by determining available resources, but also indirectly by influencing the interactions between herbivores and their parasites and predators.

Key words: arthropod; bottom-up; composition; direct vs. indirect effects; diversity; grasslands; heterogeneity; Minnesota; productivity; resources; species richness; trophic structure.

INTRODUCTION

Darwin (1859) hypothesized that higher trophic levels enhance the diversity of lower trophic levels by preventing competitive dominance by one or a few species. Theoreticians have formalized his conjectures (e.g., Cramer and May 1972, Roughgarden and Feldman 1975, Levin et al. 1977, Tilman 1986, Holt et al. 1994, Leibold 1996) and modern experiments have established the importance of this ''top-

down'' control of diversity (Hunter and Price 1992) for both plants and herbivores (e.g., Tansley and Adamson 1925, Lubchenco 1978) and for herbivores and predators (e.g., Paine 1966, 1974, Connell 1972). Darwin also hypothesized that the vegetation may influence the diversity of predators by altering the herbivore community. It has often been argued that this effect of the abundance or diversity of lower trophic levels on the diversity of higher trophic levels, ''bottom-up'' control of diversity (Hunter and Price 1992), should be important (e.g., Southwood 1978, Erwin 1982, May 1988, Hunter and Price 1992) but it is less well demonstrated than top-down effects.
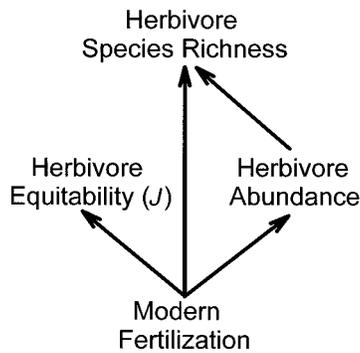
FIG. 1. Path diagram used to test among the three productivity : diversity hypotheses in an experimental study of trophic relations in a Minnesota grassland.

Effects of plants on herbivore diversity

Virtually every ecological model predicts that a more diverse resource base should support a more diverse array of consumers (e.g., MacArthur 1972, Whittaker 1975, Tilman 1986, Rosenzweig 1995) because each additional type of resource can potentially have specialized consumers. Correlational studies of natural systems support a positive relationship between plant diversity and herbivore diversity (e.g., Murdoch et al. 1972, Nagel 1979, Southwood et al. 1979, Prendergast et al. 1993). However, comparisons of agricultural monocultures and polycultures show inconsistent responses of herbivorous arthropod diversity to these differences in plant diversity (Pimentel 1961, Root 1973, Altieri and Letourneau 1982). This may be caused by correlated shifts in plant community composition that affect the nutritional value of the resources (Caswell et al. 1973, Mattson 1980) and thus the number of specialist herbivore species they support (Wilcox 1979, Strong et al. 1984). Also, experimentally increasing plant diversity often increases plant productivity (Naeem et al. 1995, Tilman et al. 1996), which may itself affect consumer diversity.

Increasing plant productivity has been hypothesized to increase consumer diversity by: (1) allowing scarce resources to become abundant enough to support additional species ("resource rarity hypothesis" [MacArthur 1969, Abrams 1995]), (2) allowing rare consumer species to become abundant enough to persist ("consumer rarity hypothesis" [Hutchinson 1959, Preston 1962a, b, Connell and Orias 1964, MacArthur 1965, Brown 1981, Abrams 1995, Rosenzweig 1995]),

or (3) increasing intraspecific density dependence ("density dependence hypothesis" [Abrams 1995]), perhaps through accumulation of specialist predators and/or parasites. These three hypotheses make explicit, testable predictions about the relationships among productivity, herbivore abundance, herbivore species richness, and herbivore equitability (Fig. 1, Table 1).

Empirical evidence supports a unimodal relationship between plant productivity and herbivore diversity on a regional scale (Rosenzweig and Abramsky 1993, Huston 1994, Rosenzweig 1995, but see Abrams 1995 for an alternative view), but this may be caused by correlated changes in plant species diversity or habitat diversity (MacArthur 1964, Pianka 1967, Lawton 1983, Rosenzweig and Abramsky 1993, Tilman and Pacala 1993). The responses of herbivore diversity to experimental changes in plant productivity have been inconsistent, insignificant, or potentially caused by associated changes in plant diversity (e.g., Southwood and van Emden 1967, Hurd et al. 1971, Morris 1971, Hurd and Wolf 1974, Morris and Lakhani 1979, Kruess and Tscharntke 1994).

Parasite and predator diversity

A high diversity of herbivores may support a high diversity of parasites and predators, thus potentially allowing the diversity of plants to "cascade" up to higher trophic levels (Hunter and Price 1992), though factors such as habitat fragmentation (e.g., Robinson et al. 1992) or colonization limitation (Kruess and Tscharntke 1994) may prevent such cascades. On the other hand, plant productivity, plant diversity, and plant species composition may affect the diversity of predators and parasites directly by, for example, influencing the supply of nectar that many parasites require as adults (Price et al. 1980, Powell 1986, Jervis et al. 1993). Increasing parasite and predator diversity may increase herbivore diversity if: (1) there are appropriate trade-offs between competitive ability and predator and parasite resistance (e.g., Cramer and May 1972, Roughgarden and Feldman 1975, Levin et al. 1977, Tilman 1986, Holt et al. 1994, Leibold 1996), (2) predators switch to feed on abundant species (e.g., Murdoch 1969, Janzen 1970, Connell 1979, Murdoch 1994), or (3) prey are clumped (e.g., May 1978, Hassell and Pacala 1990). So in addition to a simple cascade of diversity from plants to herbivores to parasites and predators, there may be a different chain of direct effects up from plant diversity to parasite and predator diver-

TABLE 1. Predicted significance levels and signs of paths in Fig. 1 under each of the three productivity: diversity hypotheses.

Path	Resource rarity	Consumer rarity	Density dependence
Productivity to herbivore abundance	no prediction	significant +	no prediction
Productivity to herbivore species richness	significant +	not significant	no prediction
Herbivore abundance to herbivore species richness	not significant	significant +	not significant
Productivity to herbivore equitability ($J = H'/\ln S$)	not significant	not significant	significant +

Note: In this experiment, modern fertilization was used as a surrogate for productivity in testing these hypotheses.

sity and then down to herbivore diversity. Path analysis is a tool that potentially can be used to discriminate among these different types of interaction chains (Mitchell 1993, Wootton 1994, Smith et al. 1997).

However, significant chains of direct effects in path diagrams may also indicate interaction modifications (see Wootton 1993, 1994). For example, plant diversity and plant composition may influence parasite and predator diversity by changing their foraging efficiency (e.g., Pimentel 1961, Strong et al. 1984, Andow and Prokym 1990) or the nutritional quality of herbivores (Price et al. 1980). Comparisons of the diversities of predators and parasites in agricultural monocultures and polycultures have found, but have not been able to explain, lower diversities of parasites and predators in polycultures (Pimentel 1961, Root 1973). This suggests that interaction modifications may be important.

I am unaware of any experiments that clearly demonstrate the effects of plant productivity and plant diversity on consumer diversity, or that test between the different mechanisms that may be responsible for these effects. The objective of this study was to answer the following questions: (1) Does decreasing the diversity of plants decrease the diversity of primary consumers (herbivores and detritivores) and secondary consumers (predators and parasites)? (2) If so, are these direct responses or indirect responses mediated through other trophic levels? (3) Does increasing plant productivity increase the diversity of primary consumers and secondary consumers? (4) If so, which of the three productivity : diversity hypotheses is the best explanation for these increases? To answer these questions, I determined how grassland arthropod communities responded to independent manipulations of plant productivity vs. plant diversity and composition, employing fertilization on two different time scales.

METHODS

Study site

This work was performed as a split-plot experiment in two upland grassland fields (B and C, in Tilman 1987; fields no. 22 and no. 69 in Inouye et al. 1987) at Cedar Creek Natural History Area (Cedar Creek), which is located ~50 km north of Minneapolis, Minnesota, USA. Fields B and C were last cultivated in 1957 and 1934, respectively (Inouye et al. 1987). Such fields at Cedar Creek are dominated by herbaceous vegetation, especially native perennial prairie plants (Inouye et al. 1987).

Long-term experiment

With the original purpose of studying the effect of nitrogen addition on the plant community, fifteen 20 × 50 m experimental plots were established by D. Tilman in 1982. Each plot received one of three fertilization treatments, with three and two experimental replicates (nine and six randomly assigned plots) located

in fields B and C, respectively. These treatments were a subset of the treatments used by Tilman (1987) and are described only briefly here. (1) Control plots received no fertilizer (treatment I in Tilman 1987). (2) Low fertilization plots (treatment E in Tilman 1987) received 5.4 g N·m^{-2}·yr^{-1} added twice a year as ammonium nitrate and small quantities of the nutrients P, K, Ca, Mg, S, Cu, Zn, Co, Mn, Na, and Mo. (3) High fertilization plots (treatment G in Tilman 1987) received 17.0 g N·m^{-2}·yr^{-1} and the same quantity of other nutrients.

After 9 yr, plots that had received greater amounts of nitrogen had greater plant productivity and lower plant diversity (Tilman 1987; D. Tilman, *personal communication*). The losses of plant species were nonrandom so that as plant diversity decreased, the plants remaining in the plot were biased toward previously rare, fast growing, nonnative C$_3$ grasses (Tilman 1996). Beginning in 1988, the same 20 × 20 m section of each plot was burned every spring, which is likely the timing and frequency of prairie fires before European settlement (Hurlbert 1969). Previous work at Cedar Creek has shown that spring fires have little long-term effect on the diversity or abundance of arthropods (Siemann et al. 1997).

New manipulations

New fertilization treatments were begun in 1993 to separate experimentally the immediate effects of nitrogen addition on plant productivity from the long-term effects on plant diversity and plant composition. Within the burned part of each 20 × 20 m plot, three 6.7 × 10.0 m plots were established, creating a split-plot experimental design with three levels of historical fertilization (related to plant diversity and composition) as the whole-plot factor (i.e., main treatment) and three new fertilization treatments, to manipulate productivity, as the split-plot factor (i.e., subplot treatment).

The goal of these new treatments was to make the productivity of the three types of split plots within each whole plot be equivalent to the productivity of the three types of whole plots prior to the new treatments. The split plots within control (I) whole plots received either treatment I, E, or G as the modern treatments to become high plant diversity and either low, medium, or high plant productivity plots, respectively. The split plots within low fertilization (E) whole plots received either treatment I, E, or G to become medium plant diversity and either low, medium, or high plant productivity plots, respectively. The split plots within high fertilization (G) whole plots received treatments E and G to become low plant diversity and either medium or high plant productivity plots, respectively. Because high amounts of nitrogen had built up in the soils of plots of these treatments compared to the other two (Tilman 1987) that might sustain high levels of productivity (Paul and Clark 1989), a different treatment was used instead of no fertilization (I) to create the

low plant diversity and low plant productivity plots. Screened, kiln-dried maple sawdust (5.28 kg·m⁻²·yr⁻¹) and table sugar (1.32 kg·m⁻²·yr⁻¹) were applied to these plots four times during the 1993 and 1994 growing seasons. This lowered productivity by providing a low nitrogen energy source to soil bacteria, which then removed available nitrogen from the soil, thus depriving the plants of it (Waring and Pitman 1985, Horner et al. 1988).

Plant measurements

In August 1994, relative cover of bare ground, litter and vegetation by species (100% total) were estimated within a marked 1.5×1.5 m area in the center of each plot. Twice in 1994 (early and late August), vegetation was clipped from a 3.0×0.1 m strip along an edge of a marked 3.0×3.0 m area in the center of each plot. These samples were sorted to species, dried, and weighed. Middle to late August is the time of peak standing crop in these fields (D. Wedin, *personal communication*). After weighing, the entire late-August sample for each plot was finely ground in a cyclone mill and measured for total carbon and nitrogen in an automated analyzer (Carlo-Erba NA 1500).

Arthropod sampling

To examine potential biases related to sampling method, two methods were used to sample arthropods: sweep nets and vacuum sampling (i.e., ''D-vac''). Prior to arthropod sampling, no one entered the experimental plots for ≥1 wk and when plots were entered for any activity other than arthropod sampling, all walking was on paving stones (total of ten 20×40 cm stones per plot) to minimize disturbance. Three times in 1994 (16 June, 22 July, and 3 September), each plot was sampled with 50 sweeps of a 37.5 cm diameter muslin net. Twice in 1994 (11 July, 17 August), each plot was vacuum sampled by collecting the arthropods from twelve 20 cm diameter areas (0.376 m² total) located in the central 3.0×3.0 m area of the plot. Each vacuum sample was gently and thoroughly mixed and then divided into 16 subsamples of approximately equal mass. Four randomly chosen subsamples of each vacuum sample and every sweep net sample in its entirety were examined under a dissecting microscope.

Specimens were identified to species, or to morphospecies within known genus or family, and enumerated. Each species was classified by trophic role based on personal observation and literature review (Siemann 1997). The parasite category included all species that are parasitic in the adult stage and parasitoids that are parasitic as larvae regardless of adult diet (primarily nectar, pollen, or host fluids [Clausen 1940]). Nonparasites were classified into three other categories: (1) herbivore, (2) predator, and (3) detritivore, based on whether adults ate primarily (1) plants, (2) animals, and (3) dead matter or fungi, respectively.

Analyses

The experiment had 45 plots (five replicates $\times$ 3 historical treatments $\times$ 3 modern treatments) in two fields (27 plots in field B, 18 plots in field C). The 44 degrees of freedom for analysis by ANOVA (analysis of variance) were: field (1 df), historical fertilization (2 df), whole-plot error (11 df), modern fertilization (2 df), historical $\times$ modern (4 df), modern $\times$ field (2 df), and split-plot error (22 df). Field was treated as a fixed effect and remaining interactions (field $\times$ historical, field $\times$ modern $\times$ historical) were assumed to be negligible. A conservative multiple-range test (Tukey's hsd) was used to compare means for different levels of field, historical fertilization, and modern fertilization.

Modern fertilization: path analysis

Path analysis was used in order to test among the three alternative productivity : diversity hypotheses. Standardized multiple regression coefficients (parameter estimates divided by the ratio of the dependent-variable sample standard deviation and regressor sample standard deviation [SAS Institute 1989]) were used to determine the magnitude and significance levels of each of the four paths (Fig. 1, Table 1). In path diagrams, the magnitudes of direct effects are simply the coefficients for the direct paths, the magnitudes of indirect effects are the products of each direct coefficient along a path, the total magnitude of indirect effects is the sum of the magnitudes of each individual path, and the sum of all possible paths between two variables is equal to their simple correlation coefficient (for more detailed discussion of the mechanics and uses of path analysis see Mitchell 1993, Wootton 1994, Smith et al. 1997).

Historical fertilization: block regression

Because typical path analysis is unable to include reciprocal effects such as those among predators, parasites, and herbivores, I used a closely related area of statistics, block regression chain modeling (both fall under the umbrella of graphical modeling [Cox and Wermuth 1993]), to test for direct and indirect effects of historical fertilization on trophic group diversity. The starting model included effects of historical fertilization on detritivore, herbivore, parasite, and predator species richness as well as all 12 possible relationships among the four trophic groups. Standardized multiple regression coefficients were used to determine the magnitude and significance levels of these paths.

Asymptotic species richness

In order to estimate whether the completeness of my sampling efforts depended on my treatments, I first constructed species accumulation curves (Colwell and Coddington 1994, Siemann et al. 1996). For each sampling method and for each plot, 20 series of increas-

ingly larger random subsamples were drawn from the set of all individuals of all species in the sample, with a maximum of 100 such random draws per series. The resulting curve for each plot and sampling method was fitted (Ordinary Least Squares) with an asymptotic, negative exponential function (Species − [Species − a] × $e^{-b \times [no. individuals]}$). The asymptote estimates the number of species that would be caught in that plot, by that sampling method, with infinite sampling effort. I tested how sampling efficiency (observed species richness divided by estimated species richness) depended on my treatments using ANOVA (same parameterization as for other response variables).

Composition

Because herbivore species composition may depend on experimental treatments even though herbivore species richness may not, I computed the Jaccard indexes of pairs of plots. The Jaccard index is the proportion of the combined set of species present in either of two plots that are present in both plots. I tested if it depended on: whether both plots were in the same field or not, the difference between their historical fertilization treatments (none = 0, low = 1, high = 2), or the difference between their modern fertilization treatments (none = 0, low = 1, high = 2).

Results

Plants

In 1994, the standing crop of plants (average of the two samples) increased significantly with modern fertilization (Fig. 2a) but was independent of field, historical treatment (Fig. 2b), and interaction terms (Table 2). Plant species richness in clipped samples was significantly greater in field C and decreased significantly with historical fertilization (Fig. 2c) but was independent of modern treatment (Fig. 2d) and interaction terms (Table 2). Foliar C:N ratio decreased significantly with historical (Fig. 2e) and modern fertilization treatments (none = 44.8, low = 38.3, high = 27.2) but was independent of field and interaction terms (Table 2). Plant species richness of relative cover samples was significantly greater in field C, decreased significantly with historical fertilization of the 2.25-m² plots (none = 11.6 spp./plot, low = 5.1, high = 1.5) and modern fertilization (none = 6.8, low = 6.6, high = 4.9) but was independent of interaction terms (Table 2). Higher rates of historical fertilization caused significant changes in the proportional cover (Fig. 2f) and species richness of C_3 grasses, C_4 grasses, and forbs (Table 2). Proportional cover of C_3 grasses and plant species richness were highly correlated ($r = -0.81$).

Arthropods

Sweep net and vacuum sampler estimates of arthropod species richness were strongly correlated (overall species richness $r = 0.82$; r values for detritivore, her-

bivore, parasite, and predator species richness = 0.69, 0.75, 0.77, 0.69, respectively) and in every case responded significantly to the same ANOVA model terms. Therefore, I will restrict further discussion to only the sweep net results. (See Appendix for totals by order and trophic group for each sampling method.)

The abundance of arthropods in the three sweep net samples combined for each plot was significantly greater in field C and increased significantly with modern fertilization (Table 2, Fig. 3). The species richness of arthropods was significantly higher in field C, and increased significantly with historical and modern fertilization (Table 2, Fig. 3). Responses of trophic groups to historical fertilization varied (Table 2, Fig. 4). Parasite and predator species richness increased significantly with historical fertilization but detritivore and herbivore species richness were independent of historical fertilization. Detritivore and predator abundance increased significantly with historical fertilization. The abundance and species richness of every trophic group increased significantly with modern fertilization although parasite abundance was highest at low fertilization (Table 2, Fig. 5). No arthropod variables responded significantly to the interaction between historical and modern treatments (Table 2).

Modern fertilization: path analysis

Modern fertilization had a significant direct effect on herbivore abundance (coefficient = +0.48, $P < 0.001$) but not on herbivore species richness ($P = 0.20$) or herbivore equitability ($P = 0.83$). Herbivore abundance had a direct effect on herbivore species richness (coefficient = +0.54, $P < 0.001$) that was significant and positive. Overall R^2 values for herbivore abundance, species richness, and equitability were 0.23, 0.41, and <0.01, respectively.

Historical fertilization: block regression

Historical fertilization had a direct effect on herbivore species richness (Fig. 6) that was significant and negative. However, there were also indirect effects of historical fertilization on herbivore species richness, mediated through parasite and predator species richness, that were significant and positive (Fig. 6). Together these indirect effects were approximately the same magnitude as the direct effect (direct = −0.54; indirect (parasite + predator = total) = +0.35 + 0.21 = +0.56 so that there was a virtually no overall effect of historical fertilization on herbivore species richness (overall = +0.02). Historical fertilization had the following effects on parasite and predator species richness: significant positive direct effects (parasite = +0.57, predator = +0.52), significant negative indirect effects mediated through herbivore species richness (parasite = −0.30, predator = −0.28), significant positive indirect effects mediated through species richness of the other group and herbivore species richness (parasite = +0.11, predator = +0.18) and overall positive
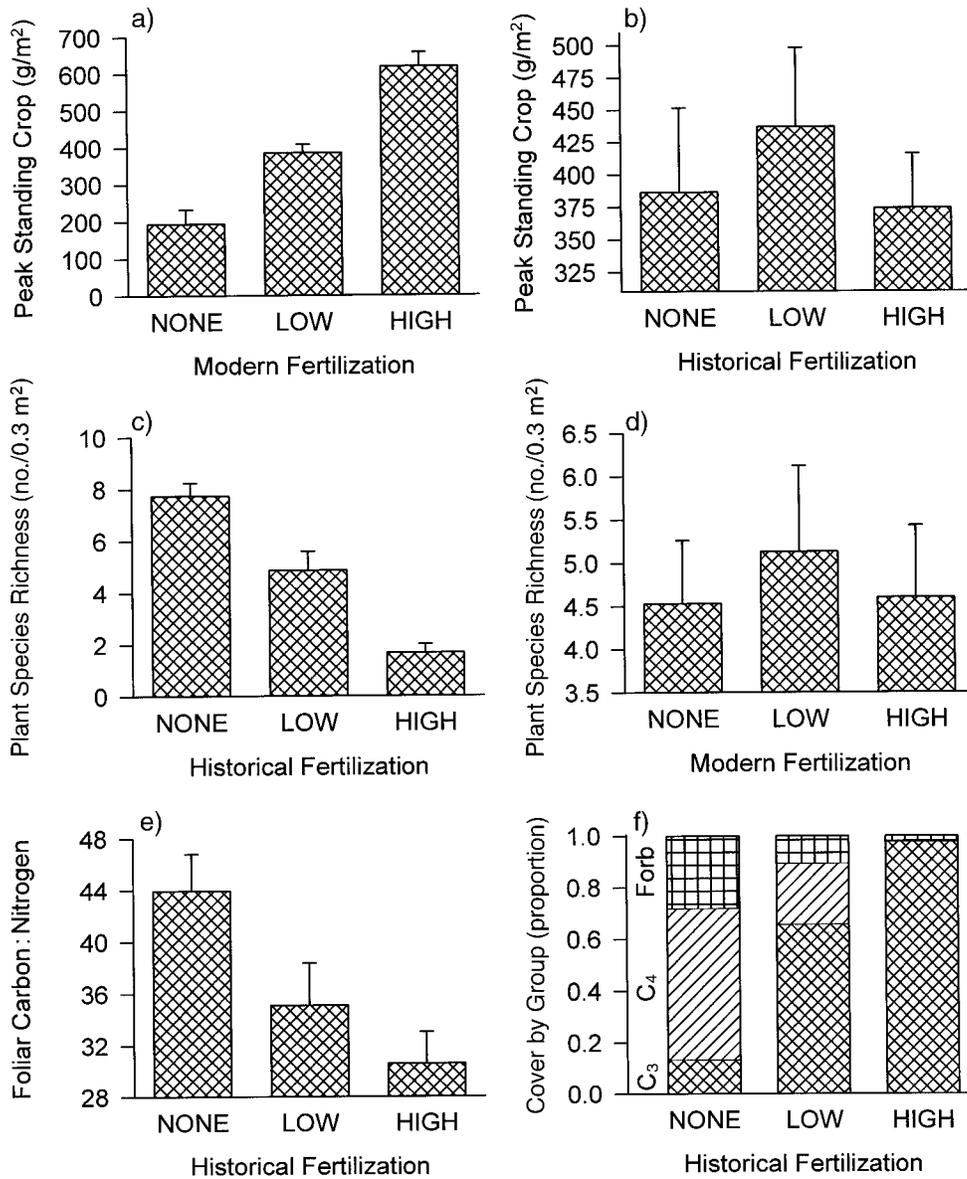
FIG. 2. The responses of vegetation variables to historical (long-term) and modern (short-term) fertilization treatments. In graphs (a)–(e), bars are means and 1 SE. (a), (b) Peak standing crop (g/m²) in 0.3-m² clipped strips; (c), (d) plant species richness in 0.3-m² clipped strips; (e) foliar C:N in clipped 0.3-m² strips; (f) proportions of total vegetation cover in 2.25 m² that were C_3 grasses (bottom), C_4 grasses (middle), and forbs (top) of individual bars. See Table 2 for more statistical information.

effects (parasite = +0.38, predator = +0.42). The direct links between parasite and predator species richness were not significant (parasite to predator, $P = 0.41$; predator to parasite, $P = 0.41$). The overall R^2 values for herbivore, parasite, and predator species richness were 0.59, 0.64, and 0.48, respectively. The links between historical fertilization and detritivore species richness ($P = 0.09$) and between detritivore species richness and species richness of each of the other three trophic groups were not significant (detritivore to herbivore, $P = 0.45$; detritivore to parasite,

$P = 0.18$; detritivore to predator, $P = 0.22$; herbivore to detritivore, $P = 0.16$; parasite to detritivore, $P = 0.30$; predator to detritivore, $P = 0.23$).

Asymptotic species richness

Accumulation curves indicated that, on average, sweep net sampling caught 74.7% of the species per plot. Sampling efficiency was independent of every ANOVA term (field $F_{1,11} = 0.02$, historical fertilization $F_{2,11} = 2.38$, modern fertilization $F_{2,22} = 0.39$, historical × modern $F_{4,22} = 0.22$, field × modern $F_{2,22} = 0.93$).

TABLE 2. Responses of plants and sweep net sampled arthropods to field, historical fertilization, and modern fertilization treatments.

Variable	Field $F_{1,11}$	Contrasts	Historical $F_{2,11}$	Contrasts	Modern $F_{2,22}$	Contrasts	Hist × Mod $F_{4,22}$	Mod × Field $F_{2,22}$
Plant responses								
Clipped biomass	0.1NS		0.7NS		77.2***	N < L < H	0.8NS	0.6NS
Clipped species richness	10.5**	B < C	25.2***	H < L < N	1.0NS		1.0NS	1.1NS
Foliar C:N	0.7NS		6.6*	H = L < N	19.3**	N = L < H	0.6NS	1.5NS
Cover species richness	18.0**	B < C	61.8***	H < L < N	4.4*	H ≤ L ≤ N	0.4NS	0.5NS
C$_3$ grass species richness	2.0NS		45.5***	N < L < H	3.0NS		0.0NS	6.0**
C$_4$ grass species richness	10.1**	B < C	8.1**	H < L = N	0.4NS		4.0*	0.8NS
Forb species richness	12.6**	B < C	23.6***	H = L < N	4.1*	N = L = H	1.1NS	5.4*
C$_3$ grass cover	0.2NS		30.3***	N < L < H	3.2NS		0.6NS	1.9NS
C$_4$ grass cover	1.3NS		25.2***	H < L < N	1.6NS		1.0NS	0.0NS
Forb cover	7.6*	B < C	13.3**	H < L < N	9.1**	H = L < N	1.4NS	8.6**
Arthropod responses								
Total abundance	8.9*	B < C	3.1NS		38.5***	N < L < H	1.9NS	6.9**
Total species richness	25.4***	B < C	6.0*	N = L < H	18.6***	N < L < H	1.2NS	0.7NS
Detritivore abundance	0.7NS		8.9**	N < L < H	34.3***	N = L < H	2.7NS	1.2NS
Detritivore species richness	35.7***	B < C	3.5NS		7.2**	N = L < H	0.8NS	1.7NS
Herbivore abundance	13.2**	B < C	3.9NS		26.1***	N ≤ H ≤ L	2.0NS	6.7**
Herbivore species richness	10.8**	B < C	0.7NS		14.6***	N < L = H	0.7NS	1.6NS
Parasite abundance	0.0NS		2.6NS		5.1*	N ≤ H ≤ L	0.9NS	1.6NS
Parasite species richness	12.8**	B < C	20.6***	N = L < H	8.2**	N < L = H	1.3NS	0.2NS
Predator abundance	0.2NS		4.6*	N = L < H	7.8**	N ≤ L ≤ H	1.4NS	3.2NS
Predator species richness	0.7NS		4.6*	N = L < H	11.7***	N ≤ L ≤ H	0.9NS	1.4NS

Notes: NS means that $P \geq 0.05$, * means that $0.01 \leq P < 0.05$, ** means that $0.001 \leq P < 0.01$, and *** means that $P < 0.001$ for significance test of parameter value difference from zero. Tukey's multiple comparison test results are displayed with treatment means (N = none, L = low, H = high) in ascending order with the following notation: = indicates that the means for the two treatments on either side were statistically indistinguishable ($P \geq 0.05$), < indicates that the mean(s) on the left were significantly less than the mean(s) on the right, ≤ indicates that the means for the two treatments immediately on either side were statistically indistinguishable and that the mean of the treatment on the left end of the list was significantly less than the mean of the treatment on the right end of the list (i.e., N ≤ L ≤ H means that there were two groups of statistically indistinguishable means {N, L} and {L, H} and N was significantly less than H).

Vacuum sampling efficiency was also independent of all factors ($0.09 < P < 0.94$)

Composition

Pairs of plots were significantly more similar in their herbivore species composition if they were in the same field than if they were in different fields (Jaccard index: same field = 0.38, different field = 0.32, $F_{1,988} = 190.7$, $R^2 = 0.16$, $P < 0.0001$). Plots with more similar historical fertilization treatments were significantly more similar in their herbivore species composition (Jaccard index = $0.37 - 0.032 \times$ (difference between treatments), $F_{1,988} = 103.8$, $R^2 = 0.10$, $P < 0.0001$) but those with more similar modern fertilization treatments were not ($F_{1,988} = 2.4$, $P = 0.12$).

DISCUSSION

Responses to historical treatment

Because virtually every plant species has some specialized arthropod herbivores, which in turn have specialized parasites and predators, all else being equal, reducing plant species diversity should reduce arthropod species diversity (MacArthur 1972, Whittaker 1975, Strong et al. 1984, Tilman 1986, Hunter and Price 1992, Rosenzweig and Abramsky 1993, Rosenzweig 1995). However, I found that long-term fertilization of grasslands, which caused a fourfold (clipped samples,

0.3 m², Fig. 2c) to nearly eightfold (cover estimates, 2.25 m²) decrease in the number of plant species and a shift to C$_3$ grasses (Fig. 2f), caused no detectable changes in detritivore or herbivore species richness (Fig. 4a, b, Table 2), significantly increased parasite and predator species richness (Fig. 4c, d, Table 2), and therefore significantly increased overall arthropod species richness (Fig. 3a, Table 2). At first glance this appears to be strong evidence against bottom-up control of arthropod diversity by plant diversity and presents two questions: (1) Why did lowering the diversity of plants not decrease herbivore diversity? (2) Why, without changing the diversity of detritivores and herbivores, did lowering plant diversity increase the diversity of parasites and predators?

Herbivore diversity

When the direct effect of historical fertilization on herbivore species richness was separated statistically from indirect effects mediated through other trophic groups, I found that increasing historical fertilization and lowering plant species richness did indeed significantly decrease herbivore species richness (Fig. 6). However, historical fertilization also significantly increased herbivore species richness indirectly by significantly increasing parasite and predator species richness (Fig. 6). Because these indirect increases in her-
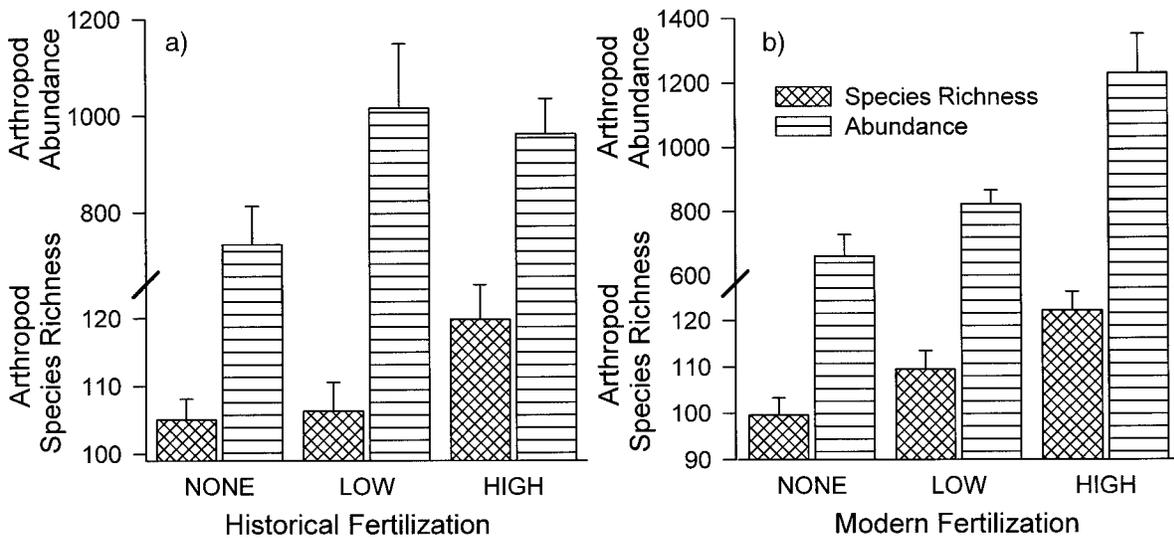
FIG. 3. The responses of arthropod species richness and abundance (each summed across all three sampling periods) in sweep net samples to (a) historical and (b) modern fertilization treatments. Bars are means and 1 SE. Note the break in each y axis between species richness and abundance. See Table 2 for more statistical information.

bivore species richness had together approximately the same magnitude as the direct effect of historical fertilization, the significant direct and indirect responses of herbivore diversity to changes in plant diversity and composition were both hidden. This suggests that, in this experiment, as plant diversity decreased along the historical fertilization gradient and the importance of bottom-up control of herbivore diversity decreased, compensating increases in the strength of top-down control by parasite and predator diversity allowed similar numbers of herbivore species and greater numbers of parasite and predator species to persist on far fewer species of plants.

This suggests that two different mechanisms may be responsible for the high local diversity of arthropod herbivores and that each may predominate in different environments. In high plant diversity environments, compartmentalization of the herbivore community into guilds associated with subsets of the plant community (Root 1967, Hawkins and MacMahon 1989, Simberloff and Dayan 1991) may allow a large number of herbivore species to coexist (May 1973, Pimm 1979). In low plant diversity systems, a high diversity of predators and parasites may keep each herbivore species at a low enough density so that a large number can coexist. The significant shift in herbivore species composition in response to historical fertilization is consistent with this idea. Because the changes in plant diversity and composition in this experiment took place gradually (over a period of 3–4 yr [Tilman 1993]) and remained at these new levels of plant diversity for another 5–6 yr before the present experiment was begun, this may explain why parasites and predators apparently were able to compensate for these losses in plant diversity

in this study even though they have not been able to in other studies (Kruess and Tscharntke 1994).

In the ANOVA (Table 2) and the block regression chain model, detritivore species richness was unrelated to historical fertilization and the species richness of every other trophic group. This result implies that there may not be much food specialization in detritivore communities (Vegter 1982, Werner and Dindal 1987). This also suggests that even though generalist consumers are required for ''top-down'' effects on standing crops to cascade down to lower trophic levels (Leibold 1989), specialist consumers may be crucial for bottom-up effects on diversity to cascade up to higher trophic levels.

Parasite diversity

Plant diversity did indeed cascade up the food chain from plants to herbivores to predators and parasites (Fig. 6). However, this cannot explain the greater species richness of parasites and predators in plots with greater rates of historical fertilization and lower plant species richness (Fig. 4c, d). Rather, the greater species richness of parasites and predators in these plots is due to what appear as direct responses to historical fertilization (Fig. 6). One possible explanation is that these are in fact direct responses to plant diversity and composition. For example, many parasites and some predators require nectar (Price et al. 1980, Powell 1986, Jervis et al. 1993) but this is unlikely to explain their responses here because the low plant diversity plots were almost entirely C_3 grasses (Fig. 2f), which do not produce nectar (Lovell 1926).

A more likely explanation is that these direct effects reflect interaction modifications (Wootton 1993, 1994).
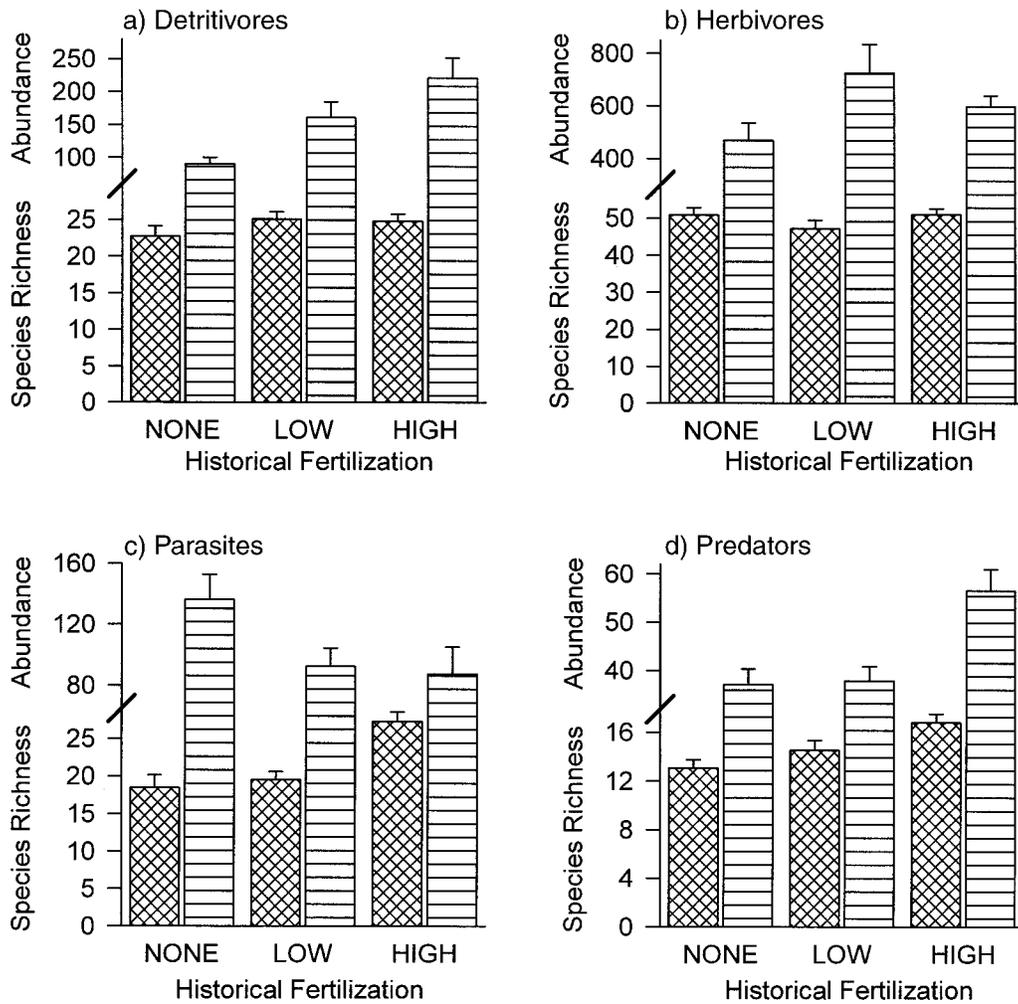
FIG. 4. The responses of species richness and abundance (each summed across all three sampling periods) of arthropod trophic groups in sweep net samples to historical fertilization treatments. Bars are means and 1 SE. Note the break in each y axis between species richness and abundance. See Table 2 for more statistical information.

Changing plant diversity and composition may have changed the interactions between herbivores and their predators and parasites, perhaps by changing the ease with which herbivores can be caught because predators and parasites have difficulty foraging in physically complex environments (e.g., Pimentel 1961, Price et al. 1980, Lawton 1983, Strong et al. 1984, Andow and Prokym 1990). Because historical fertilization also changed plant functional composition (significantly increased cover of C_3 plants and significantly decreased foliar C:N ratio, Fig. 2e, f, Table 2), parasites and predators may be sensitive to changes in the types and nutritional quality of herbivores. Because plant diversity and plant composition responses were so highly correlated in this experiment ($r = -0.81$), it is difficult to separate reliably their individual effects on the arthropod community. The path diagram also indicates, perhaps spuriously, that a diversity of parasites promotes a diversity of predators, and vice versa, by in-

creasing herbivore diversity (Fig. 6). More generally, these results suggest that the diversity, quality, and/or species composition of plants may influence the diversity of higher trophic levels not only by changing the diversity of herbivores but also by changing the food quality of herbivores and the ease with which they can be captured.

Responses to modern treatment

The abundance and species richness of arthropods increased significantly with modern fertilization, both overall (Fig. 3b, Table 2) and within every trophic group (Fig. 5, Table 2). Path analysis showed no effect of modern fertilization on herbivore equitability contrary to the prediction of the density dependence hypothesis but in agreement with the other two hypotheses (Table 1, Fig. 1). There was no significant direct effect of modern fertilization on herbivore species richness, which is evidence against the resource rarity hy-
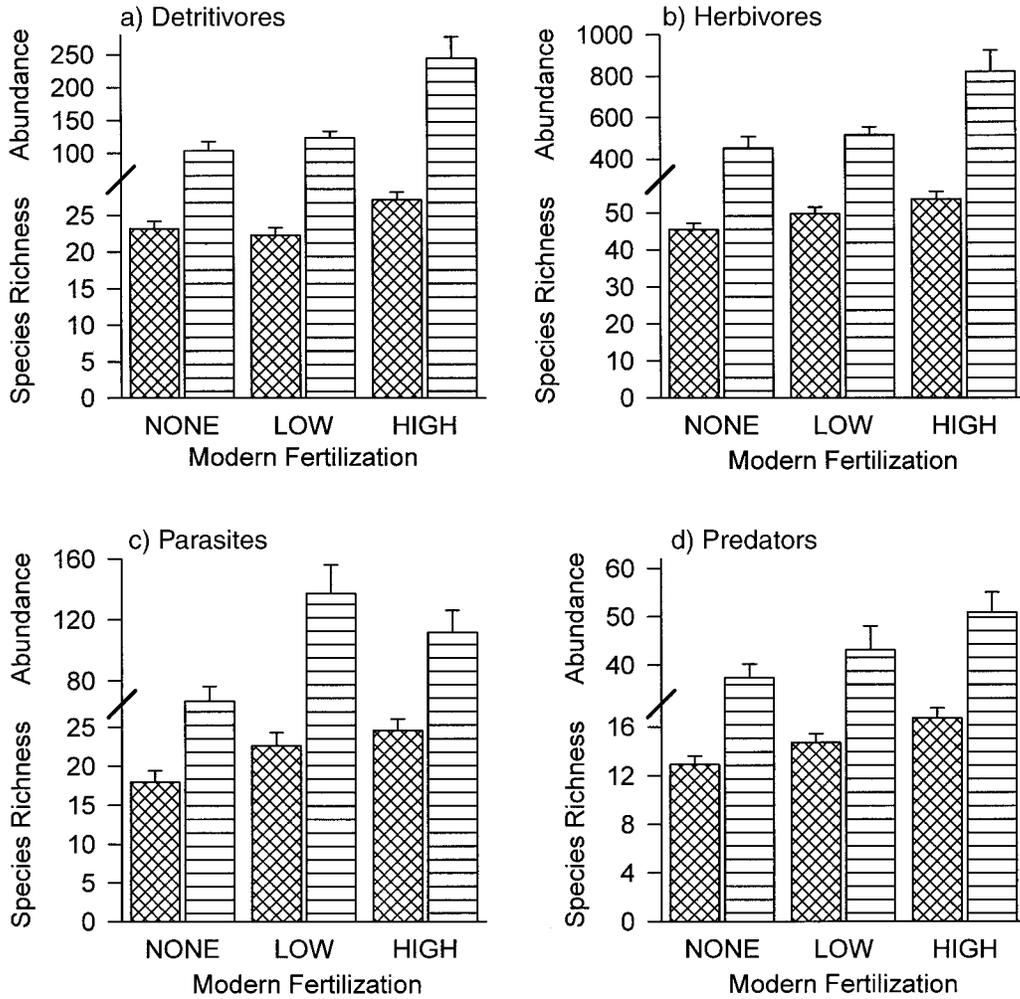
FIG. 5. The responses of species richness and abundance (each summed across all three sampling periods) of arthropod trophic groups in sweep net samples to modern fertilization treatments. Bars are means and 1 SE. Note the break in each y axis between species richness and abundance. See Table 2 for more statistical information.

pothesis (Table 1, Fig. 1). There was a significant indirect effect of modern fertilization on herbivore species richness mediated through herbivore abundance as predicted by the consumer rarity hypothesis. Together,

these results are evidence that plant productivity increases herbivore diversity by increasing the total number of herbivore individuals and allowing rarer species to persist locally (Hutchinson 1959, Preston 1962a, b,
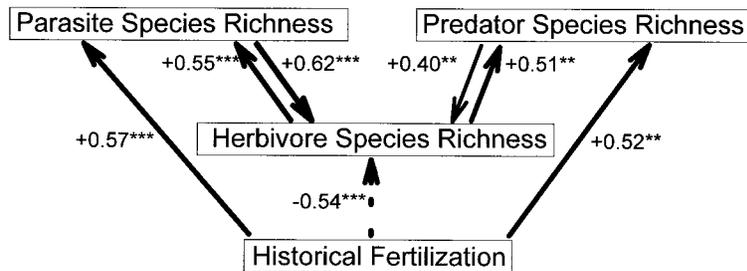
FIG. 6. Path diagram showing significant ($P < 0.05$) direct and indirect effects of historical fertilization on trophic group species richness. The number next to each arrow and the thickness of the arrow both indicate the magnitude of the path coefficient. Negative effects are shown with a dotted arrow. Significance levels: *$0.01 \leq P < 0.05$, **$0.001 \leq P < 0.01$, ***$P < 0.001$. For the sake of visual clarity, nonsignificant paths are not shown.

Connell and Orias 1964, MacArthur 1965, Brown 1981, Abrams 1995, Rosenzweig 1995). The independence of herbivore species composition and modern fertilization are also consistent with this hypothesis. These results strengthen the suggestion that the cause of unimodal productivity/diversity patterns is likely to be some factor that is correlated with productivity, such as plant and/or habitat heterogeneity, and not productivity itself (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995, Rosenzweig 1995).

Caveats

Even though path analysis offers advantages over conventional multiple regression in inferring complex mechanisms of response to manipulation of a single trophic level, path analysis still can only reveal patterns of correlation (Smith et al. 1997). Although the path analysis results in this study strongly suggest that the relationship between abundance and persistence is largely responsible for the relationship between herbivore species richness and modern fertilization, they cannot establish causation. Similarly, although block regression chain model results suggest that interactions within the arthropod community are largely responsible for their high local diversity, this is only a hypothesis. Experimental manipulations of herbivore, parasite, and predator diversity are needed to definitely establish the mechanisms allowing a high local diversity of arthropods

Artifacts

Although arthropod communities are sensitive to habitat fragmentation (e.g., Robinson et al. 1992, Kruess and Tscharntke 1994, Roland and Taylor 1997), the lack of any significant effect of the interaction between modern and historical fertilization treatments on any arthropod response variable (Table 2) indicates that the effects of modern fertilization were independent of the larger plot in which these experimental plots were imbedded. Of course, the effects of historical fertilization were confounded by being embedded in larger plots of the same plant diversity and plant composition but the split-plot analysis controls for these effects. Treatment-dependent differences in arthropod sampling efficiency are also an unlikely explanation for the results of this study because sampling efficiency was independent of every ANOVA term. Finally, these results are not likely to be artifacts of a single method of sampling arthropods because the two different sampling methods gave the same results.

Conclusions

This experiment demonstrates that (1) the species composition or diversity of plants and (2) the productivity of plants in a local area all influence the diversity of higher trophic levels. A simple cascade of diversity up the food chain from plants to herbivores and from herbivores to parasites and predators appears to be part-

ly responsible for the effects of plant diversity. Decreasing plant species diversity also potentially decreased herbivore species richness indirectly either via a chain of direct interactions or more likely by modifying the interactions between herbivores and their parasites and predators. Increasing productivity increased herbivore diversity indirectly by increasing herbivore abundance. The near ubiquity of significant effects of field in this experiment (Table 2) is suggestive that the pool of species available to colonize a local site may also be important in determining local diversity (Cornell 1993). The sensitivity of herbivore, parasite and predator diversity to simultaneous manipulations of both plant diversity and plant composition supports a need for further studies to tease apart the bottom-up forces controlling animal diversity.

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APPENDIX

Numbers of species (SR) and individuals (AB) within taxonomic and trophic groups for each sampling method.

Group	Sweep net		Vacuum sampler	
	SR	AB	SR	AB
Araneida (spiders)	32	734	38	904
Coleoptera (beetles)	64	1 569	59	1 535
Diptera (flies)	156	8 224	109	4 859
Hemiptera (bugs)	36	2 581	28	1 100
Homoptera (leafhoppers)	65	16 435	54	14 701
Hymenoptera (bees, ants, wasps)	205	6 783	163	2 745
Lepidoptera (moths)	47	680	14	287
Miscellaneous†	18	3 180	20	5 523
Orthoptera (grasshoppers)	27	506	12	48
Total	650	40 692	497	31 702
Detritivores	118	7 084	97	4 902
Herbivores	240	26 891	148	23 073
Parasites	201	4 745	153	1 626
Predators	91	1 972	99	2 101
Total	650	40 692	497	31 702

† Miscellaneous includes Acari (mites), Collembola (springtails), Ephemeroptera (mayflies), Isoptera (termites), Neuroptera (lacewings), Odonata (dragonflies), Opiliones (harvestmen), Pseudoscorpiones (pseudoscorpions), Psocoptera (barklice), and Thysanoptera (thrips).