

Community-wide trophic cascades and other indirect interactions in an agricultural community

Lee A. Dyer* and John O. Stireman III

Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, USA

Received June 10, 2002 · Accepted November 21, 2002

Abstract

A current goal in ecology is to elucidate the relative roles of primary and secondary consumers versus plant resources in determining community structure and dynamics. The complexity and diversity of terrestrial communities has been hypothesized to strongly influence the strength of these top-down and bottom-up forces, and in turn, trophic interactions are predicted to have significant consequences for species diversity within trophic levels. To examine the relative strengths of top-down and bottom-up trophic interactions and their relationship to arthropod diversity in an agricultural ecosystem, we conducted experiments in two alfalfa fields with different management regimes in which we manipulated light availability, nutrients, and arthropod abundance. We employed path analysis to examine how variation generated by these manipulations influenced top-down and bottom-up trophic pathways, focusing on alfalfa productivity and the abundance and species richness of arthropods. These analyses revealed a number of complex interactions between treatments and each of the three trophic levels. Shade structures had a strong effect on enemy, herbivore, and plant trophic levels, but much of the effect on plant biomass appeared to be mediated indirectly through changes in enemy and herbivore abundance. Potential positive effects of nutrient addition on alfalfa biomass were negated due to increases in abundance of soil microbes in the intensively managed field and herbivores in the weedy field. In the intensively managed, low arthropod abundance field, alfalfa biomass increased with herbivore diversity. However, in the lightly managed fields, herbivore diversity, which increased significantly with nutrient addition, reduced alfalfa biomass. The indirect top-down and bottom-up effects uncovered in this experiment were strong, but were not limited to the classic trophic cascades that have been the subject of intense recent investigation.

Ein derzeitiges Ziel der Ökologie ist es, die relative Bedeutung von primären und sekundären Konsumenten im Gegensatz zur Bedeutung der Pflanzenressourcen auf die Bestimmung der Struktur und Dynamik von Lebensgemeinschaften zu beleuchten. Es wurde die Hypothese aufgestellt, dass die Komplexität und Diversität terrestrischer Lebensgemeinschaften einen starken Einfluss auf die Stärke dieser „top-down“ und „bottom-up“-Kräfte hat. Daher wurde vorhergesagt, dass trophische Interaktionen ihrerseits signifikante Auswirkungen auf die Artendiversität in trophischen Ebenen haben. Um die relative Stärke der trophischen „top-down“ und „bottom-up“-Interaktionen und ihre Beziehung zur Arthropodendiversität in einem Agrarökosystem zu untersuchen, führten wir Experimente in zwei Luzernefeldern mit unterschiedlichen Bewirtschaftungsformen aus, in welchen wir die Lichtverfügbarkeit, die Nährstoffe und die Arthropodenabundanz manipulierte. Wir wendeten eine Pfad-Analyse an, um zu untersuchen, wie die durch die Manipulationen erzeugte Variation die trophischen „top-down“ und „bottom-up“-Bahnen beeinflusst, wobei wir uns auf die Luzerneproduktivität sowie die Abundanz und den Artenreichtum der Arthropoden konzentrierten. Diese Analysen deckten eine Anzahl komplexer Interaktionen zwischen den Behandlungen und

*Corresponding author: Lee A. Dyer, Department of Ecology and Evolutionary Biology, 310 Dinwiddie Hall, Tulane University, New Orleans, LA 70118 USA, Phone: 504-862-8288, Fax: 504-862-8706, e-mail: ldyer@tulane.edu

jeder der drei trophischen Ebenen auf. Schattenstrukturen hatten einen starken Effekt auf der Feind-, Herbivoren- und Pflanzen-Ebene. Allerdings schien ein Großteil des Effektes auf die Pflanzenbiomasse indirekt durch Veränderungen der Abundanz von Feinden und Herbivoren ausgeglichen zu werden. Potenzielle positive Effekte durch die Zugabe von Nährstoffen auf die Luzernebiomasse wurden durch die Zunahme der Abundanz der Bodenmikroorganismen in den intensiv gepflegten und der Herbivoren in den verunkrauteten Feldern aufgehoben. In dem intensiv gepflegten Feld mit geringer Arthropodenabundanz nahm die Luzernebiomasse mit der Herbivorendiversität zu. In den weniger intensiv gepflegten Feldern reduzierte die Herbivorendiversität, die signifikant mit der Nährstoffzugabe zunahm, die Luzernebiomasse. Die indirekten „top-down“ und „bottom-up“-Effekte, die mit diesem Experiment entdeckt wurden, sind stark, waren aber nicht auf die klassischen trophischen Kaskaden beschränkt, die Gegenstand jüngster, intensiver Forschung waren.

Key words: tritrophic interactions – alfalfa – arthropod diversity – natural enemies – herbivores

Introduction

A long-term goal of ecologists is to understand the role of trophic interactions in shaping community structure. Resource availability (“bottom-up” factors) and natural enemies (“top-down” factors) both affect various aspects of community structure, but the extent to which species diversity determines and is determined by these forces has been the subject of considerable debate (Tilman 1986, Leibold 1996, Polis et al. 2000). In general, it has been predicted that low diversity systems that have few interconnecting trophic links are much more likely to experience strong top-down trophic cascades (i.e. indirect effects of upper trophic levels on plants) than those containing many species (Polis & Strong 1996). Diverse communities may also be more likely to display high levels of intraguild predation, contain more functional redundancy (Lawton 1994), and contain more omnivores, which would further dilute the potency of top down forces (Vadas 1989, Polis & Holt 1992, Strong et al. 1999). This prediction has been upheld in some experimental field studies but not others (reviewed by Hunter 2001, Shurin et al. 2002). The effects of top-down and bottom up forces on the species diversity within various trophic levels are equally controversial and even less well understood. Some theoretical and empirical studies suggest that herbivore and natural enemy diversities increase with primary productivity (Hutchinson 1959, MacArthur 1965, Abrams 1995, Rosenzweig 1995), however many empirical studies have shown either no effect or the reverse (Hurd & Wolf 1974, Siemann 1998, Kassen, et al. 2000, Mittelbach et al. 2001, also see Aarssen 2001). Likewise, several studies have indicated that top-down forces can alter the diversity of primary producers (Paine 1966, Carter & Rypstra 1995, Wootton 1995, Schoener & Spiller 1996, Carson & Root 2000, Dyer & Letourneau 1998).

These issues of trophic dynamics and species diversity are of great theoretical interest and have important implications for a variety of applied fields, in-

cluding conservation biology (Terborgh 2001) and agriculture (Schlöpfer & Schmid 1999). An understanding of the trophic components in agricultural ecosystems and the direction and magnitude of their interactions can directly inform management practices across natural and agricultural communities. Many studies have examined the effects of specific natural enemies in agricultural systems (e.g., Jervis & Kidd 1996), but it is equally interesting to do so at the scale of the entire community (i.e. crop, weeds, herbivores, enemies). Here we present the results of two experiments that examine trophic interactions within alfalfa agroecosystems. The primary questions we seek to address are: 1) What are the relative strengths of top-down and bottom-up pathways in agricultural systems? 2) How are the diversities of herbivorous arthropods and their natural enemies influenced by the strength and direction of trophic interactions? and 3) How do these interactions affect the quantitative yield of alfalfa?

Materials and methods

The first of two experiments was conducted in 1998 in low-diversity alfalfa fields near the town of Fruita, Colorado (1375 m, 39°09'N 108°43'W), managed by the Western Colorado Research Center (WCRC). Average annual precipitation at the site is 20 cm, and the fields are irrigated by gated pipe and furrows with ditch water from the Colorado River. The alfalfa was planted in August of 1995; 448 kg per hectare of 0–45–0 (NPK) was broadcast applied then disced and plowed before planting. In February 1997 and 1998, 1 lb per acre of the herbicide, Sencor DF (metribuzin), was applied to the field, and in May 1998, 2 pints per acre of the general insecticide, Furadan 4F (carbofuran), was applied to all plots. We conducted our manipulations during the third harvest from 31 July to 18 August 1998.

The experiment employed a factorial design involving three dichotomous treatments: shade, nutrient addition, and arthropod abundance. We created forty 1.5 m² (1 m by 1.5 m) plots and randomly assigned them to treatments, such that each treatment combination was replicated 5 times. Shading and fertilizer were used to examine community effects of reduced primary productivity and enhanced mineral resources. Shade treatments were covered by a 1.5 m² sheet of 15% ambient shade cloth suspended from wooden stakes 1 m above the ground. While these manipulations cut light availability, they also provided a novel habitat for various arthropods; this is a realistic manipulation of light availability because in most terrestrial systems variation in light availability is accompanied by variation in habitat complexity. We used path analysis and a follow-up experiment (see below) to tease apart effects of light versus the novel habitat provided by the shade structures. Fertilizer treatments consisted of the application of 50 g of 18-46-0 (N-P-K) and 50 g of 0-0-50 fertilizer (Pursell Industries) to each of the treated plots. Arthropods were removed by sweeping each of the designated plots every three days with a heavy sweep net. Plots that did not receive the sweep treatment were swept with a net hoop lacking a sweep bag to control for potential direct effects of sweeping on the alfalfa plants. The goal of this sweeping treatment was to reduce the overall abundance of insects in order to generate variance in herbivore and natural enemy abundance between plots. At the beginning of the experiments, the effects of the sweeps on the arthropod community were tested by sweeping 5 of the same sized plots in the same fields and sampling these along with 5 control plots 24 hours later. For this and the second experiment, sweeping substantially reduced the abundances of herbivores and predators, and the effect appeared to be stronger for predators (Table 1); species richness was unaffected by sweeping (Table 1).

Table 1. Species richness (top numbers) and abundance (bottom numbers) of herbivores and natural enemies in pre-experimental swept and unswept plots for WCRC and MSC alfalfa fields. All sweeps for estimates of species richness and abundance were conducted 24 hours after the sweeps. Mean \pm 1 SE (N = 5) are shown for all values.

		WCRC		MSC	
		Herbivores	Enemies	Herbivores	Enemies
Sweep:	Richness	5.6 \pm 1.1	5 \pm 1	7.2 \pm 1.1	3 \pm 1.4
	Abundance	8.4 \pm 1.1	9.8 \pm 1.6	86.8 \pm 9.7	3.6 \pm 0.2
*No Sweep:	Richness	5.2 \pm 1.3	5.2 \pm 1.7	6 \pm 1.4	2.4 \pm 1.1
	Abundance	12 \pm 1.8	23 \pm 2.9	97.8 \pm 7.4	7 \pm 0.8

*All no-sweep plots were subjected to the sham treatment of sweeping with a hoop only.

In 1999 we performed a second experiment using experimental alfalfa fields (33 ha) managed by Mesa State College (MSC) that were located approximately 10 km from the WCRC fields (39°03'N 108°33'W with the same soils, rainfall, and irrigation scheme). These fields, leased to a local farmer, were under a much less intensive management regime and had not been subject to pesticide, herbicide, or fertilizer applications for at least five years preceding the inception of our experiment. They were characterized by lower yields on average and much higher diversity and abundance of weedy plant species such as *Convolvulus arvensis*, *Taraxacum officinale*, and *Chorispora tenella* (Abundance/plot [X \pm SE]: 45.8 \pm 3.5; species/plot: 4.9 \pm 0.15). The experiment was conducted during the third harvest for these fields, from June 30–July 23. The design of the experiment and number of replicates was identical to the 1998 WCRC experiment except that all plots received shade, and the shade treatment consisted either of low shade (30% ambient shade cloth) and high shade (15% ambient shade cloth). This was done to control for effects of the shade structure observed in the initial WCRC experiment.

For both experiments, all response variables were measured for all plots both at the beginning (before treatments were applied) and end (immediately prior to alfalfa cutting) of the experiments. Insect sampling was conducted from 0815 to 1000 hrs, and consisted of ten 180° sweeps per plot. Insects were sorted into morphospecies, identified to lowest possible taxon (family, genus, or species), and classified into major trophic guilds (e.g. predator, herbivore, decomposer). Alfalfa plant sampling was conducted by using plot outlines (lathe with 10 cm increments marked on it) and a random numbers table to select three plants per plot according to their coordinates. Only plants with three or more shoots were selected to gauge effects on biomass. These plants were then shade dried and weighed. For the first experiment, microbial abundance per gram dry weight of soil was measured for one randomly located soil sample from each plot (1 g of surface soil wet weight, to ca. 5 mm depth); we followed the procedures of Weaver et al. (1994) to measure abundance in these samples.

Although treatments were initially designed to alter the strength of top-down and bottom-up forces, we were not able to specifically manipulate particular trophic levels without simultaneously affecting the others. This is a common problem in field and laboratory experiments and it limits the ability to identify the causes of treatment effects (Shipley 2000). Typically manipulations that are realistic are likely to affect more than just the target variable. For these reasons, we combined our experimental approach with path analysis to test hypothesized pathways of treatment ef-

fects and relationships between response variables.

The results of each experiment were analyzed separately using similar statistical methods. Initially, MANCOVAs were used to analyze the direct effects of manipulations on arthropod diversity in both experiments, with the species richness and abundance of herbivores and natural enemies as dependent variables and fertilizer, shade, and sweep treatments as independent variables. To control for preexisting variation in diversity among plots the initial measures of abundance and species richness per plot were included as covariates. When covariates and their interactions were insignificant, they were dropped from the model. Profile analysis was subsequently used to test the null hypothesis that abundance and species richness measures did not differ in their responses to the treatments (Tabachnik & Fidell 1996). Similar ANCOVAs were used to assess the impacts of independent variables on plant biomass and microbial abundance, with initial measurements included as covariates. To investigate how particular herbivore and enemy groups responded to our manipulations, we conducted additional ANOVAs of abundance for the three most common herbivores and enemies in each experiment. All abundance variables were log-transformed to meet assumptions of normality.

We used path analysis (Mitchell 2001) to further explore the effects of treatments and diversity within trophic levels on the interactions among them. Standardized correlation coefficients between variables (SAS institute, CALIS procedure) and η^2 values were calculated and plotted as path coefficients on path diagrams constructed for each experiment. Structural equation modeling (SEM) was then used to differentiate between alternate causal hypotheses for the observed data (Ullman 1996). Due to the low species richness and strong effects of treatments on herbivore and enemy abundance in MANCOVA models, path analysis of the first experiment focused on abundance. In the second experiment we focused our path analysis on herbivore and enemy species richness due to the dominance of abundance measures by one small-bodied herbivore, *Acyrtosiphon pisum* (Aphididae). All analyses were performed using SAS (SAS Institute Inc. 1989).

Results

Arthropod abundance and species richness differed between the heavily managed WCRC alfalfa agroecosystem, and the less intensively managed MSC experimental fields (Fig. 1). The average abundance of herbivorous arthropods in the intensively managed fields was less than 5% that of the weedy MSC fields. In contrast, enemies (predators and parasitoids) were

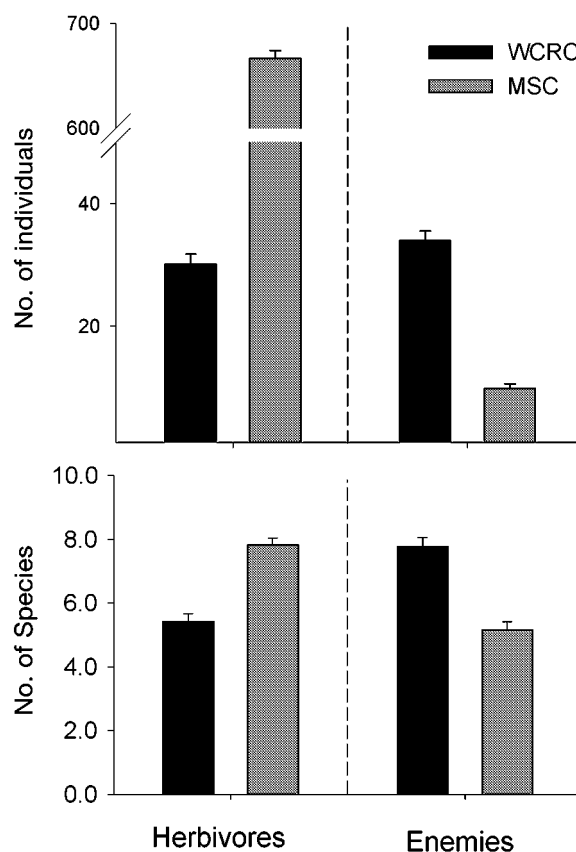


Fig. 1. Mean arthropod abundance (top) and species richness (bottom; \pm SE) for herbivores and Natural enemies in the Western Colorado Research Center (WCRC) fields and Mesa State College fields (MSC). For each field, N = forty 1.5 m² plots.

more diverse and abundant in the intensively managed fields (Fig. 1). In both experiments we found no significant relationship between initial measures of dependent variables (alfalfa biomass, arthropod abundance and species richness) and those recorded after treatments were applied; thus these covariates were excluded from ANCOVA and MANCOVA models.

Experiment One

In the WCRC experimental plots, both the shade and arthropod removal treatments had a significant impact on the alfalfa arthropod community (Table 2). The presence of shade structures increased enemy densities and decreased herbivore densities. Species richness was either lower in shaded plots (herbivores [$X \pm SE$]: 4.60 ± 0.245 versus 6.25 ± 0.315 in open plots) or was unaffected (enemies; see profile analysis Table 2). Arthropod removal (via sweeping) had a negative effect on herbivore densities, but did not significantly affect predators and parasitoids. Experimental treat-

Table 2. Arthropod diversity results from MANCOVA and profile analyses for Experiment 1 conducted in the low diversity WCRC fields. In all analyses covariates (initial measurements of variables) were non-significant and dropped from the models. Degrees of freedom for all analyses are ($F_{1,32}$). P-values less than 0.10 are accentuated in bold; the alpha for hypotheses tests was 0.05.

Factor	MANCOVA		Profile Analysis	
	F	P	F	P
<i>Herbivores</i>				
<i>Abundance vs. Richness</i>				
Shade	19.20	0.000	14.22	0.001
Nutrients	0.59	0.446	1.83	0.186
Sweep	8.26	0.007	8.95	0.005
Shade x Nutrients	0.04	0.835	0.28	0.598
Shade x Sweep	1.26	0.270	1.22	0.277
Sweep x Nutrients	1.03	0.317	0.97	0.333
Shade x Sweep x Nutrients	0.77	0.387	0.67	0.418
<i>Enemies</i>				
<i>Abundance vs. Richness</i>				
Shade	3.55	0.069	6.88	0.013
Nutrients	0.26	0.611	0.37	0.549
Sweep	2.55	0.121	1.86	0.182
Shade x Nutrients	0.29	0.595	0.03	0.855
Shade x Sweep	0.22	0.645	0.44	0.513
Sweep x Nutrients	0.62	0.435	0.48	0.495
Shade x Sweep x Nutrients	0.00	0.977	0.13	0.719

Table 3. Results from ANCOVA analyses of alfalfa biomass and soil microbe abundance for Experiment 1 conducted in the low diversity WCRC fields. In all analyses covariates (initial measurements of variables) were non-significant and dropped from the models. Degrees of freedom for all analyses are ($F_{1,32}$). P-values less than 0.10 are accentuated in bold; the alpha for hypotheses tests was 0.05.

Factor	Alfalfa Biomass		Soil Microbes	
	F	P	F	P
Shade	5.18	0.030	1.59	0.216
Nutrients	0.69	0.413	9.67	0.004
Sweep	3.65	0.065	55.5	0.014
Shade x Nutrients	2.10	0.157	6.74	0.000
Shade x Sweep	0.09	0.763	3.98	0.055
Sweep x Nutrients	0.55	0.464	3.81	0.060
Shade x Sweep x Nutrients	0.77	0.387	1.44	0.240

ments also affected alfalfa biomass and microbial diversity (Table 3). Shade resulted in a large decrease in alfalfa biomass relative to unshaded plots ($[X \pm SE]$: $18.2\% \pm 5.3$), as would be expected if rates of photosynthesis were limited. Also, rather than enhancing alfalfa productivity, nutrient addition was observed to have no significant direct effect on alfalfa biomass (Table 3; but see path analysis below for direct versus indirect effects). Contrary to expectations, the arthropod removal treatment, which decreased herbivore abundance, also decreased alfalfa biomass relative to no removal plots ($14.3\% \pm 6.7$). Fertilizer addition significantly increased soil microbe abundance, espe-

cially under high light levels. The arthropod removal treatment significantly decreased soil microbe abundance (Table 3). Interactions between arthropod removal and both fertilizer and shade also tended to affect soil microbe number, though these effects were not significant.

The most abundant herbivores in the plots, mirid bugs (primarily *Lygus* spp.), were affected significantly by both shading and arthropod removal, with higher numbers in plots with shade structures (shade: 20.7 ± 1.10 , no shade: 14.3 ± 1.145 ; $F_{1,32} = 19.96$, $P < 0.001$) and in plots subjected to arthropod removal (removal: 19.70 ± 1.44 , no removal: 15.3 ± 1.00 ; $F_{1,32} = 9.43$, $P = 0.004$). Aphids, also relatively abundant, exhibited a more complex response, responding positively to shading only in the absence of fertilizer (light x fertilizer interaction; $F_{1,32} = 11.14$, $P = 0.002$). Anthocorids (primarily *Geocoris* sp.), the most abundant predators, responded strongly to the presence of shade structures (no shade: 3.75 ± 0.542 , shade: 10.8 ± 0.996 ; $F_{1,32} = 37.8$, $P < 0.0001$), and a similar response was also suggested for spiders (no shade: 0.35 ± 0.150 , shade: 0.85 ± 0.232 ; $F_{1,32} = 3.70$, $P = 0.0632$). In contrast, the abundance of chalcid wasps (parasitoids) in shaded plots was less than half that found in open plots (6.55 ± 0.61 vs 17.75 ± 1.80 ; $F_{1,32} = 3.70$, $P = 0.0632$). No other factors significantly affected these herbivore and enemy taxa.

Path analysis of the relationships between alfalfa biomass, herbivore and enemy abundance, and treatments provides some insight into the causes of these patterns (Fig. 2). The strong direct effects of shade on

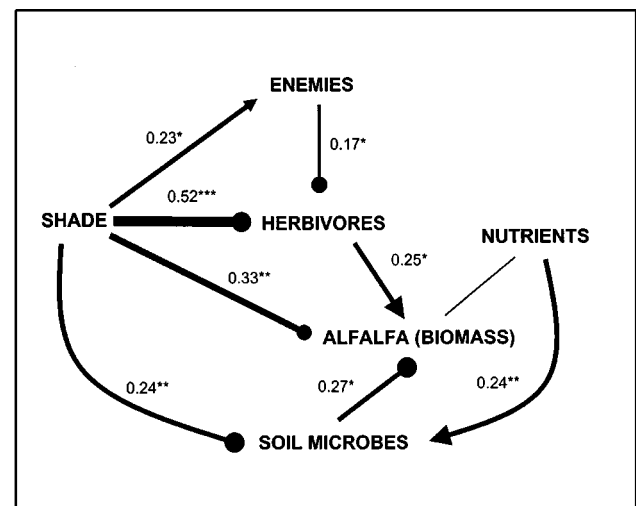


Fig. 2. Path diagrams of interactions for WCRC fields. Thickness of lines is proportional to the magnitude of the effect. Numbers beside lines represent path coefficients (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Arrowheads indicate a positive effect, circle-heads indicate a negative effect. Absence of an arrowhead indicates no effect was detected.

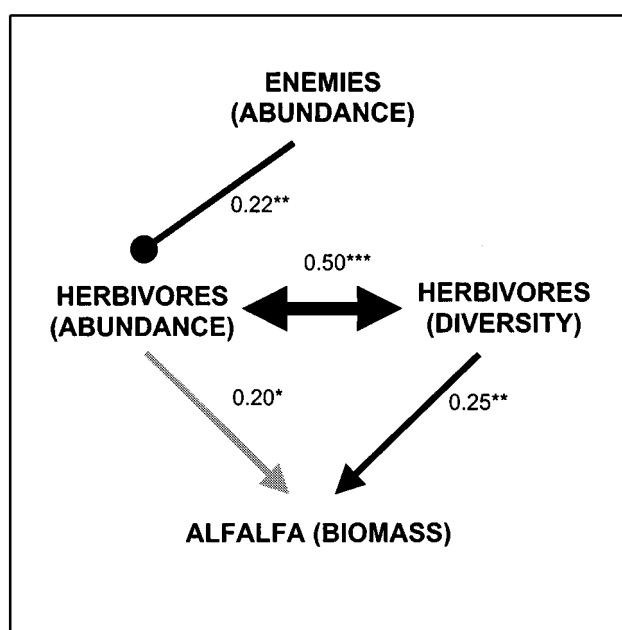


Fig. 3. Relationship between herbivore abundance and alfalfa biomass in WCRC fields. See Fig. 2 for explanation. The gray arrow indicates the pathway not supported by structural equation modeling. Absence of an arrow-head indicates no effect was detected.

each trophic level are evident. However, several indirect effects are also apparent, including the negative effects of shade and nutrients on alfalfa biomass, acting through soil microbe abundance (combined $\eta^2 = 0.13$), and the indirect impact of shade on alfalfa biomass, through its direct effects on herbivores ($\eta^2 = 0.15$). SEM revealed that the positive effect of herbivore abundance on alfalfa biomass was mediated through the strongly correlated variable of herbivore species richness (the indirect pathway is a significantly better fit than the direct pathway; $\chi^2 = 12.3$, $DF = 4$, $P < 0.001$; Fig. 3). Because we sampled insects from the entire plot and sampled all plots equally, the correlation between abundance and species richness is unlikely to have been produced solely by sampling effects.

Experiment Two

Treatment effects in the MSC fields differed from the first experiment (Table 4). No effect of shade was observed on the abundance or diversity of any trophic level. Arthropod removal also had no effect on herbivores, enemies, or alfalfa biomass, except in its interactions with nutrient level and shade (Table 4). Nutrient addition appeared to increase herbivore abundance and diversity, though this relationship was marginally non-significant in the MANCOVA ($P = 0.066$). No sig-

Table 4. Results from ANCOVA, MANCOVA, and profile analyses for Experiment 2 conducted in the high diversity MSC fields. In all analyses covariates (initial measurements of variables) were non-significant and dropped from the models. Degrees of freedom for all analyses are ($F_{1,32}$). P-values less than 0.10 are accentuated in bold.

Factor	ANCOVA/MANCOVA		Profile Analysis	
	F	P	F	P
<i>Alfalfa biomass (ANCOVA)</i>				
Shade	0.55	0.465	-	-
Nutrients	0.17	0.685	-	-
Sweep	0.05	0.817	-	-
Shade x Nutrients	0.05	0.827	-	-
Shade x Sweep	0.19	0.558	-	-
Sweep x Nutrients	0.77	0.387	-	-
Shade x Sweep x Nutrients	3.99	0.054	-	-
<i>Herbivores (MANCOVA)</i>				
			<i>Abundance vs. Richness</i>	
Shade	0.14	0.713	0.06	0.808
Nutrients	3.62	0.066	0.41	0.526
Sweep	0.66	0.423	0.74	0.396
Shade x Nutrients	0.88	0.355	0.38	0.544
Shade x Sweep	0.45	0.508	0.01	0.942
Sweep x Nutrients	2.18	0.150	0.30	0.585
Shade x Sweep x Nutrients	3.03	0.091	0.39	0.537
<i>Enemies (MANCOVA)</i>				
			<i>Abundance vs. Richness</i>	
Shade	0.35	0.561	0.51	0.480
Nutrients	1.5	0.230	3.35	0.077
Sweep	0.6	0.443	2.40	0.131
Shade x Nutrients	1.84	0.185	0.06	0.818
Shade x Sweep	0.68	0.415	0.68	0.415
Sweep x Nutrients	2.57	0.119	6.87	0.013
Shade x Sweep x Nutrients	0.28	0.600	0.00	0.969

Table 5. The effects of fertilizer addition, and arthropod removal on alfalfa biomass (X g/plant \pm SE), herbivore abundance (number per sweep, $X \pm$ SE), and enemy abundance in Experiment 2 (MSC field). Alfalfa biomass figures are under low light (15% ambient) conditions.

Fertilizer	Arthropod removal	Alfalfa biomass (g/dry plant)	Herbivores (N/sweep)	Enemies (N/sweep)
Yes	No sweep	51.82 \pm 2.45	827.1 \pm 101.5	12.5 \pm 1.4
Yes	Sweep	39.89 \pm 4.40	568.2 \pm 57.3	8.4 \pm 1.7
No	No sweep	37.36 \pm 6.40	576.4 \pm 70.1	8.6 \pm 1.1
No	Sweep	52.90 \pm 10.1	694.1 \pm 139.5	9.9 \pm 1.1

nificant effects were identified for predators in the MANCOVA model, however the profile analysis indicated that responses to nutrients and shade (interaction) differed for abundance and richness measures; the abundance of enemies was elevated in fertilized plots not subject to arthropod removal (12.5 ± 1.38 individuals compared to 9.85 ± 0.69 for all plots), but species richness differed only slightly. Alfalfa biomass exhibited an especially complicated relationship with treatment variables (Table 5). Under conditions of low light availability, arthropod removal increased alfalfa

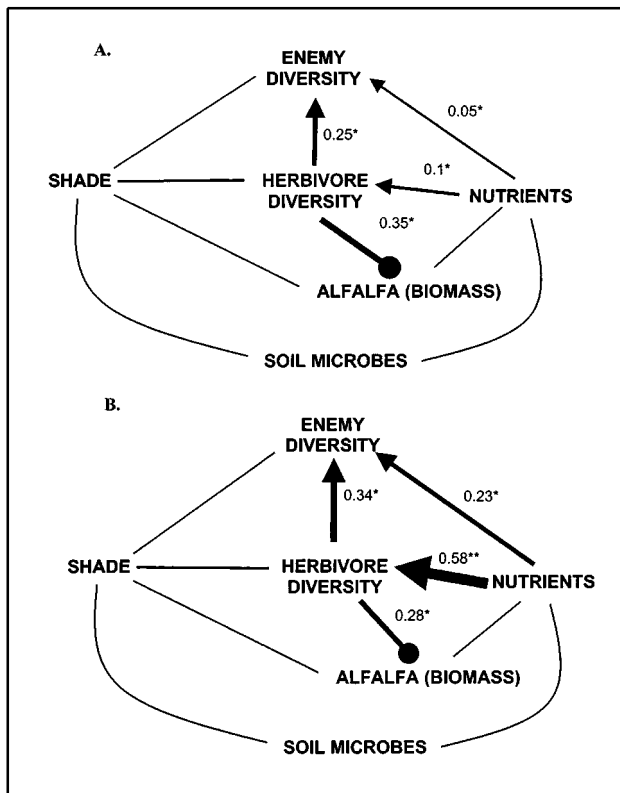


Fig. 4. Path diagrams of interactions in MSC fields for control (A) and arthropod removal (B) treatments. Thickness of lines is proportional to the magnitude of the effect. Numbers beside lines represent path coefficients (*P < 0.05, **P < 0.01, ***P < 0.001). Arrowheads indicate a positive effect, circle-heads indicate a negative effect. Absence of an arrowhead indicates no effect was detected.

biomass in the absence of fertilizer, and decreased it in the presence of fertilizer.

By far the most abundant herbivores in the MSC fields, aphids (93% of all herbivores on average), did not respond significantly to any of the experimental treatments. The large variation in aphid abundance among plots probably swamped potential effects of treatments on other herbivore species. Alfalfa weevil adults (*Hypera postica*) also showed no response to treatments. The third most abundant herbivore group, various *Lygus* species (Miridae; esp. *L. hesperus*), was also not significantly affected by any treatment, except for a complicated three-way interaction between shading, fertilizer, and arthropod removal ($F_{1,32} = 4.41$, $P = 0.044$), which is difficult to interpret. The most abundant enemies, Coccinellidae, Chalcididae, and Pteromalidae, showed no response to any treatment.

The complicated responses of the diverse MSC alfalfa arthropod community to experimental manipulations are more easily understood with an examination of the path diagram incorporating herbivore and

enemy species richness (Fig. 4a,b). Path analysis revealed that nutrient addition had a positive effect on herbivore and enemy diversity. It also reveals the strong interaction between nutrients and arthropod removal; in the absence of arthropod removal the abundance and diversity of herbivores increased with fertilizer addition, but with arthropod removal fertilizer addition tended to decrease herbivore abundance (Table 5). Enemy abundance and diversity follow the same pattern of increasing with fertilizer addition in plots not subject to arthropod removal. Any positive effects of nutrients on alfalfa biomass appear to be counteracted by significant negative effects due to herbivores, which increase in diversity and abundance in response to nutrient addition.

Discussion

Our experiments and analyses demonstrated that even in "simple" agricultural systems, complex interactions may have significant impacts on basic community properties. For example, in the low diversity WCRC fields we found that alfalfa biomass increased with herbivore abundance, a seemingly nonsensical proposition that might usually be explained by compensatory growth. However, path analysis and structural equation modeling revealed that herbivore abundance is highly correlated with herbivore diversity, and that this pathway (from herbivore diversity to alfalfa biomass) fits the observed data significantly better than the hypothesis that increased herbivory is responsible for the increase in alfalfa biomass. Increased alfalfa biomass may be associated with herbivore diversity because less diverse herbivore communities tend to be dominated by one or a few highly injurious species and few enemies, whereas more diverse communities are composed a broader array of species (including potential omnivores) whose effects are more dispersed across plant structures and species (Tilman 1982, Strong et al. 1984, Hunter & Price 1992).

Shade structures and light availability

The strong effects of shade on enemy and herbivore abundances in the WCRC experimental fields are likely due in part to an increased number of enemies, which appeared to be attracted to the shade structure. This explanation is supported by the direct effect of shade on enemies, the positive effect of crates and other habitat manipulations on spider and other predators described in other studies conducted in agricultural systems (e.g., Carter & Rypstra 1995, Landis et al. 2000), and the lack of an effect of shade on enemies or herbi-

vores in the MSC experiment. In the latter case, all plots contained shade structures and only the degree of shading was manipulated. That two of the most abundant herbivores (Miridae, Aphididae) responded positively to shade suggests that the overall negative effect of shade on herbivores was a community effect, not the response of single abundant species. The effects of shade on alfalfa biomass (Experiment 1) appear to represent the combined direct effect of shade on lowering photosynthesis levels and the indirect negative effect acting through a reduction in herbivore diversity. The hot sunny environment of these experiments, in which shade may be beneficial for many organisms, and the absence of an effect of light level in the second experiment, suggest that much of the detrimental effect of shade on alfalfa may be due to indirect causes.

Nutrients

The addition of fertilizer did not increase alfalfa biomass in either of the agricultural systems we examined, and in the first experiment, alfalfa biomass was reduced. In the low diversity WCRC fields, this appeared to be due to strong positive effects of fertilizer on the microbial community, which then may have competed with the alfalfa plants for other limiting nutrients (Jonasson et al. 1996, Scheu 2001). In the diverse MSC fields, the interactions were even more complicated. We did not detect indirect effects of nutrient additions via altered alfalfa biomass on herbivores and enemies, and it is unlikely that there was a direct effect of nutrients on arthropods. However, the MSC fields contained a diverse and vigorous population of weedy plant species in addition to the alfalfa crop. Although we did not measure changes in productivity or composition of the weed community, the positive effect of nutrient addition on primary and secondary consumers was likely mediated by direct effects of fertilizer on weed productivity and perhaps diversity. The lack of a direct effect of fertilizer on alfalfa biomass may be explained by competition between alfalfa and the productive community of weed species, many of which lack the symbiotic relationship with nitrogen-fixing bacteria found in alfalfa. The strong interaction of nutrient addition with arthropod removal suggests that the repeated removal of herbivores from the plots prevented them from responding reproductively or through immigration to the more vigorous weed community. Although increases in enemy abundance and diversity were due in part to the changes in herbivore populations, they may also be positively affected directly by weed species due to increased food resources (e.g. pollen, nectar, honeydew; Jervis et al. 1993) or increased structural habitat diversity (Andow 1991, Siemann et al. 1998).

Effects of diversity within trophic levels

In contrast to the predictions of several models (e.g., Abrams 1995) that diversity should increase with productivity, herbivore diversity was not affected by alfalfa productivity (biomass) in either experimental field. However, the reverse (top-down) pathway of herbivore species richness affecting alfalfa productivity, was significant. In the MSC plots where herbivore abundance and diversity were high, this effect was negative, whereas in the intensively managed WCRC fields it was positive. The positive influence of higher herbivore diversity on alfalfa may be attributed to the associated decreased abundance of two particularly damaging herbivores, mirid plant bugs and aphids.

Several relationships supported the donor-control perspectives of Hunter & Price (1992) and Polis & Strong (1996). First, the highly significant negative effect of arthropod removal on soil microbe abundance suggests that the soil community may strongly depend upon arthropod abundance and perhaps diversity through feces cascades, honeydew production, and/or arthropod corpses (Scheu & Setälä 2002). Second, enemy diversity tended to be dependent on bottom up forces of herbivore diversity and abundance, especially in the MSC field. Finally, in neither experiment did we find strong evidence that enemy diversity or biomass influenced the diversity of herbivorous arthropods.

In summary, our manipulations of resource availability and arthropod abundance in this relatively simple alfalfa dominated ecosystem have exposed a complex set of interactions encompassing both bottom-up and top-down effects. The most prominent of these are the strong effects of shade and/or shade structures on alfalfa, its herbivores, and their enemies, the overall lack of positive effects of nutrients on alfalfa biomass, and the hypothesized antagonistic interactions between alfalfa and weedy plant species mediated through the herbivore trophic level. At first blush, these complicated interactions may suggest that even in simple systems trophic cascades are unlikely to be strong due to the prevalence of horizontal connections that buffer the system. Nevertheless, it is clear from both experiments that a variety of complex indirect effects are responsible for large-scale changes in alfalfa biomass and the associated arthropod community. Several lines of evidence suggest that the trophic interactions described here are community wide responses rather than just species-level cascades (Polis et al. 2000), including: the strong effect of treatments on herbivore and predator species richness, the effects of species richness within these groups on other trophic levels, and community wide response of herbivore abundance to treatments in the first experiment. These indirect effects are not limited to the classic trophic cascades that have been the subject of intense recent investigation.

Acknowledgements: This study was mostly funded by a grant from the Lathrop Foundation and partially by NSF grant DEB-0074806 to LAD. Excellent technical assistance was provided primarily by W. Williams. C. Pearson, H. Horton, and A. Schaeffer also assisted in the field data collection. Soil microbes were quantified by D. McKenney. We are grateful to M. Moran, K. Ram, I. Rodden, M. Brauner, M. Tobler, G. Gentry and two anonymous reviewers for comments that improved previous drafts of the manuscript.

References

- Aarssen LW (2001) On correlations and causations between productivity and species richness in vegetation: predictions from habitat attributes. *Basic and Applied Ecology* 2: 105–114.
- Abrams PA (1995) Monotonic or unimodal diversity-productivity gradients: what does competition theory predict? *Ecology* 76: 2019–2027.
- Andow DA (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology* 36: 561–586.
- Carson WP, Root RB (2000) Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs* 70: 73–99.
- Carter PE, Rypstra AL (1995) Top-down effects in soybean agroecosystems: spider density affects herbivore damage. *Oikos* 72: 433–439.
- Hunter MD (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: Experiments, life tables, and time-series analysis. *Basic and Applied Ecology* 2: 295–309.
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724–732.
- Hurd LE, Wolf LL (1974) Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. *Ecological Monographs* 44: 465–482.
- Hutchinson GE (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* 93: 145–159.
- Jervis MA, Kidd NAC (1996) *Insect Natural Enemies: Practical Approaches to Their Study and Evaluation*. Chapman & Hall, London.
- Jervis MA, Kidd NAC, Fitton MG, Huddleston T, Dawah HA (1993) Flower-visiting by hymenopteran parasitoids. *Journal of Natural History* 27: 67–105.
- Jonasson S, Michelsen A, Schmidt IK, Nielsen EV, Callaghan TV (1996) Microbial biomass C, N and P in two arctic soils and responses to addition of NPK fertilizer and sugar: Implications for plant nutrient uptake. *Oecologia* 106: 507–515.
- Kassen R, Buckling A, Bell G, Rainey PB (2000) Diversity peaks at intermediate productivity in a laboratory microcosm. *Nature* 406: 508–511.
- Landis, DA, Wratte, SD, Gurr, GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45: 175–201.
- Lawton JH (1994) What do species do in ecosystems? *Oikos* 71: 367–372.
- Leibold MA (1996) A graphical model of keystone predators in food webs: Trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147: 784–812.
- Letourneau DK, Dyer LA (1998) Experimental manipulations in lowland tropical forest demonstrate top-down cascades through four trophic levels. *Ecology* 79: 1678–1687.
- MacArthur RH (1965) Patterns of species diversity. *Biological Review of the Cambridge Philosophical Society* 40: 510–533.
- Mitchell RJ (2001) Path analysis. Pollination. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Oxford University Press, New York, pp 217–234.
- Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Moran MD, Hurd LE (1998) A trophic cascade in a diverse arthropod community caused by a generalist arthropod predator. *Oecologia* 113: 126–132.
- Paine RT (1966) Food web complexity and species diversity. *American Naturalist* 100: 65–76.
- Polis GA, Holt RD (1992) Intraguild predation: The dynamics of complex trophic interactions. *Trends in Ecology and Evolution* 7: 151–154.
- Polis GA, Sears ALW, Huxel GR, Strong DR, Maron J (2000) When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* 15: 473–475.
- Polis GA, Strong DR (1996) Food web complexity and community dynamics. *American Naturalist* 147: 813–846.
- Rosenzweig ML (1995) *Species diversity in Space and Time*. Cambridge University Press, Cambridge.
- SAS (1989) *SAS user's guide: statistics*. SAS Institute, Cary, NC.
- Scheu S (2001) Plants and generalist predators as links between the below- ground and above-ground system. *Basic and Applied Ecology* 2: 3–13.
- Scheu S, Setälä H (2002) Multitrophic interactions in decomposer food-webs. In: Tscharntke T, Hawkins BA (eds) *Multitrophic Level Interactions*. Cambridge University Press, Cambridge, U.K., pp 201–225.
- Schlöpfer F, Schmid B (1999) Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. *Ecological Applications* 9: 893–912.
- Schoener TW, Spiller DA (1996) Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381: 691–694.
- Shipley B (2000) *Cause and correlation in biology: A user's guide to path analysis, structural equations, and causal inference*. Cambridge University Press, Cambridge.
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD, Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5: 785–791.
- Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79: 2057–2070.

- Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. *American Naturalist* 152: 738–750.
- Strong DR, Lawton JH, Southwood TRE (1984) *Insects on plants: Community patterns and mechanisms*. Harvard University Press, Cambridge, Massachusetts.
- Strong DR, Whipple AV, Child AC, Dennis B (1999) Model selection for a subterranean trophic cascade: Root-feeding caterpillars and entomopathogenic nematodes. *Ecology* 80: 2750–2761.
- Tabachnick BG, Fidell LS (1996) *Using Multivariate Statistics*. 3rd Edition. Harper Collins, New York.
- Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD, Balbas L (2001) Ecological meltdown in predator-free forest fragments. *Science* 294: 1923–1926.
- Tilman D (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tilman D (1986) A consumer-resource approach to community structure. *American Zoologist* 26: 5–22.
- Ullman JB (1996) Structural equation modeling. In: Tabachnick BG, Fidell LS (eds) *Using multivariate statistics*. 3rd edition Harper Collins, New York, pp 709–811.
- Vadas, RL (1989) Food web patterns in ecosystems: a reply to Fretwell and Oksanen. *Oikos* 56: 339–343.
- Weaver RW, Angle S, Bottomley P, Bezdicsek D, Smith S, Tabatabai A, Wollum A (1994) *Methods of soil analysis part 2: Microbiological and Biochemical Properties*. Soil Science Society of America, Inc. Madison, Wisconsin.
- Wootton JT (1995) Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade. *Ecoscience* 2: 321–328.