EFFECTS OF FIRE ON A PRAIRIE ARTHROPOD COMMUNITY

KATRINA MARIE WHITE

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ABSTRACT

In this study, I addressed how a large-scale wildfire affected a prairie arthropod community in southern Alberta, Canada. First, I looked at the general effects of disturbance on the arthropod community. Second, I addressed how processes such as competition and secondary succession may have affected diversity in this arthropod community. Third, I determined how the arthropod community trophic structure was regulated.

Results showed that the effect of disturbance on arthropods varies greatly by taxa. Factors, such as site, year, distance from disturbance edge, as well as the disturbance itself, were important in determining the abundance, biomass, richness, and diversity of the arthropod community. There were strong year-to-year differences that exceeded the disturbance effects. Results showed that the processes behind the intermediate disturbance hypothesis, succession and competition are not detectable in this arthropod community. This arthropod community was likely regulated in a bottom-up manner, in which herbivores ultimately control the abundance of predators and parasitoids.

PREFACE

For the little things

"Is it possible that humanity will love life enough to save it?"

E.O. Wilson

"In the end, we conserve only what we love.
We will love only what we understand."

Baba Dioum, Senegalese poet

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Chapter 1. General Introduction

Community ecology has been and continues to be an extensively researched field, with a long history of changing views. One contentious issue has been the assessment of the processes determining community structure (i.e. which species exist in a given community and the processes by which they interact). In the 1960's, it was believed that inter-specific competition played an important role in determining community structure (e.g. MacArthur, 1972). However, in a review of several studies, relating competition to community structure, Connell (1975) concluded that few species actually reached population densities high enough to produce competitive interaction and that tolerance to physical conditions played the more dominant role in determining community structure. The focus on the shaping of community structure began to change from competition to other factors, such as simple random distribution of species, and predation (Lubchenco, 1978; Connor and Simberloff, 1979; Duggins, 1983; Menge and Sutherland, 1987). However, by the mid- to late 1980's it became apparent that disturbance, by influencing inter-specific competition and predator-prey interactions, could affect the diversity and trophic structure of communities. Research in disturbance ecology increased in popularity and continues to be a prominent area of study today (Abugov, 1982; Holliday, 1991; Connell et al., 1997).

Huston (1994) gives a general definition of disturbance, describing it in terms of mortality of organisms. Any process which results in the sudden death of organisms within a community, significantly faster than the population growth of those organisms, is defined as a disturbance. Thus, processes such as invasion by new species, climatic changes, or succession would not be considered disturbances. Some examples of processes that would be defined as disturbances are floods, fires, severe weather conditions, and epidemics. These are all large and obvious disturbances, however there are also disturbances at the smaller scale, such as construction of burrows by small mammals or the felling of a tree.

Disturbance ecology has received increased attention in the context of biodiversity (e.g. Samways, 1989; Holliday, 1991; Wootton, 1998). Disturbances can increase biodiversity by reducing the competitive pressures of dominant species, or by creating patches that encourage immigration by new species (Connell, 1978). Disturbances can also affect the trophic structure of communities, by providing a natural manipulation of community dynamics. Thus, disturbed communities are good candidates for the study of biodiversity and community structure.

Fire is a common, natural disturbance and is often used as a rangeland management practice (e.g. Range Research Subcommittee, 1962; Daubenmire, 1968; Hulbert, 1969). Fires enhance the growth of dominant C_4 grasses which are often preferentially grazed by large herbivores (Collins, 1987). Thus, from an economic perspective, periodic burning of rangeland is beneficial. However, while many studies have looked at the effect of burning on plants, the effect of fire on arthropods is poorly understood.

Arthropods are an important component of prairie communities, based on their abundance and diversity (Schoenly et al., 1991). They also contain representatives of every trophic level above primary producer (Siemann et al., 1998). These factors make arthropods good candidates for study of the effects of disturbance on biodiversity and community structure (Duelli et al., 1999). With the heightened concern today for conservation it is important to understand the effect of common management practices on the abundance and biodiversity of different taxonomic groups (at various levels; family, genus, or species).

A prairie fire swept through the foothills in the Porcupine Hills region in southwestern Alberta in December of 1997. This fire burned approximately 200 square kilometers of native range, in an area that had not experienced fire for at least 20 years. The fire rapidly burned northeast from the ignition point, travelling a total distance of 33.5 km (Figure 1.1). The fire intensity ranged from 10,000 to 20,000 kW/m and the rate of spread was one of the highest recorded for fires in Canada (Tysmstra, 1998).

This thesis is organized in two general parts. The first characterizes the patterns of arthropod community structure in this grassland and aims to determine the effects of fire disturbance on this pattern. The second part tests two general hypotheses regarding the processes that determine arthropod biodiversity and community structure.

First, I studied the overall effects of a prairie wildfire on arthropod community structure. The effect fire has on different arthropod communities, in different areas, is quite varied and little generality of explanation can be achieved (e.g. Rice, 1932; Nagel, 1973, and see review by Warren et al., 1987). In this study I sought to determine the effects fire has on a prairie arthropod community in Western Canada, by comparing the abundance of individual families, total abundance, total biomass, family richness, and family diversity of a grassland arthropod community, in adjacent burned and unburned areas.

The second part addresses the processes behind determination of biodiversity and community structure. I looked at how prairie fire affected the diversity of the herbivore, predator, and parasitoid trophic levels in the arthropod community. Changes in biomass were assumed to reflect changes in competition within trophic levels. For example, a decrease in biomass of a trophic level should increase competition in the level above. Several studies have shown that disturbance decreases competition, which in turn increases diversity (e.g. Hemphill, 1991; Polishchuk, 1999), while other studies have not been able to show such an effect (McAuliffe, 1984; Death, 1996). Whether or not competition plays a role in determining biodiversity following a disturbance may depend on the dynamics of secondary succession in the community. This idea, presented as the intermediate disturbance hypothesis, was first proposed by Connell (1978). Immediately following a disturbance, conditions are relatively harsh and few species can make use of the patches created by the disturbance. However, as more and more species move into the area, at some intermediate point in time competitively superior species begin to eliminate other species (Connell, 1978). That intermediate point is the point of highest diversity. Wootton (1998) determined that this hypothesis does not always hold when the interactions between trophic levels are considered. I examined the effect of disturbance on a multitrophic arthropod community to address to what extent competition and succession determine biodiversity. I used the observed effect of disturbance on biomass at each consumer trophic level (herbivore, predator, parasitoid) to make and test predictions about how the diversity of these groups should be affected by disturbance.

In the third part, I addressed the debate of top-down versus bottom-up community regulation in terrestrial systems (Hunter and Price, 1992; Strong, 1992). There has been extensive study on whether top-down processes or bottom-up processes are more important in the regulation of community structure (e.g. Hunter and Price, 1992; Menge, 1992; Letourneau and Dyer, 1998; Siemann, 1998). Top-down hypotheses predict that lower trophic levels of the food web are ultimately controlled or released by higher levels, whereas bottom-up hypotheses predict that lower levels control higher ones. Disturbances tend to disproportionately affect some trophic groups more than others. Thus, the natural manipulations provided by disturbance, allowed a test of the top-down and bottom-up hypotheses by comparing undisturbed communities to those disturbed by fire. Predictions can be made about how trophic interactions will be affected following a disturbance, based on the trophic structure on undisturbed prairie. Comparing the observed trophic interactions on disturbed prairie to those that would be predicted, provides insight into how arthropod communities are structured. I used a coarse approach, grouping arthropods into three trophic levels (herbivores, predators, parasitoids) to evaluate the trophic structure of this prairie arthropod community and how it was affected by fire disturbance.

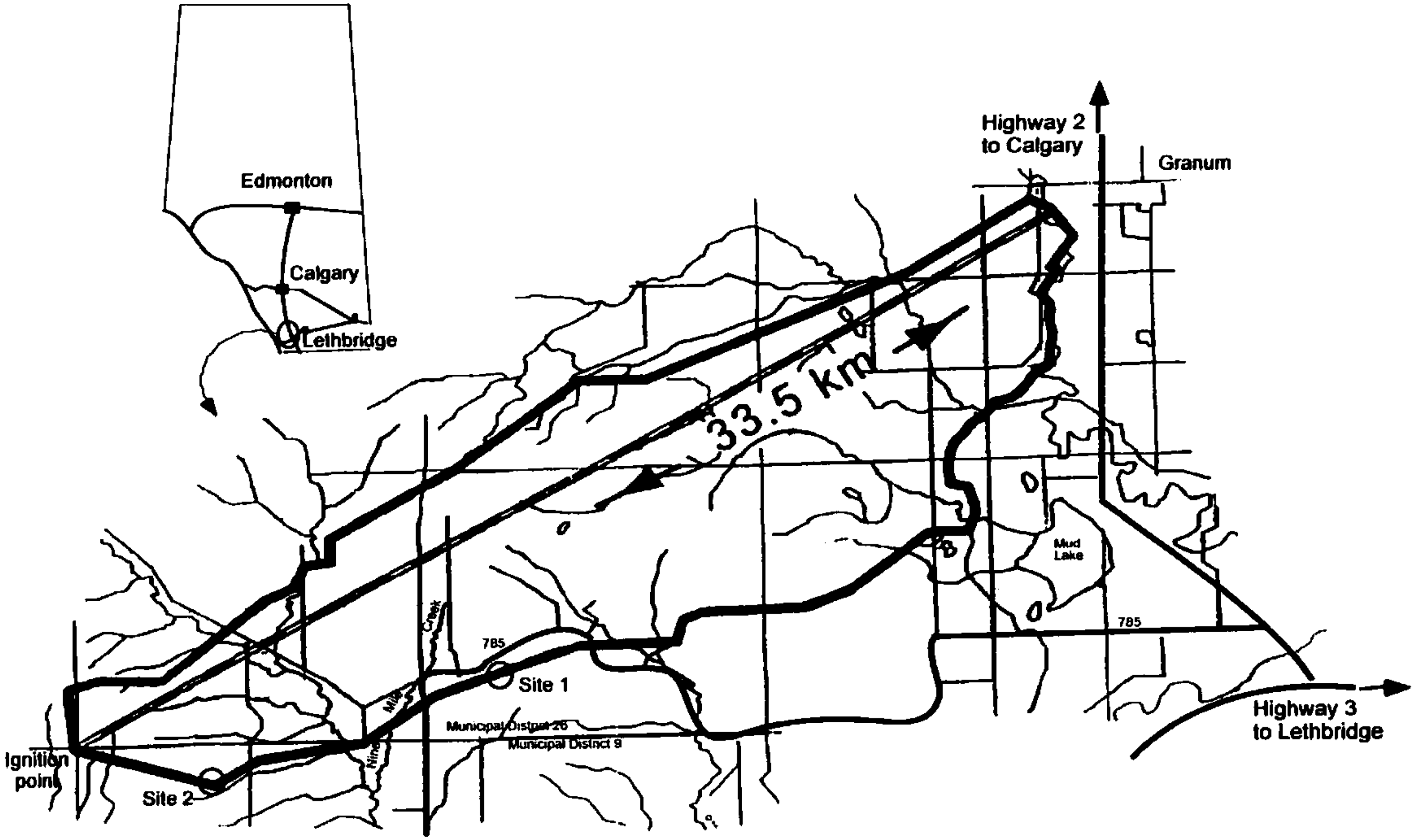

Figure 1.1. Map of the area burned in southern Alberta, Canada (Dec. 1997). The locations of study sites 1 and 2 are indicated.

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Chapter 2.

The Effect of a Grassland Fire on Arthropod Abundance and Diversity

Abstract

The aim of this study was to determine how the arthropod community was affected after a prairie wildfire in southwestern Alberta (Dec. 1997). Samples were collected from adjacent burned and unburned plots, at two study sites, in the summers of 1998 and 1999. Arthropods were identified to family and counted. Mean abundance of each family on and off the burn was compared for each year, to determine the effect of fire on different groups. There was wide variation in the effects of the fire on different arthropod taxa. Some showed no change, some increased, and some decreased on the burn compared to the unburned prairie. The effects of site, year, distance from burn edge, and treatment on total abundance, total biomass, richness, and diversity were also addressed using mixed-model ANOVA. The effect of the burn on abundance and biomass varied between sites in each year. Biomass also varied according to distance from the burn edge between burned and unburned areas, and between years. The effect of burning on family richness varied between the two sites. Richness was higher in 1999 than in 1998. Diversity was higher at Site 1 than at Site 2. The response of diversity to treatment varied between years. This study indicates that generality is hard to achieve when addressing the effects of fire on arthropod communities.

Introduction

We know very little about what determines the abundance, biomass, and diversity of prairie arthropod populations and communities. One possible explanation is disturbance. One form of disturbance that can have a large impact on prairie arthropod communities is burning. A number of studies have looked at the effect of fire on arthropod communities (Rice, 1932; Nagel, 1973; Anderson et al., 1989; reviewed by Warren et al., 1987). However, due to the varied factors associated with grassland fire, such as timing and intensity of burn, little generality of explanation has been achieved when comparing the effects of fire in different communities. This is an important shortcoming, considering the history of fire as a management practice and the general issues surrounding conservation of prairie biodiversity.

While the effect of fire on plant communities has been well studied (e.g. Old, 1969; Bragg and Hulbert, 1976; Collins, 1992), little work has been done on the effects of fire on western Canadian native grasslands and their associated arthropod communities. This study seeks to increase our understanding of the effect of prairie fire on arthropod communities in western Canada, and to add to the knowledge base that already exists from other areas (e.g. Warren et al., 1987). In this study I examine how arthropods are affected by a large grassland fire. In particular, the question addressed by this paper is: how did burning affect the total abundance, total biomass, family richness, and family diversity of prairie arthropods?

Methods

On December 13, 1997 a wildfire swept across the prairie in the foothills of southern Alberta. Approximately 200 square kilometers of prairie were burned in an area that had not experienced a fire for at least 20 years. The fire burned in a northeast direction from the starting point for a total of 33.5 km. The size and infrequency of burning makes this disturbance greater than that in other studies of arthropod communities on burned grassland (Anderson et al., 1989; Reed, 1997; Nagel, 1973; Warren et al., 1987).

Two study plots were set up in the Porcupine Hills, southwest of Granum, Alberta (see Figure 1.1 for exact locations). These sites are in the foothills fescue natural subregion. The soils are dark brown and black chernozems (Strong, 1992). The precipitation varies from 400 to 480 mm per annum. The dominant grasses are rough fescue (*Festuca campestris*), Idaho fescue (*F. idahoensis*), sedges (*Carex* spp.) and Western wheat grass (*Agropyron smithii*) (Strong, 1992). Site 1 is approximately 19 km N of Brocket, Alberta (49°43'N 113°45'W), at an elevation of 1410 m. Site 2 is approximately 18 km NNW of Brocket, (49°41'N 113°54'W), at an elevation of 1350 m.

Arthropods were collected using pitfall traps (for ground dwelling arthropods) and pantraps (for vegetation dwelling and flying arthropods), according to methods outlined in Finnamore et al. (1998). A pitfall trap consisted of two nested 450 ml plastic cups (9 cm in diameter at lip) sunk in the ground so that the lip of the top cup was level with the substrate. A gray-white, 15x15 cm ceramic tile was positioned 2.5 cm over each cup, supported by four galvanized nails, to prevent overflow by rainwater. The cups were half-filled with 50% ethylene glycol. Pantraps were aluminum food trays (22.5x15x5 cm) which were painted yellow (RGB color scale: 250, 200, 0) to increase trap rates (many insects are attracted to yellow). The pans were laid level on the ground (using a rock to prop up a corner if the ground was not level) and filled to approximately 2cm depth with 90% ethylene glycol. A rock was placed in some traps to prevent wind damage. When this was necessary the solution level was deep enough to cover the rock. Pantraps were also covered with 30 x 30 cm chicken wire mesh to prevent large vertebrates from drinking the ethylene glycol. Servicing of the traps and processing of the specimens followed protocols for prairie arthropods (Finnamore et al., 1998).

I sampled along the southern edge of the Granum burn, comparing adjacent regions on and off the burn. The edge of the burn was actually the fire break that was ploughed at the time of the fire. Four transect lines were set up at each site, perpendicular to the firebreak (approximately 2.5 to 3 m wide) and positioned 25m apart. The mid-point in the width of the firebreak was treated as the center point for the transects. Sampling stations were positioned at 10 and 50 m from the center point on both the unburned (control) side of each transect and the burned side.

At each sampling station, three pitfalls and three pantraps were laid in a 1 m radius circle (alternating trap type) around a center stake marking the distance from the center point. Samples from the 6 traps at each station were pooled for analysis. Given this set-up, arthropod collections were resolved to the level of site, burn treatment, distance from burn edge, and date. In 1998, the traps were laid out on 6 July at Site 1 and 11 July at Site 2. At Site 1, all traps were emptied and reset on July 10, 15, and 18. Traps at Site 2 were emptied and reset on July 15, 18, and 22. All traps were reset on August 6, then emptied and reset on August 10, 14, and 18. Traps were removed for the winter then reset on July 8, 1999 and emptied and reset on July 12, 16, and 20. Vegetation measurements were made on August 13, 1998 and August 19, 1999. Percent cover of common plant species was estimated using a $1m^2$ quadrat. These measurements were made at each trap, centering the quadrat over the trap. This allowed a view of the microhabitat structure immediately surrounding each trap. Mean height estimates were made using a meter stick. Cattle were excluded from the two sites during the study to eliminate grazing as a confounding factor.

Individuals were counted and identified to the family level. However, arthropods from the orders Pseudoscorpionida, Phalangida, Chilopoda, and Thysanoptera were not keyed to family due to logistic constraints. These orders, except for the Thysanoptera, occurred rarely. Biomass was estimated by weighing 10-20 randomly selected specimens from each family. Total biomass for each group was calculated by multiplying abundance by the biomass estimate for each taxon. Specimen identifications were confirmed by comparison and with the help of technicians at the Strickland Museum, University of Alberta and at the Provincial Museum of Alberta.

Samples from all pitfalls and pantraps at each distance were pooled for each four day sampling period, and a mean was calculated for all sampling dates. Differences between vegetation measurements and family abundances on the unburned and burned prairie were analyzed using Wilcoxon/Kruskal Wallis tests. The following response variables were measured: total arthropod abundance, total arthropod biomass, family richness, and family diversity. Family richness was measured as the total number of taxa (family for all but four orders not keyed to family, described above) that occurred in each sample. Diversity was calculated using Simpson's (1949) index of diversity, which is based on the probability of randomly picking two different species from a given community. Family diversity was used as a surrogate for species diversity, because specimens were only identified to the family level. Data were analyzed using JMP® (v4.0, 2000). Total abundance, total biomass, family richness, and family diversity were all transformed to normality using Box Cox transformations. Variations due to site, year, treatment, and distance were analyzed with mixed-model ANOVA. The mean abundances of each family were calculated using all of the 1998 samples, however only the July samples from 1998 were used in the ANOVA analyses to make the two years comparable. Least square means were plotted for the highest order interactions in which variables were significantly involved. A posteriori differences between treatment means were assessed using Tukey-Kramer HSD tests (P=0.05).

Results

Approximately 120,000 individual specimens were collected in July of 1998 and 1999, from 137 taxa. In 1998, a total of 49,861 specimens were collected and 69,960 were collected in 1999. Over the two years, 49,459 individuals were collected at Site 1 and 70,362 were collected at Site 2. Approximately 62,000 specimens were found on the unburned prairie, whereas approximately 58,000 were found on the burned prairie. In 1998 the percent cover of vegetation was 17.3 % less on the burn than on the unburned prairie (Table 2.1; Wilcoxon test, $\chi^2 = 145.44$, $P < 0.0001$). In 1999, the vegetation cover on the burn was 8.9 % lower than that on the unburned prairie (Table 2.1; Wilcoxon test, $\chi^2 = 105.56$, $P < 0.0001$).

Table 2.2 shows all families collected and their mean abundance on the unburned and burned prairie in both 1998 and 1999. The effect of burning varied by taxa. In 1998, many taxa showed no significant difference in abundance between burned and unburned treatments (e.g. Tachinidae, Lygaeidae, Nymphalidae). However, some taxa were more abundant on the unburned prairie (e.g. Lycosidae, Chironomidae, Aphididae), whereas others were more abundant on the burned prairie (e.g. Curculionidae, Pentatomidae, Thysanoptera). In 1999, very few taxa showed significant differences between burned and unburned treatments. However, the Phalangida, Aranaea and Neuroptera were more abundant on the unburned prairie. The Orthoptera were more abundant on the burned area.

Total abundance was affected by a 3-way interaction involving site, year, and treatment (Table 2.3). Hence, the annual changes in abundance on burned and unburned treatments were not consistent between sites (Figure 2.1). At Site 1, there was no difference in total abundance between burned and unburned prairie in 1998 or 1999 (Figure 2.1). However, the abundance at Site 1 was higher in 1999 than in 1998 (Figure 2.1). At Site 2, there was no difference between total abundance on and off the burn in 1998 or 1999 (Figure 2.1).

Total biomass was also affected by a 3-way interaction involving site, year, and treatment (Table 2.4). As with total abundance, the response of total arthropod biomass to the burn varied significantly between sites in each year (Figure 2.2). At Site 1, the total biomass of arthropods on the burned prairie was no different from that on the unburned prairie in 1998 (Figure 2.2). However, in 1999, the total biomass was higher on the burn than off at Site 1 (Figure 2.2). At Site 2 there was no difference between the total biomass on the burned and unburned prairie in either year (Figure 2.2). Biomass was also significantly affected by two 2-way interactions involving distance from burn edge (Table 2.4). At 50 m from the burn edge the biomass on burned prairie was significantly higher than that on the unburned prairie (Figure 2.3a). The effect of distance also varied between years. Biomass was higher in 1999 than in 1998 and the differences in biomass between years at 10 m were greater than the differences in biomass between years at 50 m (Figure 2.3b).

Mean family richness was affected by a 2-way interaction between site and treatment, and also by year (Table 2.5). Family richness was the same on both unburned and burned prairie at Site 1 (Figure 2.4a). At Site 2, the family richness was significantly higher on the unburned prairie than on the burned prairie (Figure 2.4a). Family richness was also significantly higher in 1999 than it was in 1998 (Figure 2.4b).

Mean family diversity was significantly affected by site and by a 2-way interaction between year and treatment (Table 2.6). The diversity at Site 1 was higher than that at Site 2 (Figure 2.5a). In 1999, there was no difference between family diversity on the unburned and burned prairie, however, in 1998, the family diversity was significantly higher on the unburned prairie (Figure 2.5b). Diversity was also significantly higher on the burn in 1999 than it was on the burn in 1998 (Figure 2.5b).

Discussion

Consistent with other studies (Cancelado and Yonke; 1970; Warren et al., 1987; Anderson et al., 1989), this study showed that fire disturbance has a varied effect on the abundance, biomass, richness, and diversity of various arthropod taxa. While fire appears to be beneficial to some taxa, it is deleterious to others. This varied response is likely due to a number of factors. The timing and rate of burning can greatly affect how it will affect given insect groups (Reed, 1997). Life-history may also influence how a fire will affect arthropod taxa. The over-wintering location of arthropods can determine the effect fire will have on them during a winter burn (Algren, 1974). Whether arthropods are generalists or specialists also affects their ability to recolonize and survive in a disturbed habitat (Swengel, 1996).

Total abundance, total biomass, family richness, and diversity were all significantly affected by combinations of year, site, treatment, and distance. There were strong year effects in total abundance of arthropods on burned and unburned prairie at Site 1, but not at Site 2. At Site 1 in 1998, the total abundance was lower than in 1999. Total biomass was higher on the burned prairie than the unburned at Site 1 in 1999. An apparent overgrazing of unburned prairie at Site 2 prior to the fire and less intense burning, may explain the disparity between the effect of burning each year at the two sites. In 1998, the total percent cover of vegetation was only 17% lower on the burn than off at Site 2, whereas at Site 1 the percent vegetation cover on the burn was 40% lower than that on the unburned prairie. A common explanation for increased arthropod abundance following a fire is that large numbers of phytophagous insects move into the area to feed on the lush vegetation regrowth (Hurst, 1971). Both the burned and unburned areas at Site 2 would have had new growth, making the two habitats relatively similar, and thus minimizing the effect of burning. At Site 1, there was nearly 100% cover on the unburned area, much of which was from the previous year's growth, making any new growth less obvious. On the burned plot all the cover was due to new growth, and was likely more attractive to herbivorous arthropods.

The interaction between distance and burning provides insight into edge effects between two distinct habitats. The fact that the total biomass at 10 m from the burn edge on the burned prairie was not different from that on the unburned prairie indicates that arthropods were likely moving between these two communities. The significant difference between the burned and unburned samples at 50 m from the burn edge suggests that the arthropod communities were affected by the burn, but that the spatial scale of this study may have been too small to see the effects on abundance and diversity.

The variation between the effect of disturbance on diversity and on family richness at each site likely occurred due to reasons given for site disparity earlier. The significant effect of year on family richness and on the effects of disturbance on diversity should be expected. Factors that fluctuate from year to year, such as temperature and precipitation, also have a large impact on arthropod development and will influence which taxa are present in a community from year to year (Borror et al., 1976). Also, the differences in number of taxa, while statistically significant, are actually quite small. Only 17 families were collected in 1998 that were not recorded in 1999, and only 12 were recorded from 1999 that were not recorded in 1998. All of these taxa were very rare and thus simply may have not encountered the traps in both years, even if they were present throughout.

This study shows that there are many factors that influence the abundance, biomass, richness, and diversity of arthropods in prairie communities. The area studied, the year, and the effects of disturbance, and the distance from a disturbed edge all had an impact on this grassland arthropod community. Factors such as these are what makes finding generality among studies dealing with arthropod responses to disturbance difficult. This study has shown that (unmeasured) properties of the habitat and seasonal variation can also affect arthropod communities. Greater generality may be achieved if more studies were conducted on disturbances that occurred in the same types of habitats at the same time of year, and with similar intensities and rates of burning.

The heterogeneity of arthropod communities also makes interpretation of results difficult as different taxa will respond differently to burning (Warren et al., 1987). Conservation of biodiversity is a popular topic in community ecology (e.g. Morowitz, 1991; Ehrlich, 1992; Tilman, 1999) and the search for management practices that allow preservation of the highest diversity is just beginning. The present study further indicates that it is difficult to determine how common management practices affect arthropod communities and that generality is difficult to attain. Given the informational constraints, management and conservation practices must be set up using educated guesses, on a case by case basis.

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Table 2.1. Percent cover and diversity of vegetation on unburned and burned prairie in 1998 and 1999. Rank means (% or D/station) ± 1 standard error are given. P values are Bonferroni-corrected.

Measurement	**Unburned**	**Burned**	**Wilcoxon test statistics**
% cover – 1998	96.69± 1.00	68.18 ± 1.25	$\chi^2 = 39.92$ $P < 0.0004$
% cover – 1999	93.57 ± 1.06	78.23 ± 0.86	$\chi^2 = 105.56$ $P < 0.0004$
Diversity – 1998	0.18 ± 0.014	0.51 ± 0.014	$\chi^2 = 126.15$ $P < 0.0004$
Diversity - 1999	0.24 ± 0.014	0.32 ± 0.018	$\chi^2 = 6.03$ $P = 0.056$

Table 2.2. Mean abundance of all families collected on burned and unburned prairie in 1998 and 1999. The overall effect for each order is also given following the family listings for that order. * indicates significant difference between burned and unburned rank means in each year (Wilcoxon test, P < 0.05). P values were Bonferroni corrected, for each year comparison. Trophic classification for each family is noted (used in Ch 3).

Family	Unburned 1998 n=94	Burned 1998 n=141	P< .05	Unburned 1999 n=44	Burned 1999 n=66	P< .05	Tophic category
Ixodidae	4.24±0.92	0.13±0.04	*	0.27±0.07	0.16±0.10		pestiferous
Phalangida	5.10±0.51	4.90±0.72		0.42±0.07	0.17±0.04	*	detritivore
Clubionidae	0.59±0.14	0.25±0.06		0.09±0.03	0.09±0.02		predator
Gnaphosidae	0.36±0.08	0.14±0.03		0.04±0.01	0.05±0.01		predator
Lycosidae	8.35±1.33	3.62±0.56	*	2.17±0.29	0.98±0.14	*	predator
Salticidae	0.78±0.12	0.11±0.03	*	0.19±0.04	0.07±0.02		predator
Tetragnathidae	0.11±0.04	0.14±0.04		0.03±0.01	0.02±0.01		predator
Thomisidae	1.98±0.20	0.70±0.08	*	0.64±0.09	0.38±0.05		predator
Total Araneae	12.16±1.39	4.97±0.59	*	3.16±0.39	1.59±0.18	*	NA
Acroceridae	0.00	0.01±0.01		0.03±0.02	0.01±0.00		parasitoid
Agromyzidae	3.09±0.58	2.49±0.45		0.95±0.14	0.80±0.10		herbivore
Asilidae	0.34±0.06	0.62±0.09		0.01±0.01	0.01±0.00		predator
Bibionidae	0.01±0.01	0.05±0.02		0.00	0.01±0.01		detritivore
Bombyliidae	0.14±0.05	0.17±0.04		0.02±0.01	0.02±0.01		parasitoid
Calliphoridae	0.14±0.04	0.49±0.08		0.19±0.06	0.38±0.11		pestiferous
Ceratopogonidae	0.00	0.00		0.01±0.01	0.00		pestiferous
Chironomidae	60.87±4.78	36.88±2.47	*	18.31±1.29	14.50±1.07		herbivore
Chloropidae	23.48±2.44	35.74±3.57		2.89±0.52	2.41±0.29		pestiferous
Conopidae	0.04±0.02	0.16±0.04		0.02±0.01	0.02±0.01		parasitoid
Culicidae	0.05±0.04	0.01±0.01		0.00	0.00		pestiferous
Dolichopodidae	8.45±0.84	9.09±0.56		0.44±0.08	0.46±0.05		predator

Table 2.2 continued

Family	Unburned 1998	Burned 1998	P< .05	Unburned 1999	Burned 1999	P< .05	Trophic category
Drosophilidae	1.98±0.57	0.94±0.25		0.06±0.03	0.04±0.02		detritivore
Heleomyzidae	6.76±0.42	12.50±0.64	*	2.48±0.48	2.14±0.28		herbivore
Lonchopteridae	0.00	0.00		0.01±0.01	0.00		herbivore
Muscidae	16.17±0.88	25.45±1.42	*	7.73±0.46	10.01±0.55		omnivore
Mycetophilidae	0.24±0.13	0.04±0.02		0.45±0.10	0.27±0.04		detritivore
Otitidae	0.12±0.03	0.11±0.03		0.04±0.02	0.05±0.01		herbivore
Phoridae	9.67±0.66	4.36±0.46	*	2.23±0.24	2.26±0.20		detritivore
Pipunculidae	1.17±0.14	0.72±0.09		0.63±0.11	0.33±0.06		parasitoid
Psychodidae	0.34±0.20	0.15±0.07		0.00	0.00		pestiferous
Ptychopteridae	0.54±0.23	0.45±0.10		0.03±0.01	0.02±0.01		detritivore
Rhagionidae	0.02±0.01	0.01±0.01		0.05±0.03	0.03±0.01		predator
Sepsidae	0.06±0.04	0.02±0.01		0.67±0.17	0.54±0.11		detritivore
Stratiomyidae	0.14±0.04	0.18±0.04		0.05±0.02	0.05±0.01		herbivore
Syrphidae	1.18±0.16	1.91±0.25		0.02±0.01	0.04±0.01		herbivore
Tabanidae	0.01±0.01	0.00		0.01±0.01	0.04±0.01		pestiferous
Tachinidae	10.12±0.84	13.23±0.86		2.24±0.22	2.65±0.21		parasitoid
Tephritidae	1.50±0.30	0.21±0.04	*	0.66±0.19	0.16±0.04		herbivore
Therevidae	0.07±0.03	0.06±0.02		0.03±0.01	0.03±0.01		herbivore
Tipulidae	0.03±0.02	0.07±0.02		0.00	0.01±0.00		herbivore
Total Diptera	146.73±5.77	146.11±4.84		40.24±2.27	37.26±1.53		NA
Andrenidae	0.65±0.11	0.73±0.10		0.06±0.02	0.09±0.03		herbivore
Anthophoridae	0.01±0.01	0.01±0.01		0.00	0.00		herbivore
Aphelenidae	0.01±0.01	0.01±0.01		0.09±0.04	0.04±0.02		parasitoid
Apidae	4.14±0.53	4.11±0.51		0.39±0.06	0.31±0.04		herbivore
Braconidae	4.52±0.33	2.96±0.23	*	0.59±0.09	0.99±0.15		parasitoid
Chalcididae	0.21±0.06	0.23±0.05		0.01±0.01	0.01±0.01		parasitoid
Chrysididae	0.78±0.10	1.21±0.13		0.11±0.03	0.18±0.03		parasitoid
Colletidae	0.01±0.01	0.00		0.05±0.02	0.03±0.01		herbivore
Eurytomidae	0.50±0.13	0.44±0.08		0.34±0.12	0.15±0.03		omnivore
Formicidae	62.71±18.79	114.5±23.47	*	8.28±2.82	7.78±1.47		omnivore
Halictidae	1.98±0.21	3.16±0.25		0.76±0.12	1.01±0.14		herbivore
Ichneumonidae	3.48±0.34	3.18±0.23		0.58±0.06	1.32±0.16		parasitoid
Megachilidae	0.14±0.07	0.09±0.03		0.02±0.01	0.01±0.00		herbivore
Platygasteridae	0.02±0.01	0.00		0.02±0.01	0.01±0.01		parasitoid
Pompilidae	1.15±0.14	0.55±0.09	*	0.12±0.03	0.19±0.04		predator
Pteromalidae	29.17±1.27	24.72±1.11		11.24±0.99	11.53±1.30		parasitoid
Scelionidae	14.64±1.40	9.96±0.75		1.25±0.28	1.67±0.34		parasitoid
Sphecidae	1.07±0.13	1.01±0.11		0.12±0.03	0.21±0.04		predator
Tenthredinidae	0.02±0.01	0.01±0.01		0.15±0.04	0.11±0.03		herbivore
Tiphiidae	0.00	0.01±0.01		0.00	0.00		parasitoid
Vespidae	0.11±0.04	0.04±0.02		0.02±0.01	0.04±0.01		predator
Total Hymenoptera	125.3±19.61	166.9±23.33		24.18±3.43	25.70±2.57		NA

Table 2.2 continued

Family	Unburned 1998	Burned 1998	P< .05	Unburned 1999	Burned 1999	P< .05	Trophic category
Adelgidae	0.00	0.00		0.06±0.02	0.03±0.01		herbivore
Aphididae	15.13±1.08	7.97±0.63	*	1.05±0.17	10.83±6.93		herbivore
Cercopidae	0.02±0.02	0.00		0.01±0.01	0.00		herbivore
Cicadellidae	67.18±3.20	58.74±2.48		32.53±3.91	19.54±1.60		herbivore
Cixiidae	3.02±0.34	0.63±0.09	*	1.00±0.16	0.30±0.04	*	herbivore
Coccoidea (Superfamily)	0.15±0.15	0.00		0.00	0.00		herbivore
Dictyopharidae	0.00	0.01±0.01		0.00	0.00		herbivore
Issidae	0.04±0.02	0.00		0.06±0.02	0.00		herbivore
Membracidae	0.89±0.17	0.43±0.15		0.02±0.01	0.00		herbivore
Psyllidae	0.00	0.00		0.03±0.01	0.03±0.01		herbivore
Total Homoptera	86.44±3.18	67.78±2.79	*	34.77±4.08	30.72±7.09		NA
Alydidae	1.27±0.17	1.84±0.19		0.05±0.01	0.29±0.06		herbivore
Anthocoridae	0.00	0.04±0.02		0.00	0.01±0.00		predator
Coreidae	0.03±0.02	0.08±0.02		0.00	0.01±0.01		herbivore
Geocoridae	0.40±0.09	0.77±0.10		0.00	0.00		predator
Lygaeidae	0.16±0.05	0.30±0.06		0.04±0.01	0.19±0.05		herbivore
Miridae	1.89±0.26	1.90±0.15		0.46±0.08	0.39±0.06		herbivore
Nabidae	0.09±0.03	0.11±0.03		0.02±0.01	0.03±0.01		predator
Pentatomidae	0.03±0.02	0.26±0.05	*	0.04±0.02	0.09±0.02		herbivore
Rhopalidae	0.01±0.01	0.06±0.02		0.00	0.00		herbivore
Rhyparochromidae	0.00	0.07±0.02		0.00	0.00		herbivore
Reduviidae	0.00	0.00		0.00	0.02±0.01		predator
Scutelleridae	0.02±0.01	0.02±0.01		0.00	0.00		herbivore
Thyreocoridae	0.00	0.01±0.01		0.00	0.00		herbivore
Tingidae	0.13±0.05	0.00		0.02±0.01	0.00		herbivore
Total Heteroptera	4.03±0.31	5.48±0.36		0.64±0.11	1.02±0.15		NA
Coleophoridae	3.97±0.62	0.72±0.10	*	1.73±0.23	1.04±0.13		herbivore
Gelechidae	10.49±1.46	3.95±0.36	*	2.74±0.30	4.53±0.68		herbivore
Geometridae	0.35±0.09	0.30±0.06		0.02±0.01	0.02±0.01		herbivore
Hesperidae	1.57±0.27	1.65±0.24		0.05±0.02	0.03±0.01		herbivore
Lycaenidae	0.16±0.06	0.06±0.02		0.05±0.02	0.02±0.01		herbivore
Noctuidae	0.47±0.08	0.42±0.06		0.26±0.03	0.21±0.05		herbivore
Nymphalidae	0.54±0.09	0.33±0.05		0.21±0.03	0.11±0.02		herbivore
Pieridae	0.09±0.04	0.05±0.02		0.01±0.01	0.00		herbivore
Pterophoridae	0.03±0.02	0.04±0.02		0.00	0.00		herbivore
Pyralidae	0.35±0.07	0.26±0.05		0.27±0.04	0.19±0.03		herbivore
Satyridae	0.71±0.14	0.48±0.09		0.02±0.01	0.02±0.01		herbivore
Total Lepidoptera	18.73±0.26	8.26±0.45	*	5.36±0.42	6.15±0.76		NA
Bruchidae	0.00	0.02±0.01		0.02±0.01	0.03±0.01		herbivore
Buprestidae	0.00	0.01±0.01		0.00	0.00		herbivore
Byrrhidae	0.01±0.01	0.00		0.00	0.00		herbivore

Table 2.2 continued

Family	Unburned 1998	Burned 1998	P< .05	Unburned 1999	Burned 1999	P< .05	Trophic category
Cantharidae	0.00	0.00		0.01±0.01	0.00		predator
Carabidae	1.18±0.16	1.23±0.13		0.07±0.02	0.12±0.03		omnivore
Cerambycidae	0.00	0.00		0.01±0.01	0.01±0.00		herbivore
Chrysomelidae	0.16±0.05	0.11±0.03		0.01±0.01	0.01±0.00		herbivore
Cleridae	0.43±0.07	0.38±0.05		0.11±0.03	0.07±0.01		predator
Coccinellidae	0.32±0.06	0.54±0.08		0.05±0.02	0.06±0.02		predator
Curculionidae	1.15±0.13	3.07±0.23	*	0.16±0.03	0.31±0.04		herbivore
Dytiscidae	0.01±0.01	0.01±0.01		0.00	0.00		predator
Elateridae	0.03±0.02	0.03±0.01		0.01±0.01	0.00		herbivore
Haliplidae	0.03±0.02	0.12±0.03		0.02±0.01	0.03±0.01		herbivore
Histeridae	0.05±0.02	0.06±0.02		0.01±0.01	0.00		predator
Lyctidae	0.02±0.01	0.02±0.01		0.00	0.00		herbivore
Meloidae	0.05±0.03	0.06±0.02		0.06±0.02	0.06±0.01		herbivore
Melyridae	0.67±0.13	0.25±0.05		0.08±0.02	0.05±0.01		predator
Mordellidae	0.19±0.05	0.11±0.03		0.16±0.04	0.16±0.03		herbivore
Mycetophagidae	0.77±0.15	0.67±0.11		0.14±0.03	0.24±0.07		detritivore
Pedilidae	0.05±0.02	0.01±0.01		0.06±0.02	0.20±0.07		herbivore
Phalacridae	0.45±0.10	0.55±0.11		0.05±0.02	0.46±0.15		herbivore
Scarabaeidae	0.02±0.01	0.03±0.01		0.01±0.01	0.00		herbivore
Silphidae	0.00	0.00		0.00	0.03±0.02		detritivore
Staphylinidae	0.34±0.08	0.43±0.07		0.14±0.03	0.15±0.03		predator
Tenebrionidae	0.01±0.01	0.06±0.03		0.00	0.01±0.00		herbivore
Total Coleoptera	5.95±0.46	7.76±0.44		0.62±0.04	1.99±0.30		NA
Chrysopidae	0.01±0.01	0.02±0.01		0.01±0.01	0.01±0.01		herbivore
Coniopterygidae	8.00±1.58	1.32±0.81	*	0.60±0.11	0.18±0.03		predator
Rhaphidiidae	0.35±0.23	0.06±0.06		0.05±0.02	0.04±0.01		herbivore
Total Neuroptera	8.36±1.67	1.40±0.82	*	0.66±0.11	0.23±0.03	*	NA
Thysanoptera	57.71±5.95	100.91±8.29	*	24.62±1.94	27.17±1.77		herbivore
Isotomidae	2.64±0.53	0.56±0.13	*	0.27±0.17	0.13±0.03		detritivore
Poduridae	0.07±0.03	0.04±0.02		0.48±0.38	0.00		detritivore
Sminthuridae	0.00	0.00		0.02±0.02	0.00		detritivore
Total Collembola	2.71±0.53	0.60±0.13	*	0.77±0.42	0.13±0.03		NA
Acrididae	7.56±0.56	8.90±0.51		0.99±0.16	2.69±0.38	*	herbivore
Gryllacrididae	0.21±0.08	0.09±0.03		0.01±0.01	0.01±0.00		omnivore
Gryllidae	0.00	0.02±0.02		0.00	0.00		omnivore
Total Orthoptera	7.78±0.56	9.01±0.51		1.00±0.16	2.70±0.38	*	NA
Halictophagidae (Strepsiptera)	0.15±0.06	0.03±0.01		0.03±0.01	0.01±0.00		parasitoid
Chilopoda	0.00	0.04±0.02		0.00	0.01±0.01		predator

Table 2.3. Summary ANOVA statistics for the effects of site (1 vs. 2), treatment (burned vs. unburned), year (1998 vs. 1999), and distance (10 vs. 50 m from burn edge) on the total abundance of prairie arthropods.

Source of variation	df	Sum of squares	F Ratio	P-value
Site(Random)	1	0.14	13.67	0.0006
Treatment	1	0.02	2.34	0.13
Year	1	0.82	78.73	<0.0001
Distance	1	0.02	2.24	0.14
Site*Treatment	1	0.02	1.54	0.22
Site*Year	1	0.18	17.06	0.0001
Site*Distance	1	0.01	1.12	0.29
Treatment*Year	1	0.002	0.15	0.70
Treatment*Distance	1	0.003	0.28	0.60
Year*Distance	1	0.03	3.11	0.08
Site*Treatment*Year	1	0.09	8.54	0.005
Site*Treatment*Distance	1	3.0*10-8	0.00	0.99
Site*Distance*Year	1	0.02	1.80	0.19
Treatment*Distance*Year	1	0.01	1.19	0.28
Site*Treatment*Distance*Year	1	6.3*10-6	0.0006	0.98

Table 2.4. Summary ANOVA statistics for the effects of site, treatment, year, and distance on the total biomass of prairie arthropods.

Source of variation	df	Sum of squares	F Ratio	P-value
Site(Random)	1	3.0*10-6	0.002	0.97
Treatment	1	0.004	1.78	0.19
Year	1	0.17	78.87	<0.0001
Distance	1	5.0*10-5	0.03	0.87
Site*Treatment	1	0.002	1.00	0.32
Site*Year	1	0.26	120.93	<0.0001
Site*Distance	1	0.0004	0.22	0.64
Treatment*Year	1	0.03	11.78	0.001
Treatment*Distance	1	0.02	8.69	0.005
Year*Distance	1	0.01	4.65	0.04
Site*Treatment*Year	1	0.02	8.13	0.006
Site*Treatment*Distance	1	0.005	2.33	0.13
Site*Distance*Year	1	0.001	0.2825	0.60
Treatment*Distance*Year	1	4.0*10-5	0.02	0.89
Site*Treatment*Distance*Year	1	6.2*10-4	0.29	0.59

Table 2.5. Summary ANOVA statistics for the effects of site, treatment, year, and distance on the family richness of prairie arthropods.

Source of variation	df	Sum of squares	F Ratio	P-value
Site(Random)	1	9.01	54.19	<0.0001
Treatment	1	4.63	27.85	<0.0001
Year	1	9.30	55.95	<0.0001
Distance	1	0.03	0.20	0.66
Site*Treatment	1	0.85	5.11	0.03
Site*Year	1	0.39	2.39	0.13
Site*Distance	1	0.02	0.14	0.71
Treatment*Year	1	0.66	3.99	0.05
Treatment*Distance	1	0.06	0.38	0.54
Year*Distance	1	0.006	0.03	0.85
Site*Treatment*Year	1	0.08	0.47	0.50
Site*Treatment*Distance	1	0.09	0.56	0.46
Site*Distance*Year	1	0.19	1.18	0.28
Treatment*Distance*Year	1	0.10	0.61	0.44
Site*Treatment*Distance*Year	1	0.0007	0.004	0.95

Table 2.6. Summary ANOVA statistics for the effects of site, treatment, year, and distance on the family diversity of prairie arthropods.

Source of variation	df	Sum of squares	F Ratio	P-value
Site(Random)	1	0.07	27.45	<0.0001
Treatment	1	0.02	7.46	0.009
Year	1	0.03	9.53	0.003
Distance	1	0.002	0.64	0.43
Site*Treatment	1	0.002	0.87	0.36
Site*Year	1	0.002	0.88	0.35
Site*Distance	1	0.007	2.56	0.12
Treatment*Year	1	0.03	11.36	0.002
Treatment*Distance	1	0.0007	0.24	0.63
Year*Distance	1	0.001	0.38	0.54
Site*Treatment*Year	1	0.002	0.91	0.34
Site*Treatment*Distance	1	0.006	2.36	0.13
Site*Distance*Year	1	0.005	1.89	0.17
Treatment*Distance*Year	1	3.4*10-5	0.01	0.91
Site*Treatment*Distance*Year	1	0.0004	0.13	0.72

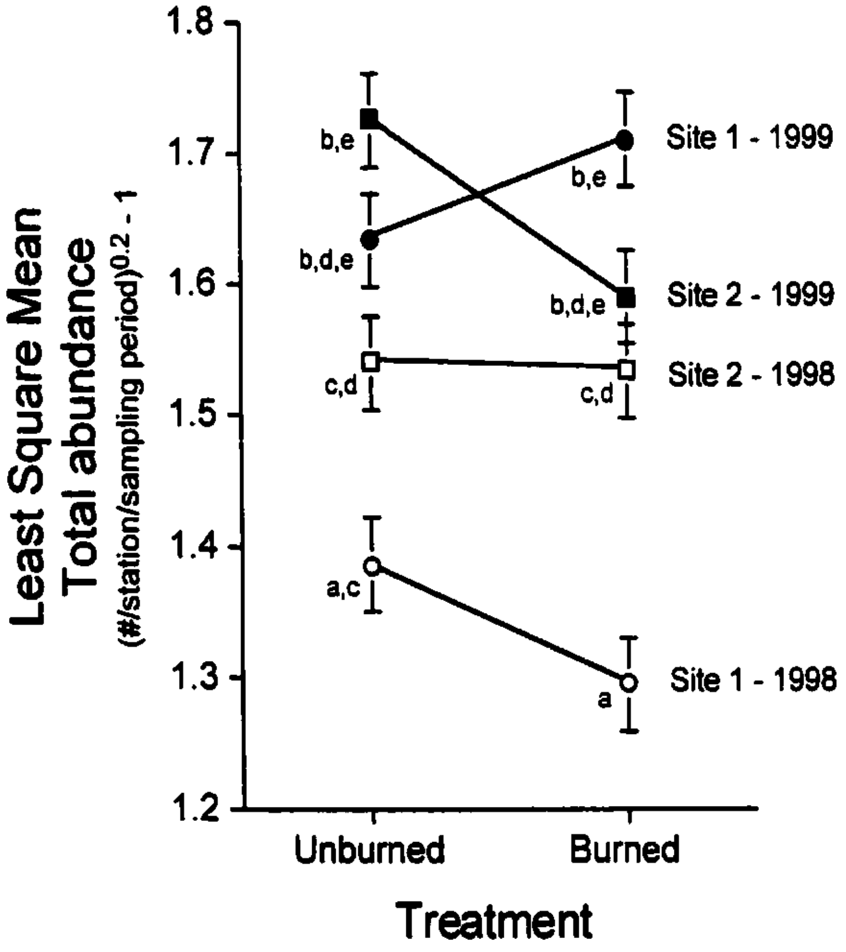

Figure 2.1. Relationship between total abundance and treatment on Sites 1 and 2 in each year (1998 and 1999). Means ± one standard error are given. The least square means are from the analysis presented in Table 2.3. Letters indicate groups of means that are not significantly different from each other (Tukey-Kramer HSD test, $P < 0.05$).

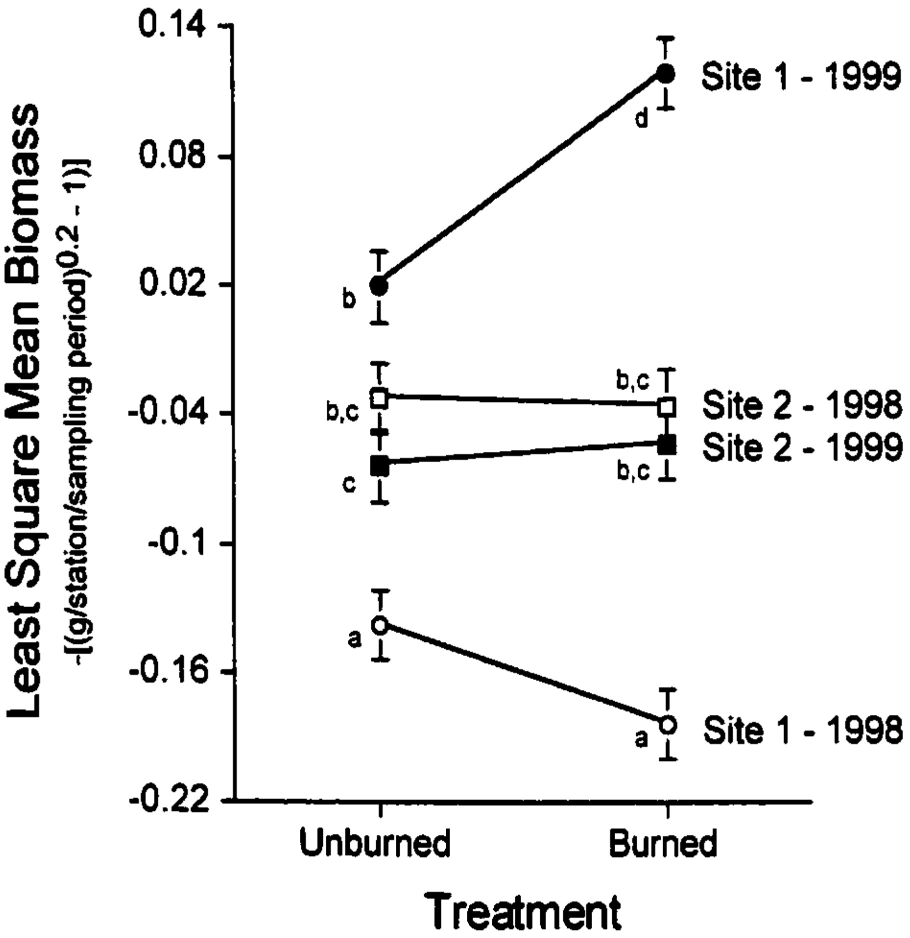

Figure 2.2. Relationship between total biomass and treatment on Sites 1 and 2 in each year (1998 and 1999). Means ± one standard error are given. The least square means are from the analysis presented in Table 2.4. Letters indicate groups of means that are not significantly different from each other (Tukey-Kramer HSD test, $P < 0.05$).

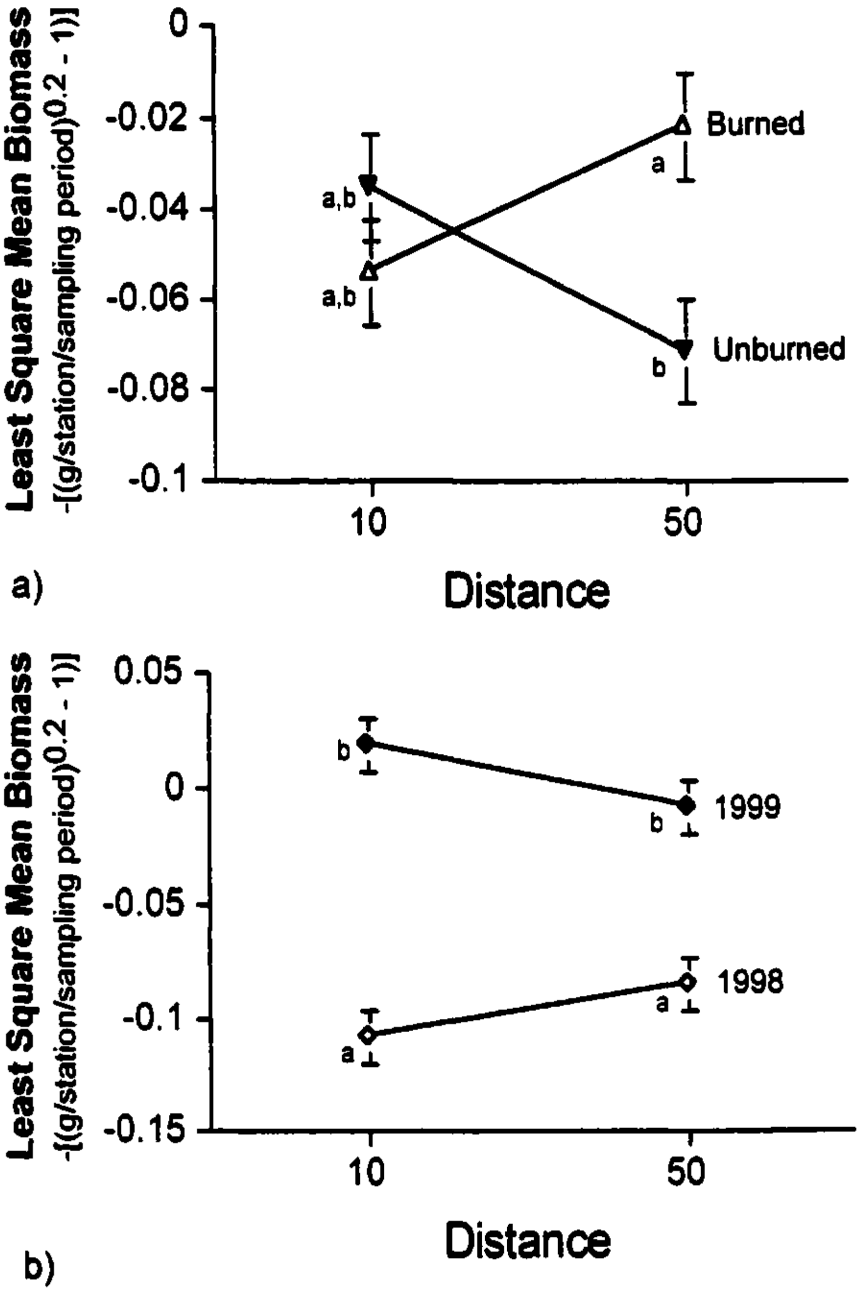

Figure 2.3. Relationship between biomass and distance for a) burned and unburned treatments, and b) each year. Means ± one standard error are given. The least square means are from the analysis presented in Table 2.4. Letters indicate groups of means that are not significantly different from each other (Tukey-Kramer HSD test, $P < 0.05$).

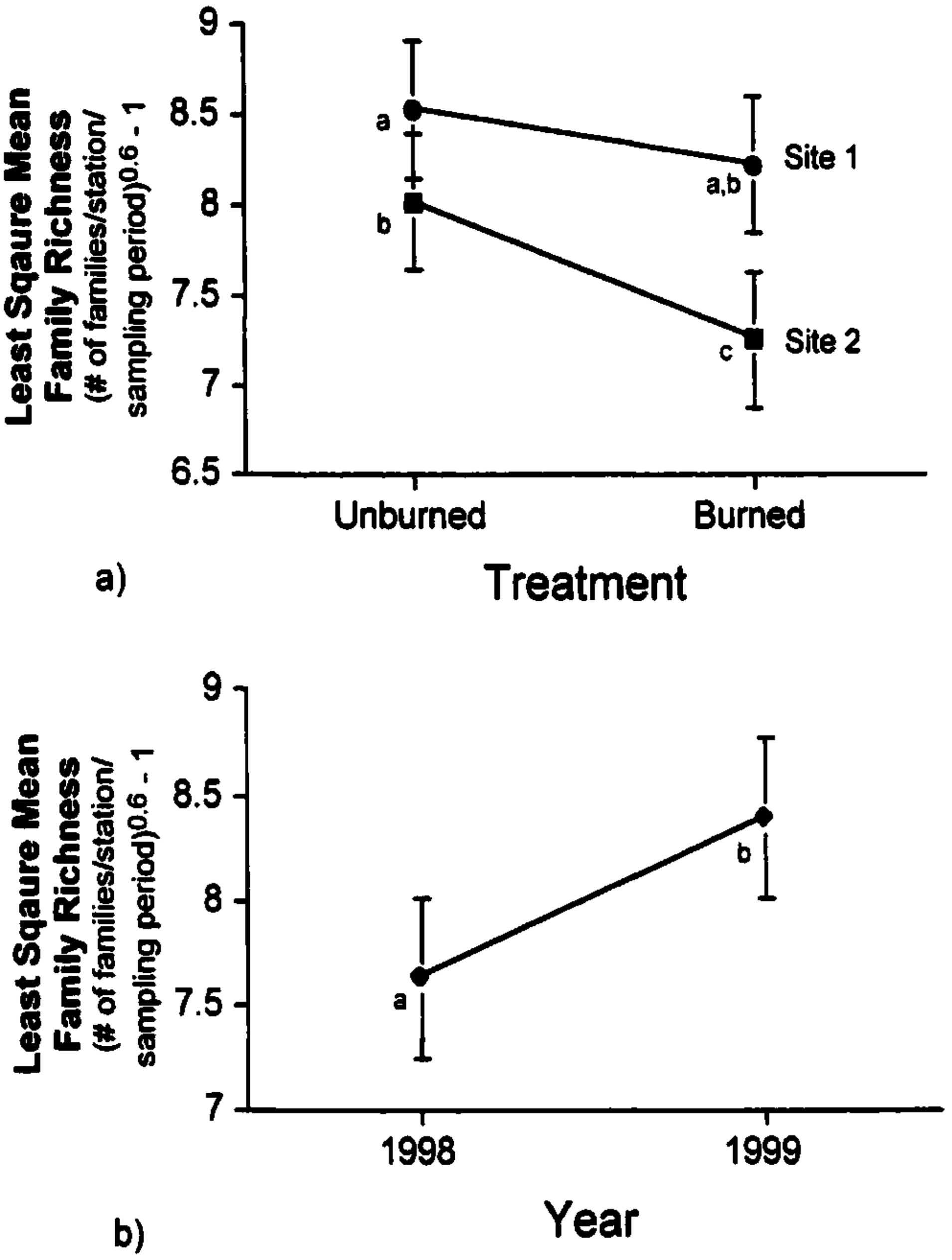

Figure 2.4. Relationship between family richness and a) treatment at each site, and b) year. Means ± one standard error are given. The least square means are from the analysis presented in Table 2.5. Letters indicate groups of means that are not significantly different from each other (Tukey-Kramer HSD test, $P < 0.05$).

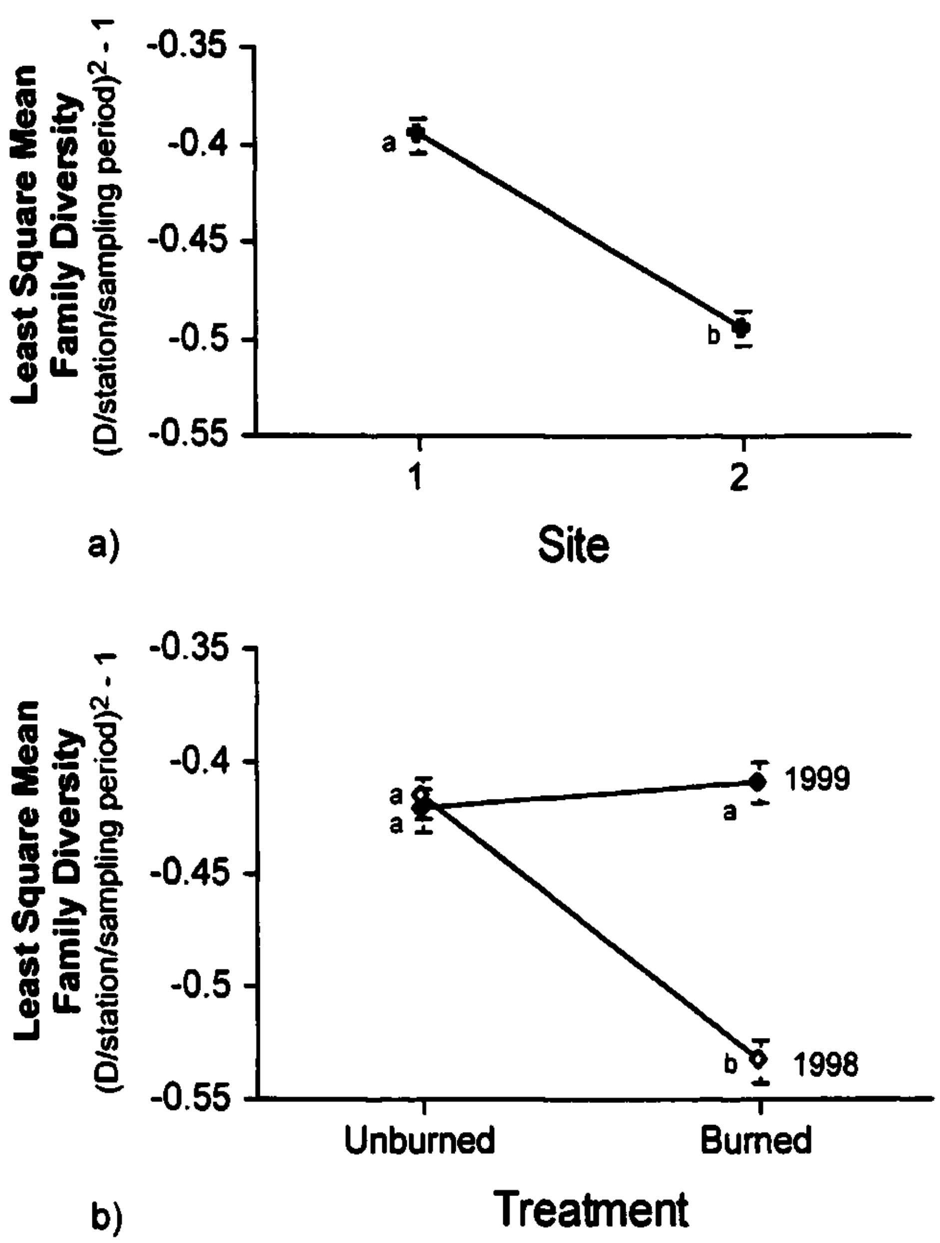

Figure 2.5. Relationships between family diversity and a) site, and b) treatment in each year. Mean ± one standard error are given. The least square means are from the analysis presented in Table 2.6. Letters indicate groups of means that are not significantly different from each other (Tukey-Kramer HSD test, $P < 0.05$).

Chapter 3.

The effects of burning on diversity in a prairie arthropod community: Does competition within tropic levels matter?

Abstract

In general, a disturbance that reduces interspecific competition within a trophic level should increase diversity, while a disturbance that increases competition should decrease diversity. However, it may be that immediately following a disturbance recolonization is more important in determining diversity than competitive pressures. If this is true, diversity may be initially low following a disturbance, but should increase thereafter. These predictions were tested in the summers of 1998 and 1999 with a prairie arthropod community on, and adjacent to, a burn that occurred in December 1997. The burn lowered predator biomass in both summers, lowered parasitoid biomass in 1998, and did not affect herbivore biomass. These changes in biomass were assumed to reflect changes in competition within trophic levels. Based on the changes in biomass of plants and herbivores, we predicted decreased herbivore diversity on the burn. This prediction was not supported: the family diversity of herbivores did not differ between treatments in 1998 or in 1999. In 1998 and 1999, we expected decreased competition and increased predator diversity on the burn. This prediction was not supported in 1998, but was in 1999. In 1998, we predicted that there should be no change in parasitoid competition and that diversity should be the same on the burned and unburned prairie. This prediction was weakly

supported, as there was no difference in the diversity between treatments. In 1999, the parasitoid biomass was higher on the burn and the combined predator and herbivore biomass was lower, so we predicted a decrease in competition and an increase in diversity. This prediction was not supported as the family diversity of parasitoids was not different between treatments in 1999. If succession is more important than competition in determining diversity following this disturbance, the diversity of all groups on the burn should have been higher in 1999 than in 1998. There was no difference in the change in diversity (unburned minus burned) of the herbivores and parasitoids between years. The change in diversity of predators was lower in 1999 than 1998. These results do not support the prediction of increased diversity following disturbance, due to secondary succession. Given this lack of overall support, interspecific competition and succession do not seem to be important in determining diversity in this community.

Introduction

Disturbance can be an important determinant of species abundance and diversity in ecological communities (Connell, 1978; Paine and Levin, 1981, Sousa, 1985). Disturbances range from natural sources such as ocean waves on the rocky intertidal community (Sousa, 1979) to anthropogenic sources such as clear-cut logging (Strayer et al., 1986), and affect many types of communities, including plants (Collins, 1992), invertebrates (Holliday, 1991), and vertebrates

(Abramsky et al., 1979). The diversity of organisms in these communities appears to be increased by moderate disturbances, due to reduced competition from dominant species (Connell, 1978).

Although several studies have supported the hypothesis that disturbance enhances diversity by reducing competition (e.g. Hemphill, 1991; Polishcuk, 1999), the evidence is not universal. For example, disturbance had little impact on diversity in freshwater invertebrates (Thorp and Bergey, 1981; McAuliffe, 1984; Death, 1996). The positive relationship between disturbance and diversity is best supported by studies where species compete for space or space-associated resources, and these species are often primary producers (Wootton, 1998). Conversely, studies that do not support this relationship usually involve mobile consumers.

The previous hypotheses represent a portion of Connell's (1978) intermediate disturbance hypothesis (IDH). However, we must recognize that the effects of disturbance on diversity go beyond simple changes in competition. The IDH predicts that the relationship between competition and diversity is only important at some intermediate time after succession has occurred in the disturbed area. Immediately following a disturbance, the conditions created in the community are so harsh that only a few species can survive (Figure 3.1). As time goes on, succession occurs and more and more species move into the area. Eventually, competitive dominants begin to take over and force other species out of the community. The point at which this switch occurs, intermediate along a time scale appropriate to the community in question, is the point of highest diversity (Connell, 1978; Polishchuk, 1999).

Generally, studies of disturbance and diversity look only at the effects at one trophic level, ignoring the interactions between levels. However, interactions between trophic levels are important when we address the processes of succession and competition, upon which the intermediate disturbance hypothesis is based. In his theoretical analysis of simple multitrophic systems, Wootton (1998) determined that the interactions between trophic levels affect the predicted consequences of disturbance. He suggests that diversity may only be affected by a disturbance when that disturbance affects one trophic level disproportionately. If all trophic levels are proportionately disturbed there is no relative change in the intensity of competition or predation and we should not necessarily expect changes in diversity. However, disproportionate effects of disturbance on one or more trophic levels will affect competition or predation at each trophic level and should result in changes in diversity.

In this paper, inspired by Wootton's (1998) approach, I examine the effects of disturbance on family diversity in a multitrophic community. In particular, I look at the effects of a large-scale fire on family diversity in a prairie arthropod community. I first address the effect of changes in biomass (presumed to reflect changes in competition) on diversity. If disturbance affects all trophic levels equally, we should not see changes in diversity in a community, because the degree of competition within a trophic level for resources in the trophic level below is unaffected by the disturbance (Figure 3.2a). However, if one or more trophic levels are disproportionately affected by disturbance, there is the potential for increased diversity in the trophic levels experiencing reduced competition. For example, a reduction in the abundance of herbivores would favour an increase in plant diversity (Figure 3.2b). However, if this community is still on the left of Figure 3.1 with succession playing a more important role than competition, we should initially see overall decreases in diversity followed by increases on the burned prairie in the second year.

In this study I looked at the effects of a prairie fire disturbance on three trophic levels of the arthropod community. In particular, I tested whether we can understand the effects of disturbance on diversity of a community by looking at trophic structure. To do this, I used the observed effect of disturbance on the biomass of each trophic level (herbivores, predators, and parasitoids) to make and test predictions about how the diversity of these groups should be affected by the disturbance, based on hypothesized effects of interspecific competition and time since disturbance.

Methods

For site description and set-up design please refer to Chapter 2. Sampling methods, identification protocols, and methods for calculation of diversity indices are also given in Chapter 2.

All taxa were classified into a trophic group based on adult feeding habits (determined by literature review). Arthropods were classified as herbivores when the adults fed on plant matter, as predators when the adults fed on other arthropods, and as parasitoids based on larval habits, regardless of the adult diet (see Ch. 2 – Table 2.2 for each taxon's trophic categorization). These groupings follow conventions of other authors (e.g. Siemann, 1998). Insects not falling into these categories (i.e. detritivores, omnivores, pestiferous) represented about 26% of the total number of arthropods collected. Specimen identifications were confirmed by comparison to known specimens and with the help of technicians at the Strickland Museum, University of Alberta and at the Provincial Museum of Alberta.

In food web analyses, biomass is a better measure of resource acquisition than is abundance (Marquis et al., 1995). However, because diversity measurements are based on the relative abundances of individuals, I viewed these trophic-based systems in terms of the numbers of individuals. Thus, for this study, a Mahalanobis outlier analysis (JMP4.0,2000) was used to exclude points (i.e. one sampling station over 4 days) where the numbers of arthropods were not representative of their total biomass (e.g. arthropods that were numerous but also small).Overall, 9% of the original data were excluded. When analyses were done with these data included, the overall results were unchanged.

To assess the effects of succession on diversity I looked at the diversity on and off the burn in both 1998 and 1999. Because the diversities on the unburned prairie between years were significantly different, the change in diversity was calculated as the diversity on the unburned prairie minus the diversity on the burned prairie for each data point (6 traps/4 days). This calculation minimized the effect of year-to-year differences when comparing the diversity on the burn between years.

Results

Of the 129 families caught, 65 were herbivorous, 22 were predacious, and 12 were parasitoid. On the unburned prairie, 61 herbivorous, 20 predatory, and 10 parasitoid families were caught. On the burned prairie, 60 herbivorous, 21 predatory, and 11 parasitoid families were recorded. The number of families in each habitat was independent of trophic level ($\chi^2 = 0.075$, $P = 0.963$).

The overall effect of the fire disturbance on each trophic level in 1998 is shown in Figure 3.3. Predator biomass was significantly lower on the burned than on the unburned prairie (Wilcoxon test, $\chi^2 = 33.4$, $P < 0.0001$). Parasitoid biomass was also lower on the burned prairie (Wilcoxon test, $\chi^2 = 5.82$, $P = 0.02$). There was no change in herbivore biomass on the burned compared to the unburned prairie (Wilcoxon test, $\chi^2 = 0.35$, $P = 0.55$). In 1998, there was also no change in the combined herbivore and predator biomass (Wilcoxon test, $\chi^2 = 0.008$, $P = 0.93$). The burn reduced vegetation cover (used in place of biomass, as plant biomass was not measured directly) by 17.3% in 1998 (Chapter 2). In 1999, predator biomass was significantly lower on the burned prairie than on the unburned (Figure 3.4, Wilcoxon test, $\chi^2 = 7.98$, $P = 0.005$). Herbivore biomass was no greater on the burn than off (Figure 3.4, Wilcoxon test, $\chi^2 = 3.55$, $P = 0.06$). The combined biomass of herbivores and predators was also no greater on the burn than off in 1999 (Wilcoxon test, $\chi^2 = 1.49$, $P = 0.22$). There was no difference between the biomass of parasitoids on and off the burn in 1999 (Figure 3.4, Wilcoxon test, $\chi^2 = 1.43$, $P = 0.23$). The cover of vegetation was 8.9 % lower on the burn than off in 1999 (Chapter 2).

Increased interspecific competition is expected to decrease diversity (Connell, 1978; Hemphill, 1991; Polishcuk, 1999). Therefore, competition among herbivores should be higher following disturbance, because there was no change in herbivore biomass (Figure 3.3) but a decrease in vegetation. Thus, herbivore diversity on the burn should decrease in 1998. This prediction was unsupported. There was no difference in the diversity of herbivores on and off the burn (Figure 3.5; Wilcoxon test, $\chi^2 = 0.00$, $P = 0.99$). The predictions for 1999 are similar to those for 1998. The diversity of herbivores should decrease due to increased competition for resources. However, there was no difference in the diversity of herbivores between treatments in 1999 (Figure 3.6; Wilcoxon test, $\chi^2 = 1.04$, $P = 0.31$).

On the burn, the competition between predators should decrease in 1998 because predators are fewer, but they have the same resource base of herbivores as the predators off the burn. Thus, predator diversity on the burn should be higher. This prediction was unsupported. The diversity of predators was lower on the unburned prairie than on the burned prairie (Figure 3.5; $\chi^2 = 10.47$, $P = 0.001$). In 1999, we should again expect the diversity of predators to increase on the burn, due to reduced competition. This prediction was supported, as the diversity of predators was significantly higher on the burn than off (Figure 3.6; Wilcoxon test, $\chi^2 = 10.86$, $P = 0.001$).

In 1998, the diversity of parasitoids could increase on the burn, because the parasitoid biomass decreased while the combined herbivore and predator biomass remained unchanged, resulting in decreased competition. There was no difference in the diversity of parasitoids on and off the burn (Figure 3.5; Wilcoxon test, $\chi^2 = 2.28$, $P = 0.13$). In 1999, the diversity of parasitoids was expected to increase due to decreased competition for predators and herbivores on the burned prairie. The prediction was not supported. There was no difference in the diversity of parasitoids on and off the burn (Figure 3.6; Wilcoxon test, $\chi^2 = 0.03$, $P = 0.87$).

An alternative hypothesis is that succession or dispersal into the burn following this disturbance was a more important determinant of diversity. If this was true we would predict that the diversity in 1999 on the burned prairie should be higher than that in 1998. Figure 3.7 shows the change in diversity (unburned – burned) in 1998 and 1999. If this community was on the left of Figure 3.1 (i.e. succession played a more important role in determining diversity than competition) than the change in diversity in 1999 should be higher than that in 1998. This prediction was unsupported. The changes in diversity for herbivores and parasitoids were no different between years and the change in diversity of the predators was lower in 1999 than 1998 (Wilcoxon test, herbivores - $\chi^2 = 0.1$, $P = 0.76$; parasitoids - $\chi^2 = 0.04$, $P = 0.85$; predators - $\chi^2 = 13.37$, $P < 0.0003$).

Discussion

In 1998, the fire lowered predator and parasitoid biomass, and left herbivore biomass unchanged. The decrease in predator biomass likely leads to a decrease in competition for herbivore resources and should increase predator diversity. However, contrary to expectations, this decrease in the biomass of the predators did not translate into an increase in their diversity. Predator diversity was lower on the burn than the unburned prairie. Competition between parasitoids should have decreased given that the herbivore and predator biomass was unchanged. Thus, their diversity should have increased. This prediction was unsupported. Herbivore biomass was similar on and off the burn, while vegetation was much less abundant on the burn. Thus, competition between herbivores on the burn was likely higher than off the burn. This change did not, however, result in a decrease in their diversity. In 1998, the diversity-competition hypothesis was unsupported by results for predators and herbivores and only weakly supported by parasitoids. In 1999, predator biomass was lower on the burn and diversity was higher. This supported the predictions. However, neither the herbivores nor parasitoids supported the predictions in 1999. Overall, we have one strong result supporting it (predators in 1999). The remaining five results provide no support. Thus, it would appear that we can not simply use expected changes in competition to predict what a disturbance will do to diversity in this multitrophic system. Rambo and Faeth (1999) also found that changes in competition did not affect diversity following grazing disturbance in a grassland community in Arizona.

As suggested in the introduction, it may be that this community is still in the early stages of succession following the fire. Several studies have shown that disturbances result in initially low diversity, followed by increases in diversity (e.g. Paine and Levin, 1981; Polishchuk, 1999). The size of this fire and the infrequency of fire disturbance in the area suggest that this community may not recover quickly from the disturbance and that it may still have been in early successional stages at the time of the study. However, this hypothesis was not supported by either the herbivores or parasitoids, which showed no difference in the change in diversity between years, or by the predators, whose change in diversity was actually lower in 1999. Thus, the predictions of the effect of succession on diversity, posed by the IDH, gain no support from the data presented in this study.

The lack of change in herbivore biomass following the fire may be due to rapid re-growth of lush vegetation. Vegetation grows more rapidly in burned areas (Rice, 1932; Kucera and Ehrenreich, 1962), which encourages the quick return of herbivorous arthropods to the disturbed area (Rice, 1932). Also, the rapid growth and likely higher nutritional quality of the new vegetation may allow the smaller (in terms of percent cover) resource base on the burn to support the same number of phytophagous insects as the unburned area. On the unburned prairie a large percentage of the total cover was from dead grasses left standing from growing seasons in earlier years, whereas on the burned prairie nearly all of the vegetation was new growth.

In this study, diversity was measured at the family level rather than the species level, as logistic constraints prevented the identification of all specimens to species. Because many families occurred both on and off the burn (Jaccard's index = 85.9%), family diversity is primarily a measure of the relative proportions of each family. Does this focus on diversity at the family level affect my conclusions? Williams and Gaston (1994) showed that family diversity and species diversity of British ferns, butterflies, and Australian passerine birds are strongly and positively correlated. Thus, higher-taxon diversity may be a useful surrogate for species diversity. Also, in this study, the measures of diversity are only used in a relative sense to make comparisons between the undisturbed and disturbed arthropod communities. Thus, for the purposes of this study the lack of finer taxonomic resolution is not a problem.

The reduced structural complexity of the microhabitat on the burn may have increased the trapability of more active arthropods, which likely would encounter the traps more frequently (Ausden, 1996). Pitfall traps in particular often reflect the activity of the insects they catch rather than the actual abundances (Spence and Niemela, 1994). This may be of concern in this study as most of the predatory arthropods (eg. spiders) were caught in pitfall traps rather than pantraps, whereas the herbivorous and parasitoid arthropods were predominantly caught in pan traps. However, since the biomass of predators was lower on the burned prairie than on the unburned prairie, the problem of increased trapability due to ease of activity is not likely to be of considerable concern in this study.

In this study, the relationship between competition and disturbance as a regulator of diversity was not as would be expected from several other studies (e.g. Petraitis et al., 1989; Olff and Ritchie, 1998). We should expect interspecific competition to be inversely related to diversity (Huston, 1979). Disturbances tend to reduce competition from dominant species, allowing less competitive species to persist in the community. However, although intermediate level disturbances may allow increased diversity due to reduced competition, intense or frequent disturbances may reduce diversity, by eliminating species (Connell, 1978). The relationship between diversity and competition depends on the effect properties of disturbance have on succession following that disturbance. With low frequency or low intensity disturbances, competitively superior species can still maintain dominance because few patches open up and the community does not change overall. After a more intense disturbance, competitive pressures are released and other species can move in and thus, diversity increases. As succession occurs, the more competitive species again begin to gain control of resources and diversity decreases. Thus, diversity is highest at some intermediate time following disturbance. The intermediate disturbance hypothesis has been extensively studied (e.g. Paine and Levin, 1981; Holliday, 1991; Weigand et al, 1998) and is often used as a basis for management practices (e.g. Range Research Subcommittee, 1962). This study was unable to show support for the intermediate disturbance hypothesis based on either the negatively correlated relationship between competition and diversity, or succession immediately following a disturbance and increases in diversity.

I found striking year effects on diversity. The diversities of all groups in 1999 are lower than those in 1998 (Figure 3.5 vs. Figure 3.6). Indeed, this change in diversity from one year to the next dwarfs the within-year differences in diversity across burn treatments (Chapter 2). This result is all the more remarkable when one considers the enormous physical changes wrought by the burn. Other factors, such as temperature and precipitation, can have strong influences on the arthropod community and may explain some of the large among-year differences in diversity in this study. Regardless, any explanations for diversity invoking competition and/or disturbance must account for among-year differences in diversity that dominate among-habitat differences.

There are many unanswered questions in the area of disturbance ecology and the regulation of biological diversity, including diversity in grassland communities. This study suggests that decreasing competition does not always decrease diversity. The next most obvious explanation is that this study only occurred during the early stages of succession before competition has a strong regulatory effect on diversity. However, this hypothesis was unsupported as well. Thus, it seems that the intermediate disturbance hypothesis is not always a useful tool for predicting the effects of disturbance on diversity, as was suggested by Wootton (1998). Further work should seek to provide insight into how factors other than competition and disturbance severity and succession may influence biodiversity.

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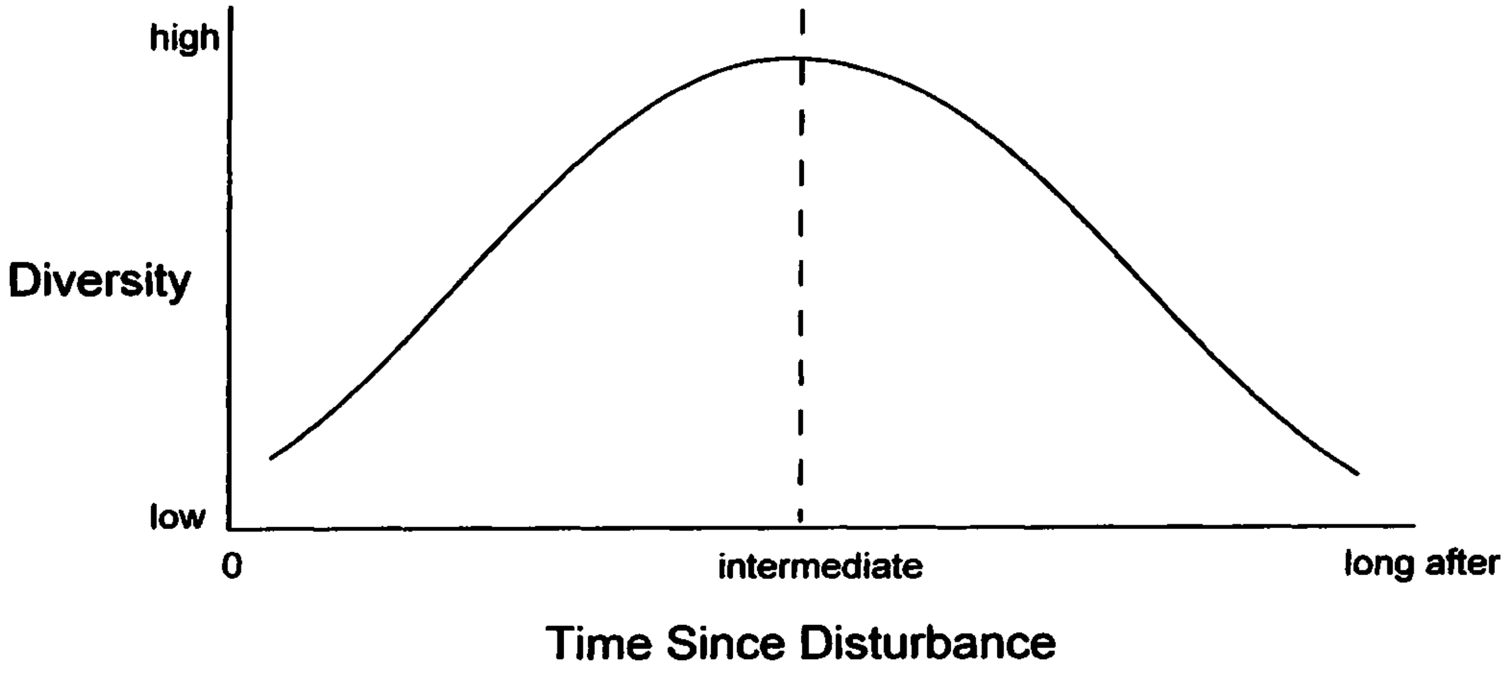

Figure 3.1. Graphical representation of intermediate disturbance hypothesis (after Connell, 1978).

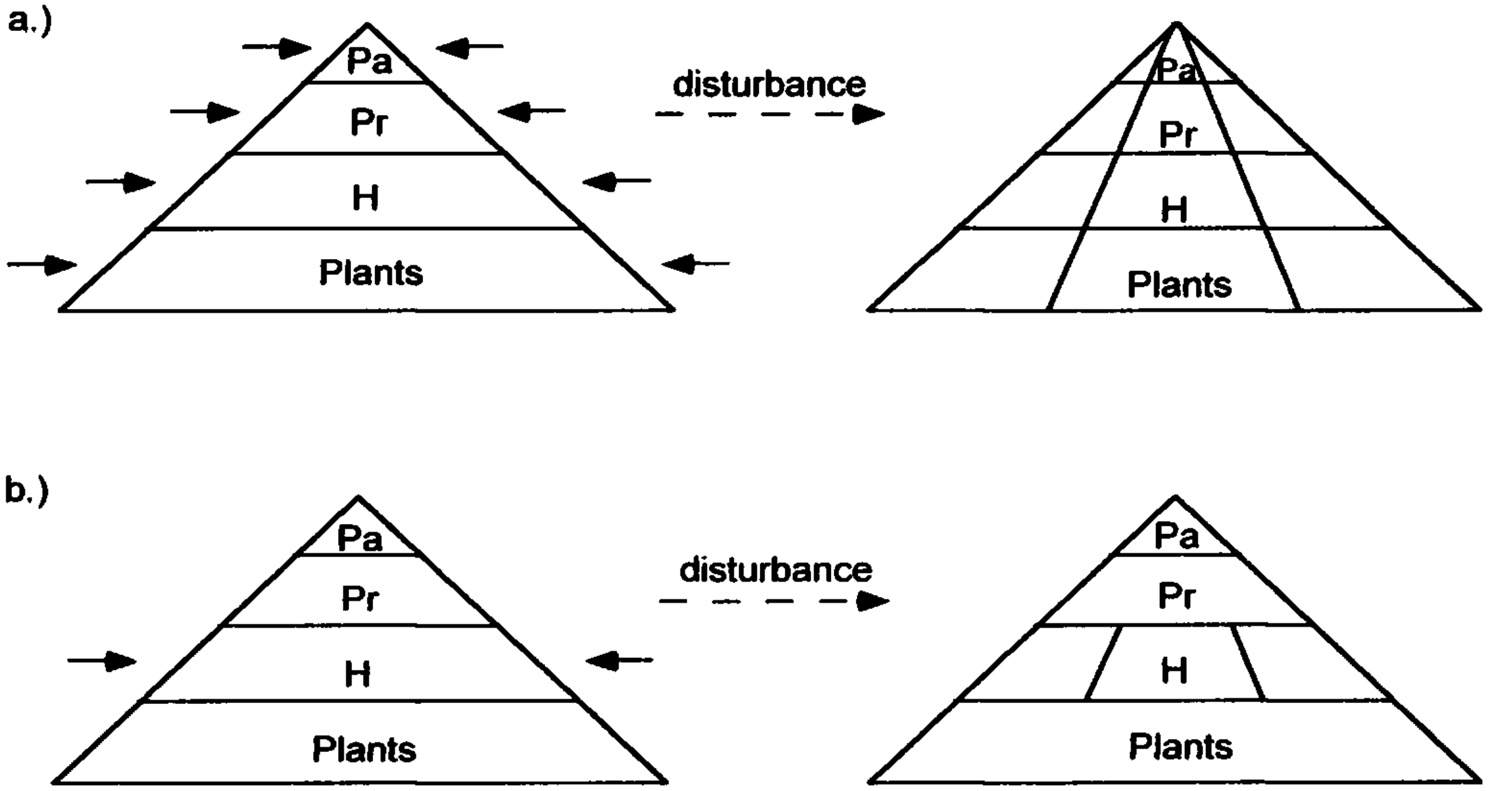

Figure 3.2. Theoretical model of the effects of disturbance on a multitrophic community. Solid arrows represent effect of disturbance on a trophic level. Each area indicates abundance of different trophic level; H = herbivores, Pr = predators, Pa = parasitoids. a) disturbance acts on all trophic levels proportionately (no change in relative abundance), b) disturbance affects a single trophic disproportionately to the others. (After Wooton, 1998)

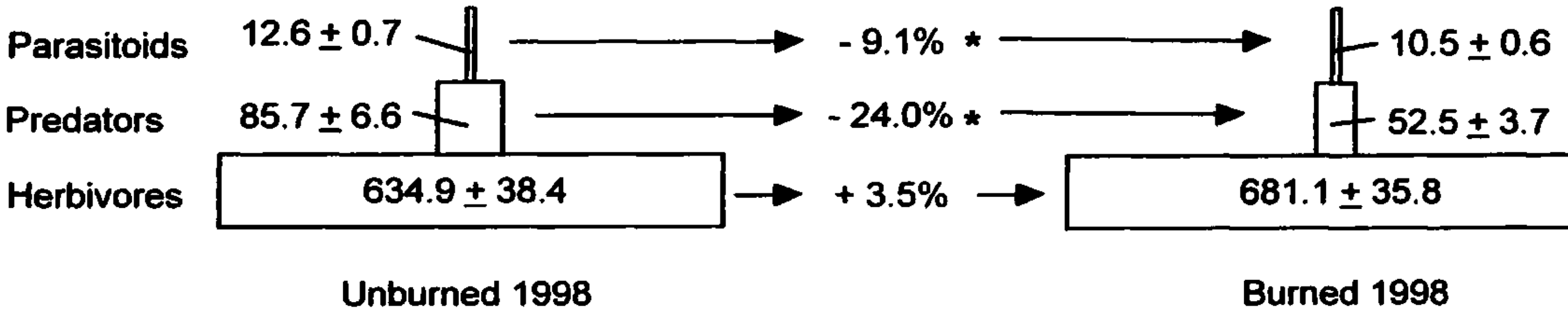

Figure 3.3. Biomass of herbivores, predators, and parasitoids on unburned and burned prairie in July and August, 1998. Means in milligrams ± one standard error are given. Percent change is given along arrow. * indicates significant change.

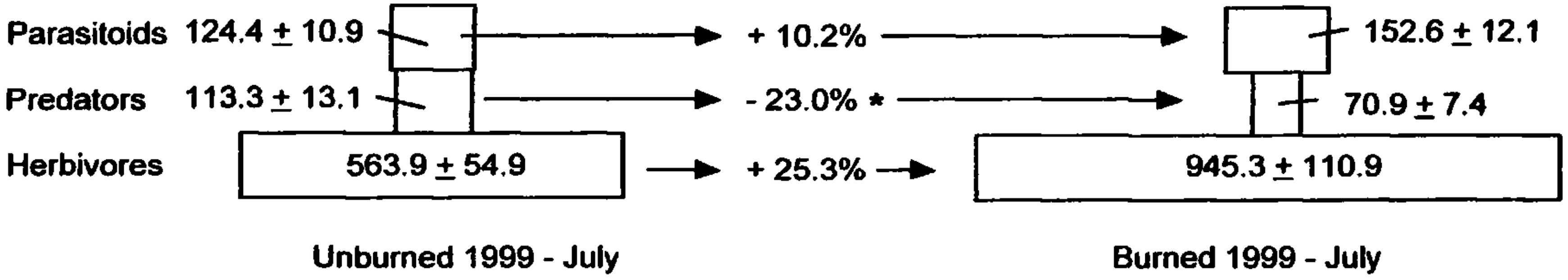

Figure 3.4. Biomass of herbivores, predators, and parasitoids on unburned and burned prairie in July, 1999. Means in milligrams ± one standard error are given. Percent change is given along arrow. * indicates significant change in biomass.

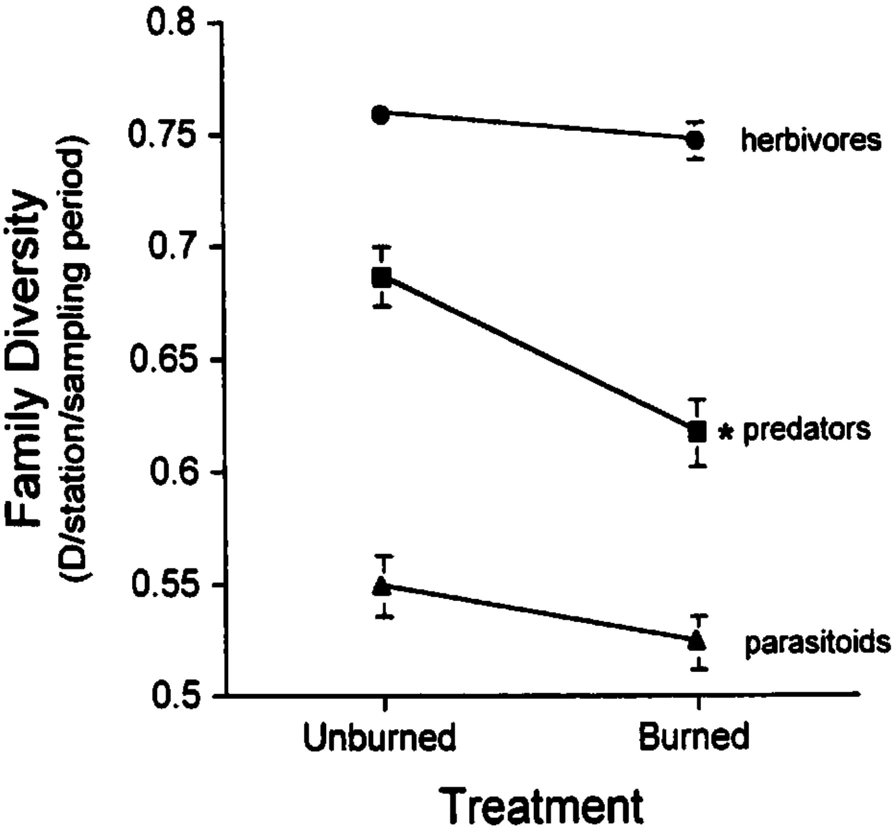

Figure 3.5. Family diversity of herbivores, predators, and parasitoids on unburned (n = 94) and burned (n = 141) prairie in 1998. * indicates significant difference between treatments ($P < 0.05$). Standard error bars are given.

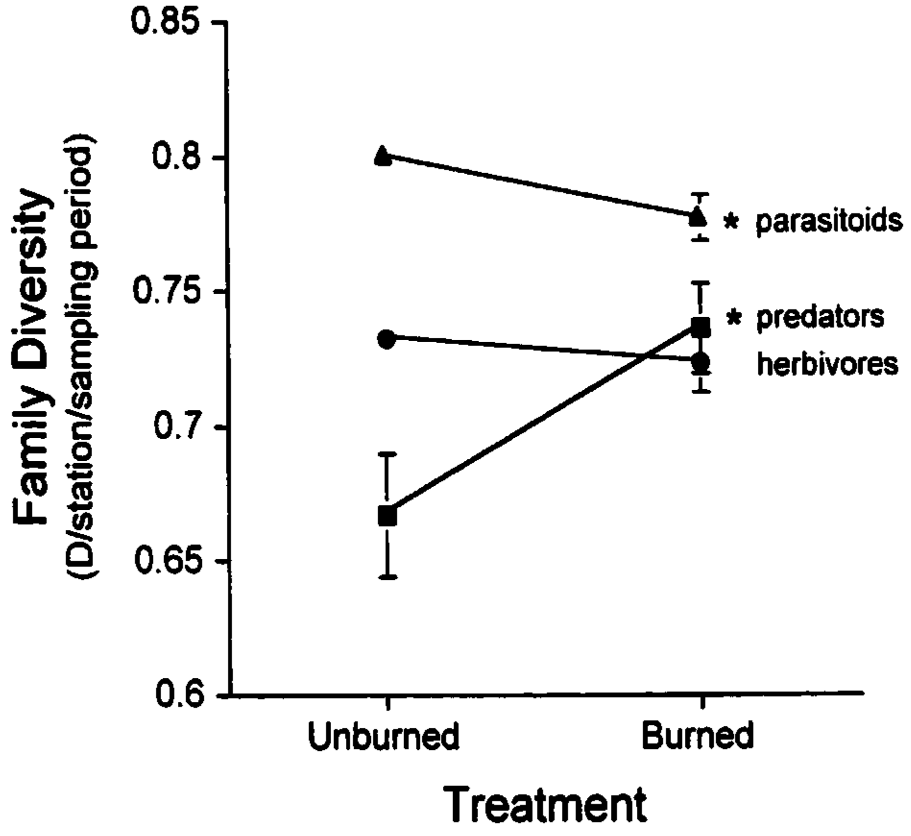

Figure 3.6. Family diversity of herbivores, predators, and parasitoids on unburned (n = 44) and burned (n = 61) prairie in 1999. * indicates significant difference between treatments ($P < 0.05$). Standard error bars are given.

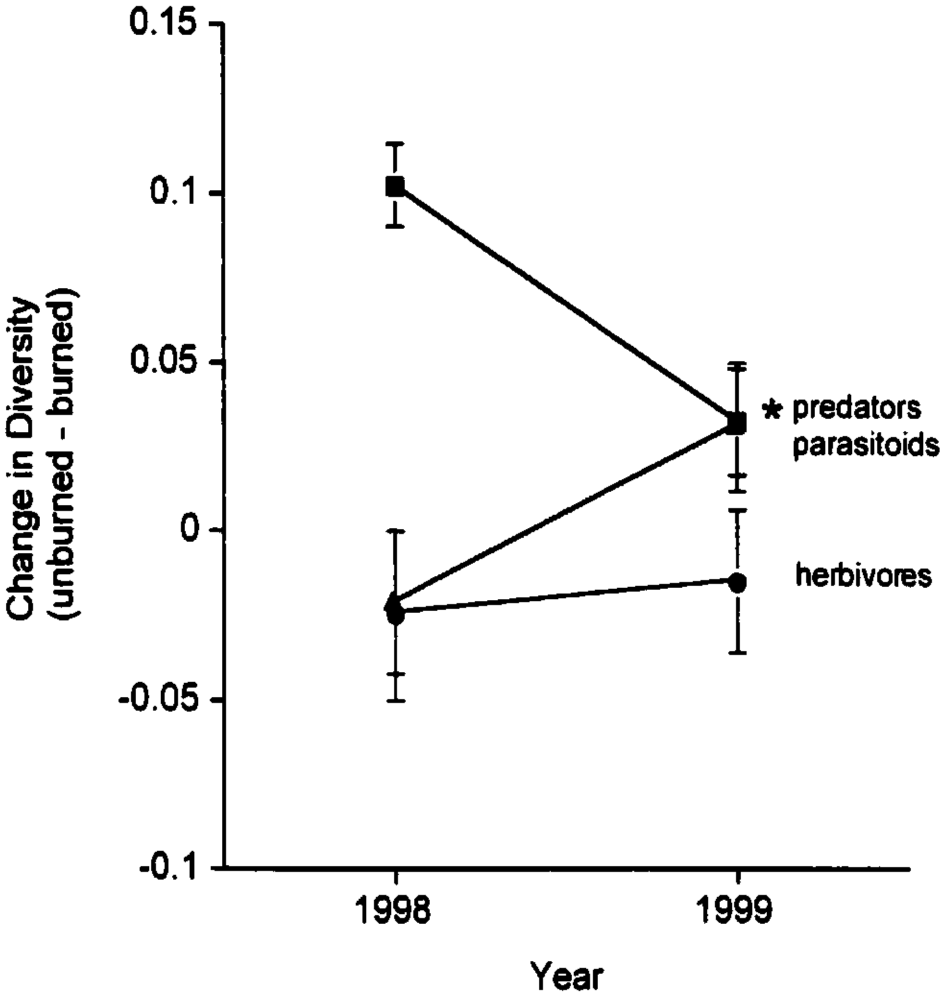

Figure 3.7. Change in family diversity between 1998 (n = 94) and 1999 (n = 44). Error bars indicate ± one standard error. * indicates significant difference between years.

Chapter 4.

The trophic-based structure of prairie arthropod communities: A comparison of disturbed and undisturbed habitats

Abstract

This study takes a coarse approach in addressing the debate of top-down vs. bottom-up community regulation in terrestrial systems. A grassland arthropod community was divided into three hierarchical trophic levels (herbivores, predators, and parasitoids) to examine the general interactions between them. In the summers of 1998 and 1999, arthropods were collected at two sites on the edge of a large prairie fire that burned in December 1997. These arthropods were counted, identified to family-level and categorized by trophic status. Three hypotheses for regulation of the community were tested: bottom-up control, top-down control, and a mixture of the two. Based on path analyses, bottom-up regulation was best supported in this arthropod community, in both unburned and burned areas. However, the interactions between trophic levels were weaker on the disturbed prairie, possibly due to decreased predator and parasitoid abundance, and no change in herbivore abundance, in the burned habitat. This study suggests that, when viewing grassland arthropod communities at a coarse level, the major driving force is bottom-up regulation. This study lends further support to the idea that top-down regulation may be unlikely in terrestrial systems due to high diversity at all trophic levels.

Introduction

There has been much debate regarding the relative importance of top-down versus bottom-up effects in structuring communities (Hunter and Price, 1992; Menge, 1992; Power, 1992). Some studies support top-down community regulation, where lower elements of a food web are ultimately controlled or released by higher elements (Letourneau and Dyer, 1998; Siemann et al., 1998). Others support bottom-up community regulation, where the converse is true (Chase, 1996; Siemann, 1998).

Habitat appears to partially explain these differences. The effects of top-down and bottom-up processes in aquatic communities are well-studied (e.g. Paine, 1966; Lubchenco, 1978; Carpenter et al., 1985). In aquatic systems, top-down forces are the dominant regulator of community structure, perhaps due to relatively low species diversity in these communities, and the ability of a few species to have a strong impact on the community (Strong, 1992). Diversity is high in terrestrial systems, and thus the likelihood of strong regulation from top-level consumers should be lower. Although experimental manipulation of elements of terrestrial communities, such as plant cover or predator abundance, has provided support for both hypotheses, few general patterns have emerged (Stiling and Rossi, 1997; Siemann, 1998).

Many studies employ experimental manipulation (usually removals or exclusions) of a trophic level to determine the strength of bottom-up and top-down forces in a given community (e.g. Stiling and Rossi, 1997; Chen and Wise, 1999). This is a powerful method, but typically limited in scope to a few interacting species. Another approach is to use observational data to correlate natural abundances of trophic groups to those of groups with which they likely interact (Siemann, 1998). This provides a generality not typically found in experimental studies. However, causation is difficult to establish with this approach. Experimental manipulations reveal the mechanisms behind the patterns observed (Siemann, 1998). A unique way around this problem is to use comparisons between trophic interactions on disturbed and undisturbed areas. Disturbances tend to disproportionately affect some trophic groups, and thus provide a natural manipulation of community dynamics. In the undisturbed community no manipulations will have occurred. Thus comparing disturbed and undisturbed communities allows evaluation of community structure. Fire is a common natural disturbance in prairie ecosystems. It has an obvious effect on the physical structure of vegetation, favours some plant species over others, and produces a nutrient pulse, which influences plant growth and quality (Tscharntke and Greiler, 1995).

The present study compares undisturbed and disturbed communities afforded by a prairie wildfire to examine the trophic-based structure of a grassland arthropod community. Arthropods are a dominant component of prairie communities (Schoenly et al., 1991) and contain representatives of every trophic group except primary producer (Siemann et al., 1998). Thus, arthropod communities are good candidates to study community structure, due to their abundance and diversity.

Figure 4.1 shows three hypotheses for how arthropod communities with three trophic levels may be structured. The top-down model accounts for herbivore abundance. It predicts that parasitoids should have a negative impact on predators. This may result in a cascading effect: if parasitoids decrease predator numbers sufficiently, herbivores may be released from predation pressure and increase in abundance. Parasitoids may also have a direct negative effect on herbivores, or a positive indirect effect mediated through their negative effect on predators. The bottom-up model accounts for parasitoid abundance. It hypothesizes that herbivore numbers should have a positive effect on predator and parasitoid numbers, and that increased predator numbers will also increase parasitoid numbers. The combined model combines top-down and bottom-up up effects to account for predator abundance. This model predicts that increased herbivore abundance will increase predator abundance, and that increased parasitoid numbers will decrease predator numbers. The interaction between parasitoids and herbivores may be positive or negative depending on the strength of indirect effects.

Previous studies on the trophic relationships of arthropod groups have typically looked at species-level interactions within specific food webs (Chase, 1996; Stiling and Rossi, 1997; Letourneau and Dyer, 1998; Chen and Wise, 1999). These studies measure interactions between small parts of complete communities. In this study, I take a coarse approach to consider the trophic structure of the arthropod community, grouping arthropods into three trophic groups: herbivores, predators, and parasitoids. Comparing the observed trophic interactions on disturbed prairie with those that would be predicted following a disturbance, based on the trophic interactions on undisturbed prairie, provides further insight into how arthropod communities are structured in grassland communities and the extent to which disturbance shapes community structure. This approach analyzes the diverse arthropod community (Chapter 2) at a general level, to determine the relative importance of top-down and bottom-up forces.

Methods

Site description, set-up, sampling and identification methods, as well as protocols for classification by trophic level, are given in Chapter 2. Use of Mahalonobis outlier analysis for total abundance versus total biomass is outlined in Chapter 3.

Path analyses were used to test which of the three hypothesized models best fit the data. Path analyses test how well observed data fit a hypothesized model, using a combination of correlation and multiple regression analyses (Mitchell, 1992). In path diagrams the direction of the arrow indicates the direction of influence, from a causal variable to a dependent variable, and the sign of the arrow indicates the expected effect of that influence. Path coefficients for the hypothesized models were determined by parametric correlations and standardized partial regression coefficients from multiple regression analysis. I used the amount of variation explained by a path model, the coefficient of determination (R^2), as one measure of adequacy of model fit.

Because the path analyses contained data from the same places at different times, the data were not independent. To determine the importance of this non-independence, separate path diagrams were constructed for each date (pooling across sampling stations) and for each sampling station (pooling across dates), separating samples from burned and unburned habitats. The best fitting model for each of these sets of paths was chosen. Adequacy of fit was determined by the highest R^2, as well as by the number of significant paths in the direction predicted by the hypothesis being tested. The number of times each model best fit the data, and did not contain significant non-supportive paths (i.e., paths that oppose the predictions of the model, Figure 1), was tallied and a sign test was used to determine significance.

This study was conducted over two years following the fire, to address how secondary succession may affect the trophic interactions in this arthropod community.

Results

Figure 4.2 shows the path diagrams for the unburned prairie in 1998. Based on R^2, the bottom-up model best fit the observed data. It is also the only model that contained no significant non-supportive paths. The bottom-up model was also best supported by both the station- and date-level analyses (Figure 4.2; sign tests, station $P = 0.059$, date $P = 0.008$).

In 1999, the bottom-up model was again best supported (Figure 4.3). While the top-down model had the highest coefficient of determination, all of its paths were non-supportive of the model. For example, it suggests that parasitoids increase, not decrease, predator populations. The analyses of each station could not be done, due to too few data points, however there was anecdotally more support (i.e. all three dates) for the bottom-up model when analyzed by date (Figure 4.3).

In 1998, burning decreased predator and parasitoid abundance, but had no effect on herbivore abundance (Figure 4.4; One-way ANOVAs, predators: $F_{1,233} = 26.5$, $P < 0.0001$, parasitoids: $F_{1,233} = 12.7$, $P = 0.0004$, herbivores: $F_{1,233} = 0.21$, $P = 0.65$). By 1999, only predator numbers were different between burned and unburned habitats (Figure 4.5; predators: $F_{1,108} = 11.7$, $P = 0.0009$, herbivores: $F_{1,108} = 3.2$, $P = 0.08$, parasitoids: $F_{1,108} = 0.15$, $P = 0.70$).

Given that the bottom-up model best explains the arthropod community on the unburned prairie, and given the effects of burning on each trophic group (Figures 4.4 and 4.5), we predicted that the fire would not change the overall trophic structure of the community. With bottom-up regulation, no change in herbivore abundance, coupled with decreased predator and parasitoid abundance, imply no change in the overall trophic structure, but weakened interactions between trophic groups. However, predator and parasitoid numbers should increase dramatically following the initial disturbance-induced mortality, due to the large herbivore base.

The bottom-up model was also best supported on the burned prairie in 1998 (Figure 4.6) and in 1999 (Figure 4.7), as it had the highest coefficient of determination, no non-supportive paths, and best support from date-by-date and station-by-station analysis.

The bottom-up model did not fit the data as well on the burned prairie as on the unburned prairie in 1998, but better explained the data on the burn in 1999 (Figures 4.2, 4.3, 4.6, and 4.7). In 1998, the interaction between predators and parasitoids was weaker on the burn than off the burn (Figure 4.2 and 4.6; partial regression coefficients, unburned $ß_{PrPa} = 0.40$, burned $ß_{PrPa} = 0.29$). In 1999, the interaction between herbivores and parasitoids was much stronger on the unburned prairie than the burned (Figure 4.3 and 4.7; partial regression coefficients, unburned, $ß_{HPa} = 1.1$, burned $ß_{HPa} = 0.39$). However, the interaction between predators and parasitoids and predators and herbivores was much stronger on the burn than in the unburned habitat (Figure 4.3 and 4.7; partial regression coefficients, unburned $ß_{PrPa} = -0.22$, $ß_{HPr} = 0.76$, burned $ß_{PrPa} = 0.47$, $ß_{HPr} = 0.83$).

Stronger support for the bottom-up model may have resulted from parasitoid numbers being less variable and, therefore, easier to explain statistically, than herbivore and predator numbers. However, predator numbers were always more variable (CV for 1998 and 1999 respectively; 64.6, 81.2) than parasitoid numbers (27.1, 25.6), which were always more variable than herbivore numbers (14.5, 20.2). Thus, support for the bottom-up model is not a simple consequence of lower variability in the parasitoids.

Discussion

The bottom-up model was best supported in the undisturbed prairie arthropod community. Given that the fire disturbance did not change herbivore abundance, but decreased predator and parasitoid abundance, we predicted that the dominant regulatory forces should not change, but that the interactions between trophic levels should be weakened. In general, the results obtained on the burned prairie are consistent with this prediction.

These results fit with other studies that have indicated that we should not expect dominant top-down forces in terrestrial ecosystems (Strong, 1992; Polis and Strong, 1996). Strong (1992) suggested that top-down forces should only be dominant in communities with low diversity, where a few top species can have a strong influence on other species in the community. The arthropod community in this study had a relatively high diversity of predatory and parasitoid arthropods, as well as herbivores (Chapter 3). Thus, we should not expect the higher trophic levels to strongly regulate lower levels, due to the inability of one or a few species to monopolize the diverse herbivore resource base. In other words, communities are generally made up of a diversity of specific interactions, with most of the parasitoids and many of the predators acting as specialists.

The bottom-up model better described the community on the unburned versus burned prairie. It may be that following the fire disturbance, factors other than resource rarity (bottom-up forces) had a stronger influence on the arthropod community. Abiotic factors can mask the effects of trophic influences, whether they are top-down or bottom-up. Thermal conditions had a much stronger influence on small grass-feeding grasshoppers than did primary productivity (measured as soil nitrogen) (Ritchie, 2000). Changes in the microhabitat may also be more important in determining community structure soon after the fire. Chase (1996) reported significant effects of top predators in a top-down regulated community when abiotic conditions were altered. In his study, shading (reducing temperature and radiation) reduced time available for feeding by grasshoppers. The shaded grasshopper population was not able to compensate for spider predation by increased feeding, and densities were reduced by the spiders.

Following a burn, soil temperature should increase and fluctuate more, due to carbon-rich soil and reduced vegetation cover (Nagel, 1973). This would likely affect the abundance and type of arthropods in the area. The altered vegetation structure may also affect the number of arthropods moving around on the burned prairie, due to reduced microhabitat complexity and thus, affect the interactions between trophic groups.

Hunter and Price (1992) suggest that bottom-up control is always more important than top-down control because removing higher trophic levels leaves those below intact, but removing the primary producers affects the whole system. Power (1992) further supports bottom-up dominance by suggesting that top-down forces are weakened by factors that reduce consumer efficiency, such as habitat complexity. This may be a good argument for the strength of bottom-up forces in this system. The relative complexity of the unburned grassland community may reduce the efficiency with which flightless predators can move around to hunt prey. Thus, the ability of predators to control herbivore numbers in this community may be weakened. The bottom-up forces on the burn may not be as strong as those on the unburned prairie due to reduced microhabitat complexity.

The non-supportive paths in the top-down and combined models actually support the bottom-up model by indicating that overall the interactions between trophic levels in this community are positive. The significantly non-supportive path, between predators and parasitoids, in the bottom-up model for the unburned prairie in 1999 (Figure 4.5) is problematic. However, this model is still a much better fit than the other two and the weak negative interaction may simply reflect the stronger interactions between herbivores and their predators and parasitoids.

There are obvious among year differences in the trophic interactions in this community (Chapter 2). This result is not surprising because there are so many other factors, such as climate changes, distribution patterns, and population structure that differ among years. Secondary succession of the community is also a likely explanation for the among-year differences (Connell and Slayter, 1977). As the plant community fills in the gaps created by the burn, the arthropod community is also affected by changes in community parameters such as microhabitat, detritus build-up, and resource availability.

Another statistical approach in determining trophic community structure is lag analysis. For example, the number of herbivores at a given time may be better explained by the number of predators at an earlier time. Lag analyses, to the order of two, were done for each of the models tested here, but lagged variables were of weak and inconsistent significance, and did not clarify any of the hypotheses tested in this paper.

One possible problem with comparing the hypothesized models presented here is that each model predicts a different variable. That is, the bottom-up model seeks to explain parasitoid abundance, the top-down model explains herbivore abundance and the combined model explains predator abundance. The bottom-up model may best fit because variation in parasitoid numbers is more easily explained by variation in the predators and herbivores than vice versa. However, the variation in parasitoid abundance is higher than that in the herbivore abundance. Given this, if the differences in variation were important we should expect the bottom-up model to give the poorest fit. Thus, it is not likely that differences in variation are a problem in this study.

The models tested are not based on known species interactions. As noted in the introduction, it may be more clear to choose a well known food web, in which all the individual species interactions have been determined and experimentally test whether top-down or bottom-up forces are more dominant (e.g. Stiling and Rossi, 1997). Instead, I simply characterized arthropods more coarsely by trophic level, and then tested for general interactions between them. Some of the herbivorous arthropods may have no arthropod predators, and thus do not biologically contribute to the arthropod food webs tested here. However, this may be more of an advantage than a shortcoming. Despite the coarsely-resolved trophic structure, this study was able to show support for the bottom-up hypothesis, consistent with other studies in terrestrial communities, while attaining a generality not found in those studies, by looking beyond the known interactions between a few species (e.g. Strauss, 1987; Chen and Wise, 1999).

Several authors report that because top-down and bottom-up forces act simultaneously, the division of the two is often artificial (Oksanen et al., 1981; Leibold, 1989; Hunter and Price, 1992). However, it can still be useful to explore which of these two forces is dominant, as long as we recognize that both can operate simultaneously. Hunter and Price (1992) suggest that the question of regulation of community structure is more interesting when viewed in terms of the variation at different trophic levels and abiotic factors and how these influence top-down and bottom-up forces. They point out that not all plants are equally edible, not all herbivores equally damaging and not all predators equally efficient. Thus, it is necessary to understand the interactions between these heterogeneous factors at all trophic levels (Hunter and Price, 1992). The present study has taken the next step in the study of multi-trophic community structure, to determine the relative importance of top-down and bottom-up forces, while recognizing the importance of heterogeneity over all trophic levels. The coarse approach used here ensures that the heterogeneity of each trophic level is included in the determination of dominant ecological forces in the food web.

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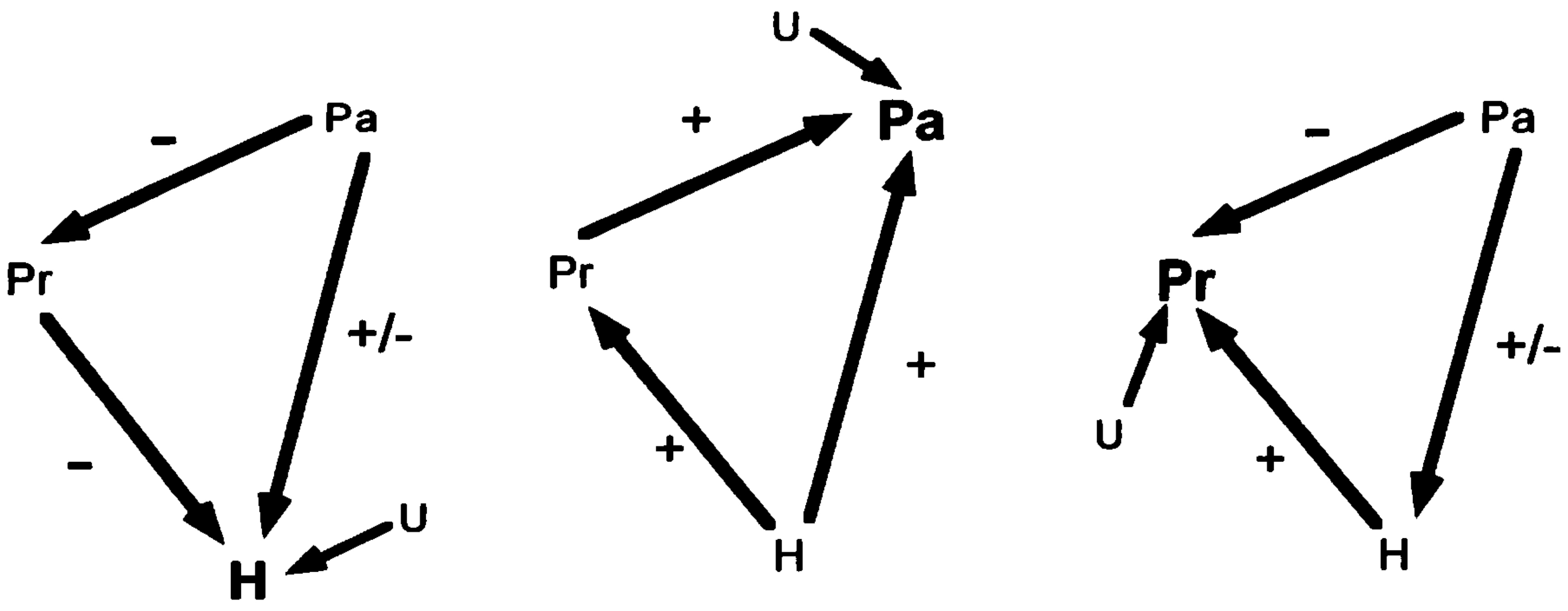

Top-down model

Bottom-up model

Combined model

Figure 4.1. Hypotheses for regulation of the arthropod community, presented as path diagrams. Pa = parasitoids, Pr = predators, H = herbivores. The group in bold indicates the variable being explained by the model. The U indicates unexplained variation in the variable.

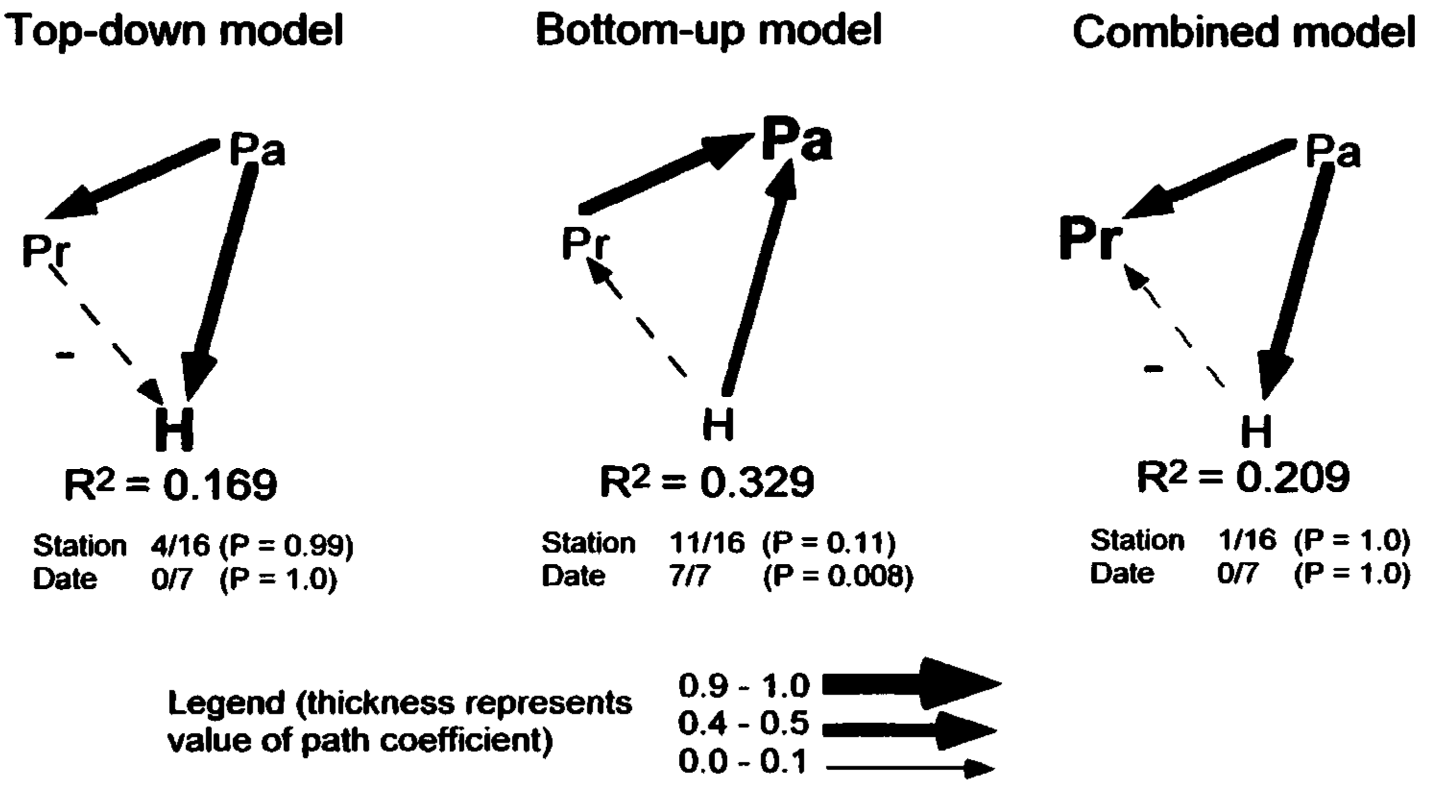

Figure 4.2. Path diagrams for unburned prairie in 1998 (n = 93 for each model). Thickness of the arrows indicates magnitude of the path coefficient. Non-significant paths are dashed. The negative signs indicate a negative path coefficient. Paths that are non-supportive of the model's logic are shown in grey. R^2 is the coefficient of determination. The table below each diagram indicates the number of times (out of the total tested) each model was supported when each station or each date was analyzed separately.

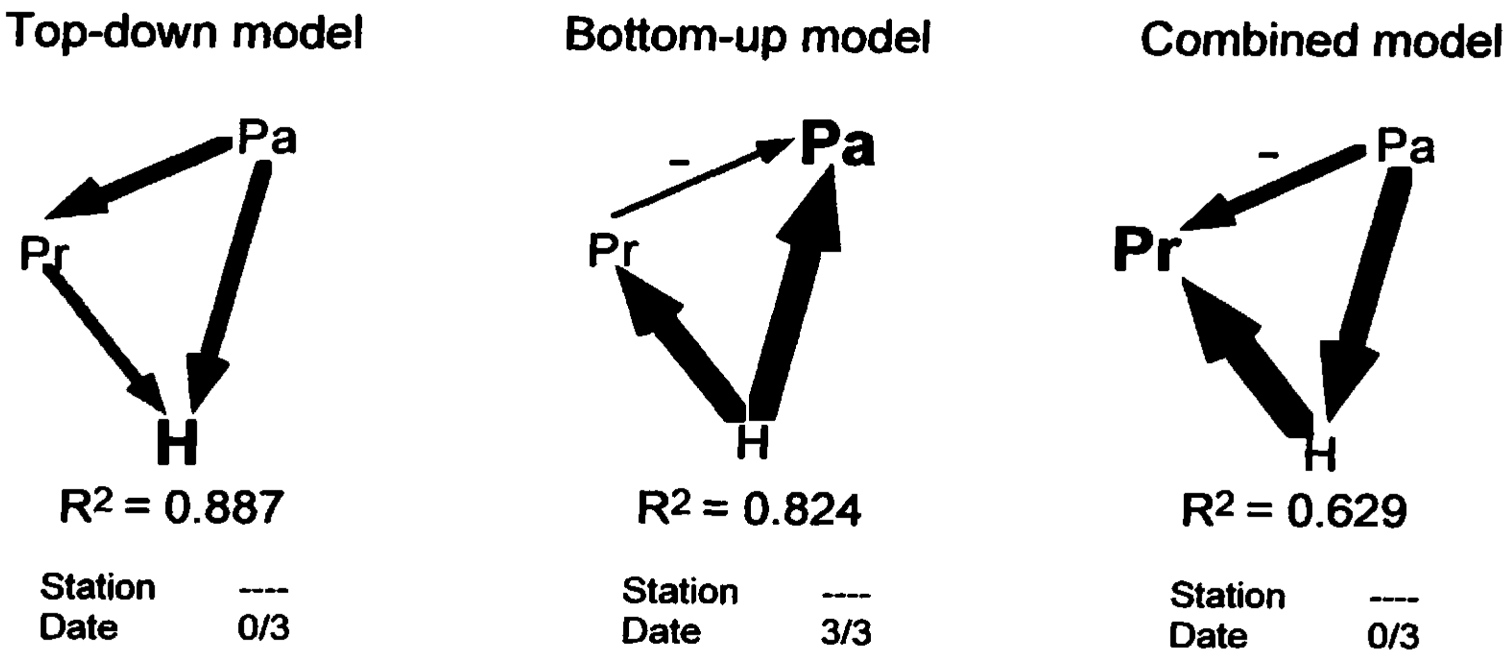

Figure 4.3. Path diagrams for unburned prairie in 1999 (n = 44 for each model). Figure labels as in Figure 4.2. The by-station analysis could not be done because of insufficient data.

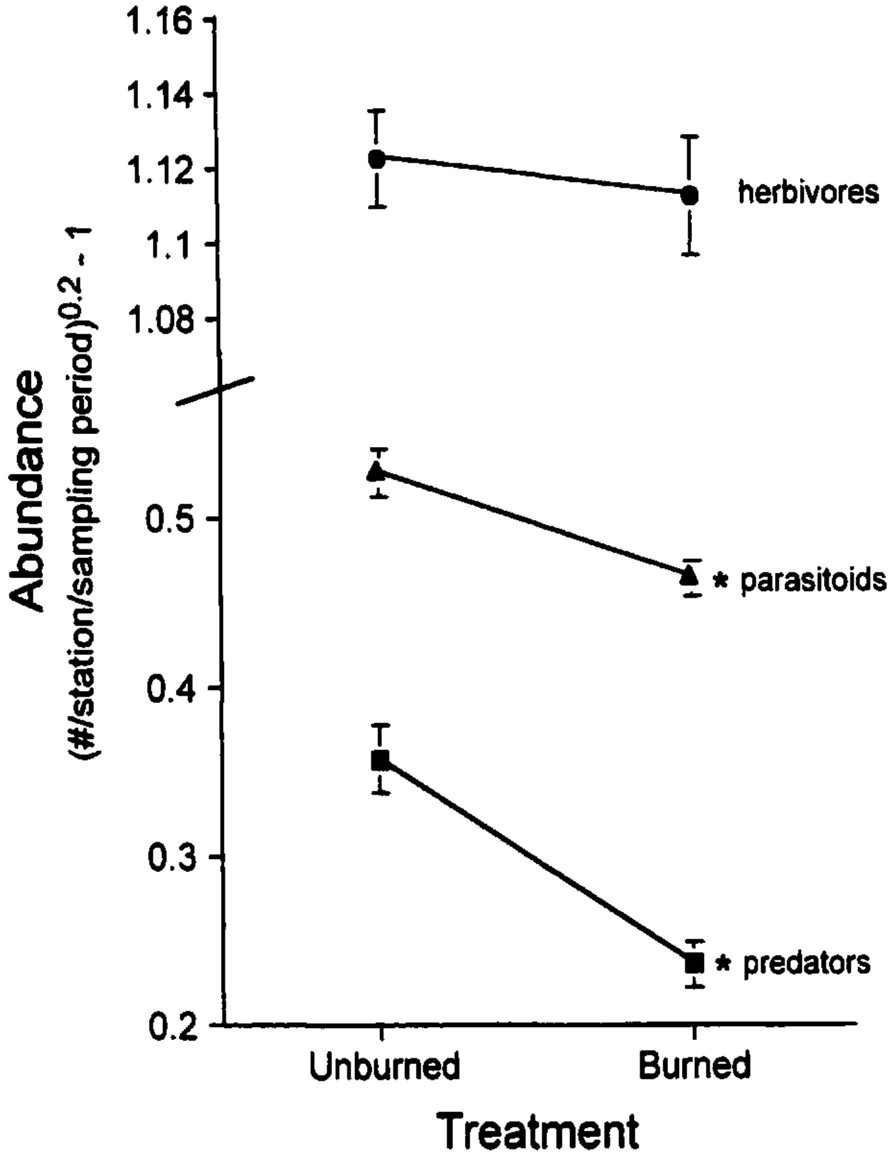

Figure 4.4. Abundance of herbivores, predators, and parasitoids on burned (n = 136) and unburned (n = 93) prairie in 1998. Error bars show ± 1 standard error. * indicates significant difference between treatments ($P < 0.05$)

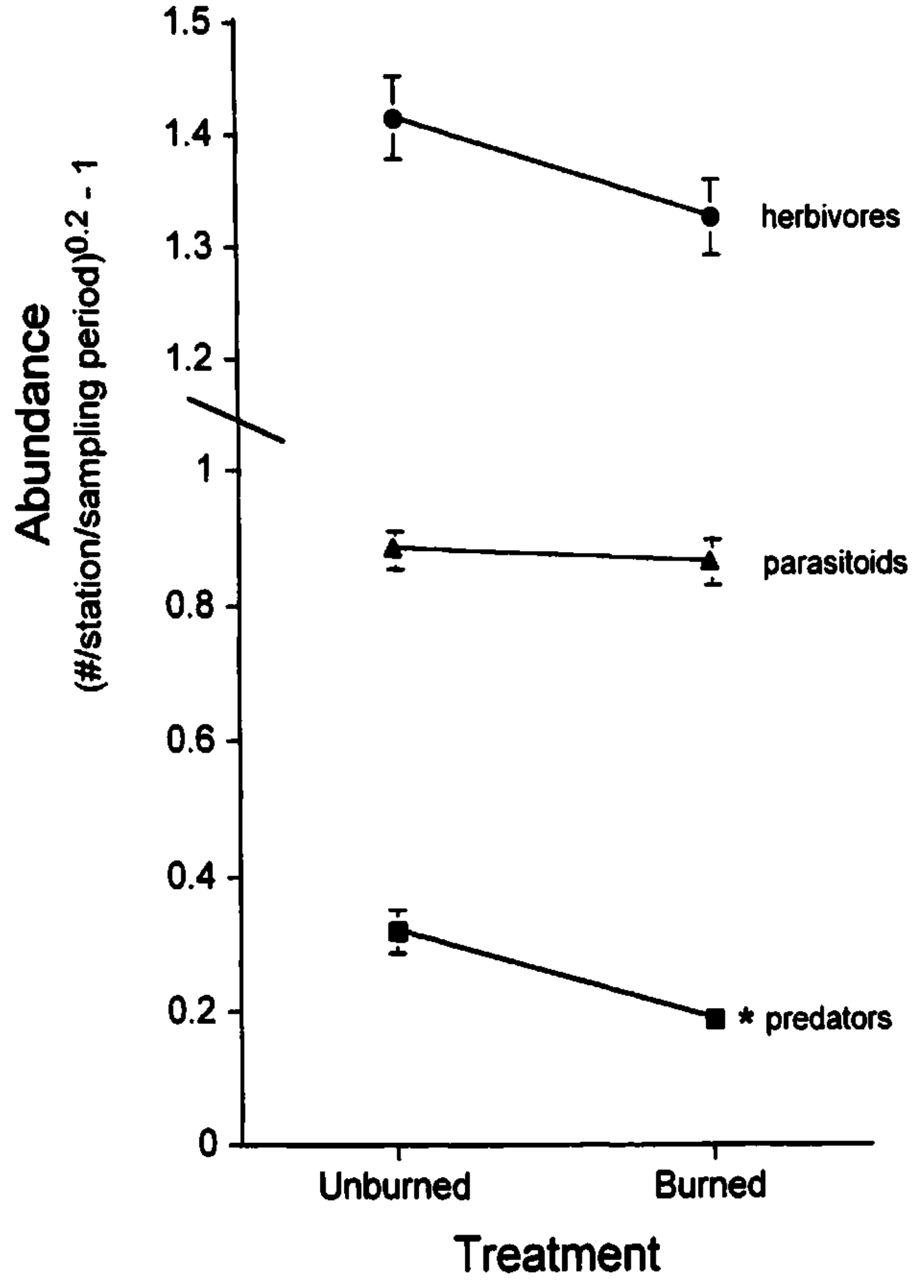

Figure 4.5. Abundance of herbivores, predators, and parasitoids on burned (n = 61) and unburned (n = 44) prairie in 1999. Error bars show ± 1 standard error. * indicates significant difference between treatments ($P < 0.05$)

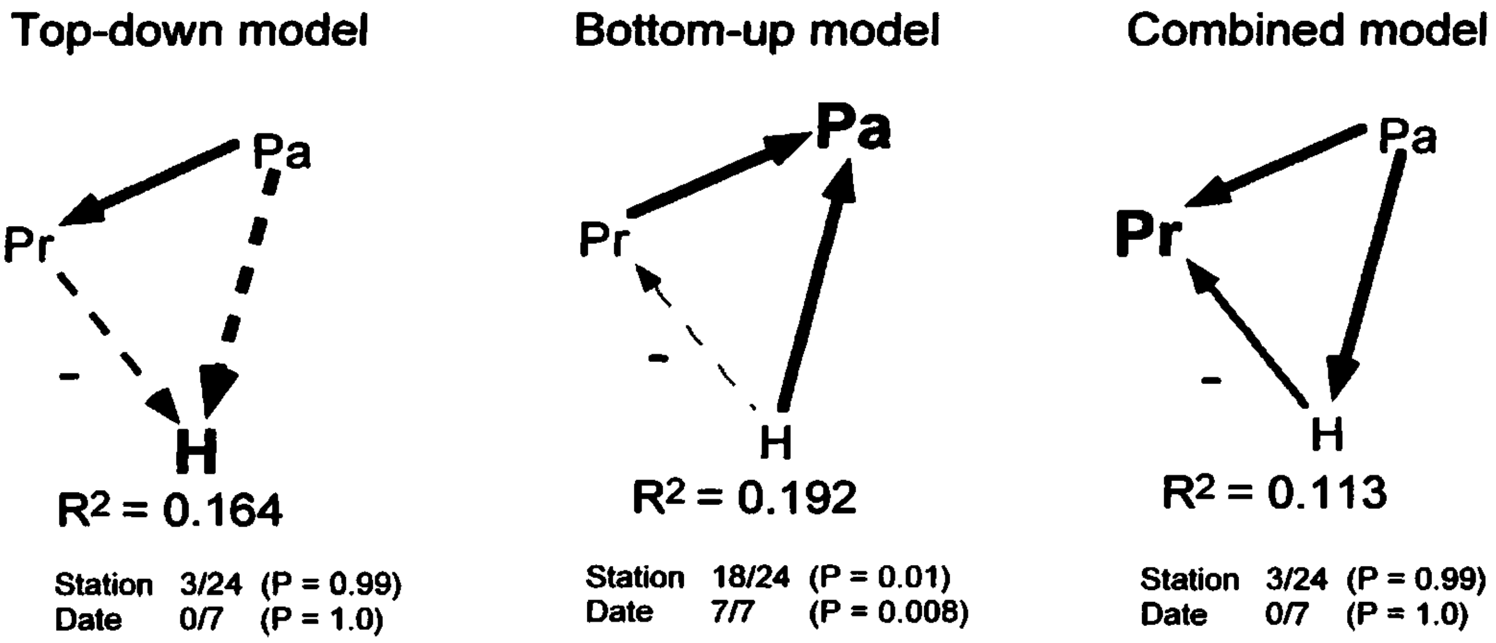

Figure 4.6. Path diagrams for burned prairie in 1998 (n = 136 for each model). Figure labels as in Figure 4.2.

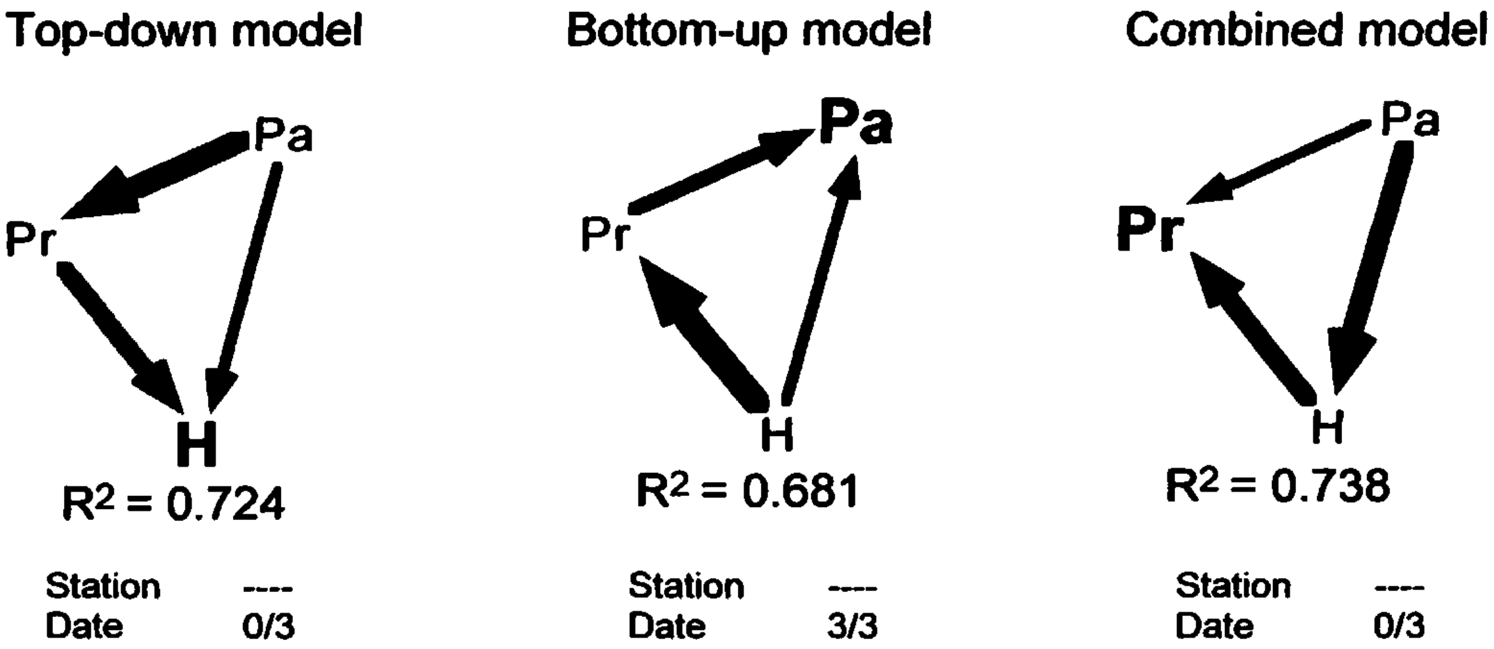

Figure 4.7. Path diagrams for burned prairie in 1999 (n = 61 for each model). Figure labels as in Figure 4.2. The by-station analysis could not be done because of insufficient data.

Chapter 5. General Conclusion

In the field of ecology there has been much debate regarding the processes that determine biodiversity and community structure (MacArthur, 1972; Lubchenco, 1978; Menge and Sutherland, 1987). A relatively recent view is that disturbance plays a dominant role in determining biodiversity and community structure. In this thesis I addressed how disturbance affected a prairie arthropod community. I first examined the patterns of arthropod community structure in this grassland and determined the effects of fire disturbance on this pattern. Second, I tested two general hypotheses regarding the processes that determine those patterns of arthropod biodiversity and community structure.

Patterns of arthropod community structure:

The effects of disturbance on arthropods in this grassland community varied greatly. Some taxa were more abundant on the burn (e.g. Curculionidae, Acrididae) and some were less abundant (e.g. Aranaea, Homoptera), but these patterns varied between years and sites. Clearly, it is difficult to predict the effect fire will have on a community as a whole. This inability to achieve generality is likely due to a number of unmeasured factors, such as properties of the disturbance itself, climate, and arthropod biology. The total abundance, total biomass, family richness, and family diversity were all significantly affected by combinations of site, year, treatment, and distance from burn edge. It is evident that generality is very difficult to attain due to the varied factors associated with arthropod communities and with disturbances.

Disturbance, competition and diversity in prairie arthropods:

This study provided little support for the predictions of the intermediate disturbance hypothesis. Presumed changes in competition following disturbance did not result in predicted changes in diversity. For example, a decrease in predator biomass, without a change in herbivore biomass (i.e. reduced competition) did not increase predator diversity as would be expected. Predator diversity actually decreased on the burn. It was clear from this study that probable changes in competition were not strong determinants of diversity. The next most obvious explanation for changes in diversity following disturbance, as proposed by the intermediate disturbance hypothesis, was succession. However, the hypothesis that succession following a disturbance should increase overall diversity also was unsupported by this study. It seems evident that there may be processes more important than just competition and succession that determine biodiversity. However, it may be that these are very important and the tests of this study were not powerful enough to detect subtle changes.

Abiotic factors, such as temperature and microhabitat structure, may have profound impacts on recolonization of burned areas (Warren et al., 1987). Also, in this study most of the groups collected were found both on and off the burn indicating that there were few burn or unburned prairie specialists. It is possible that, with a wide diversity of generalists on the unburned prairie, the burned area immediately adjacent to it could be rapidly recolonized by local arthropods, maintaining the diversity present prior to burning.

Trophic structure of a prairie arthropod community:

This study showed that, consistent with other studies (Strong, 1992; Polis and Strong, 1996), a bottom-up model best describes this terrestrial arthropod community. Although the bottom-up model best described the community on both the unburned and burned prairie, it better fit the observed data off the burn. As noted in the previous two sections, there are many factors that can influence biodiversity and community structure following a disturbance. Abiotic changes in disturbed habitats have been shown to affect the trophic dynamics in communities (Chase, 1996; Ritchie, 2000). Soil temperatures can be much higher on burned prairie (Nagel, 1973), which could affect the abundance and types of arthropods in the area. Looking at these trophic interactions at a coarse level ensures that heterogeneity at each level is included in determination of the dominant ecological forces in the food web, as well as making results obtained here comparable to similar studies in other areas. Hunter and Price (1992) suggest that a key component of community ecology is to view regulation of community structure in terms of how variation at different trophic levels and abiotic factors influence top-down and bottom-up processes. This work is a step in that direction.

Perspectives:

Although there is evidence from this and other studies that the many effects of a fire disturbance are negligible 2 to 3 years after burning (e.g. Anderson et al., 1989; Bock and Bock, 1991) some groups may have a delayed response and changes may go unnoticed. It may be necessary to study the effects of burning for several years post-burn before we truly understand its implications from a conservation biology perspective. From an economic perspective, this 2-3 year time period seems promising if vegetation is of higher quality and some deleterious arthropod groups are decreased. The key issue then is to find the balance between economic and conservation concerns. The difficulty here is that most species, while valuable in a biological sense, have no economic value (Morowitz, 1991). This balancing act is an important and difficult task for rangeland managers. Scientists must continue to enhance our understanding of ecological processes on native range, to find novel practices that will give the best of both worlds, economy and biological diversity. As suggested by Wootton (1998), further work on the effects of disturbance on diversity should seek to understand how processes other than those behind the predictions of the intermediate disturbance hypothesis may regulate biodiversity. These predictions should be used with caution when considering range management and conservation practices for real multitrophic communities (Wootton, 1998).

There are still many unanswered questions in the area of disturbance ecology. We still cannot definitively predict what processes may regulate the diversity and structure of a given community. Previous published reports showed that the effects of disturbance are varied and that it is difficult to attain generality on what processes drive those effects. As scientists, we have an obligation to do more than just report patterns. We must strive to understand the processes that produce those patterns. The key to this is recognizing that all processes addressed throughout the history of ecology (e.g. competition, predation, disturbance, random influences, etc.) may play some role in determining biodiversity and community structure. The next step is to determine under what conditions any one of these will dominate and how they all interact.

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