

# Plant-Feeding Hemiptera and Orthoptera Communities in Native and Restored Mesic Tallgrass Prairies

Kristine T. Nemeč<sup>1,2</sup> and Thomas B. Bragg<sup>1,3</sup>

## Abstract

Aboveground Hemiptera and Orthoptera communities were compared among three native and three restored mesic tallgrass prairies along the Platte River in central Nebraska to assess both the relative success of restored sites and the relationship between insect and plant communities. Hemiptera and Orthoptera were sampled using sweep nets in early June, mid-July, and mid-August 2000. Plant species composition was assessed in early June and mid-August. A total of 89 Auchenorrhyncha (71 Cicadellidae, 15 Fulgoroidea, and 3 Membracidae) and 23 orthopterans (15 Acrididae and 8 Tettigoniidae) were collected. Eighty-five plant species were observed in combined study sites. Shannon diversity was significantly higher at restored prairie for Cicadellidae ( $H' = 1.38$ ), Fulgoroidea ( $H' = 0.796$ ), and Membracidae ( $H' = 0.290$ ), which comprised the majority of individual insects collected, but significantly higher at native prairie

for Acrididae ( $H' = 0.560$ ) and Tettigoniidae ( $H' = 0.480$ ) ( $p \leq 0.05$ ). Species richness was comparable except for Acrididae which were significantly higher in restored prairie. Density of insects generally followed species diversity but was only significantly higher in restored areas for Membracidae. The number of remnant-dependent species collected was comparable for both native prairie ( $n = 15$ ) and restored prairie ( $n = 15$ ). These results suggest that, at least for Hemiptera, differences in insect communities between native and restored prairie may best be explained by the presence of insect host plants rather than by whether a site is native or restored.

**Key words:** Acrididae, Auchenorrhyncha, Cicadellidae, Fulgoroidea, insect communities, invertebrates, Membracidae, mesic tallgrass prairie, Orthoptera, prairie restoration, Shannon diversity, Tettigoniidae.

## Introduction

The tallgrass prairie (*Andropogon–Panicum–Sorghastrum*) (Küchler 1964) once covered over 64 million ha of central North America, extending from southern Manitoba to southern Texas (e.g., Transeau 1935). However, since European settlement, more than 99% of the ecosystem has been lost primarily from conversion to cropland (Samson & Knopf 1994) making the tallgrass prairie one of the most critically endangered ecosystems of the United States (Noss et al. 1995). The loss threatens regional biodiversity and adversely affects ecosystem services, such as those affecting soil erosion and water quality (Ostlie et al. 1997). In the mid- to late-1900s, conservation-focused organizations initiated efforts to restore tallgrass prairie. Although, conceptually, such restored sites were intended

to offset effects of the tallgrass prairie decline, their ability to do so is still being evaluated. Currently, these evaluations focus on community attributes such as floral and faunal diversity and ecosystem attributes such as soil characteristics.

In general, prairie restoration is a slow process with recovery of some soil characteristics requiring 5–10 years (e.g., soil aggregation; Jastrow 1987) and that of plant communities even longer (e.g., Kindscher & Tieszen 1998). For invertebrates, however, native species may return more rapidly because of their greater sensitivity to small-scale environmental conditions (Hamilton 1995; Mortimer et al. 1998; Ahlering et al. 1999), thus serving as good indicators of the potential success of a restored site (Maczey et al. 2005).

Several studies have described invertebrates of native tallgrass prairies (e.g., Kopp & Yonke 1970; Blocker & Reed 1976; Cwikla & Blocker 1981; Whitcomb et al. 1987a,b; Wilson et al. 1993; Whitfield & Lewis 2001; Stoner & Joern 2004; Hines & Hendrix 2005), whereas others have evaluated restored tallgrass prairies (e.g., Henderson, Bautz, Maurer, & Sauer 2002, unpublished data). Only a few, however, have compared invertebrate communities

<sup>1</sup> Department of Biology, University of Nebraska at Omaha, 6001 Dodge Street, Omaha, NE 68182-0040, U.S.A.

<sup>2</sup> Present address: U.S. Army Corps of Engineers, 106 S. 15th Street, Omaha, NE 68102, U.S.A.

<sup>3</sup> Address correspondence to T. B. Bragg, email tbragg@mail.unomaha.edu

of both native and restored sites (e.g., Sesler & Schramm 1990; Reed 1995; Debinski & Babbitt 1997; Ahlering et al. 1999; Foster & Kettle 1999; Bomar 2001). Comparative studies on butterflies (Order Lepidoptera) often give contradictory results, with some showing higher diversity at native prairie and others showing higher diversity at restored prairies (e.g., Sesler & Schramm 1990 vs. Debinski & Babbitt 1997). Different results from these studies may reflect variables such as different fire and mowing histories. For bees, wasps, flies, and moths in Minnesota (Reed 1995) and Acrididae in Wisconsin (Bomar 2001), higher invertebrate diversity was observed in native than in restored prairies. The absence of the mound-building ant *Formica subsericea* (Formicidae) in Kansas 41 years after restoration (Foster & Kettle 1999) suggests slow ant recovery.

In our study, we hypothesize that both the diversity and the proportion of remnant-dependent Hemiptera and Orthoptera will be higher in native than in restored prairies. Further, we hypothesize a direct relationship between invertebrate diversity and floral diversity.

## Methods

### Study Sites

The study was conducted along a 55-km reach of the Platte River between the towns of Kearney and Alda in central Nebraska (lat 40°41'–40°46'N, long 98°29'–98°50'W) (Fig. 1). Treatment designations for this study were either *native prairie* or *restored sites*. Three native prairies and three restored sites were selected, all of which were classified as wet-mesic sites (Steinauer & Rolfsmeier 2000) which occur in floodplains and which may have standing water during the spring or after heavy rains. Characteristic plant species include Big bluestem (*Andro-*

*pogon gerardii*), Maximilian sunflower (*Helianthus maximiliani*), Yellow stargrass (*Hypoxis hirsuta*), Prairie blazing star (*Liatis pycnostachya*), Switchgrass (*Panicum virgatum*), Rosinweed (*Silphium integrifolium*), and Indiangrass (*Sorghastrum nutans*). Restored areas had been used for row crops, primarily corn, for many years but were seeded to native prairie species in 1993 (Ruge93), 1994 (Dahms94), and 1995 (Dahms95) (Nemec 2003). All seedlings were a mix of from 100 to 200 native prairie species collected locally (C. Helzer 2001, The Nature Conservancy, Aurora, NE, personal communication). In general, native sites all had a recent history of occasional burning. Restored sites had recently been either burned or mowed. Burns at native and restored sites were most recently conducted in 1998–1999. Neither native nor restored sites had a history of grazing by cattle. In addition to similar restoration efforts, sites were selected that had comparable surface hydrogeology. Comparably sized prairies were sought, but in the end, one native prairie (Rowe) was much larger than the others. All sites were located approximately the same distance from the Platte River, and all restored sites were adjacent to native, although mostly degraded, prairie remnants. Due to a limited number of potential locations, study sites unavoidably differed in past management (Nemec 2003).

### Field Collections

At each site, sampling was conducted along two parallel, centrally located 20-m-long transects that were selected to be representative of the extant plant community. End-points of transects were marked with 1-m-tall metal poles to facilitate subsequent resampling. Transects were oriented from west to east and separated by 40 m, a procedure intended to minimize the effect of different prairie sizes by sampling the same sized area within each site. To minimize edge effect, transects were a minimum of 24 m from the study site boundary. Both insects and plants were sampled because of the close association between the two (e.g., Panzer & Schwartz 1998).

**Aboveground Insect Sampling.** Aboveground insects were sampled 5–7 June, 14–18 July, and 9–11 August 2000 to ensure sampling the greatest number of taxonomic groups irrespective of seasonal presence. A single year's sampling limited the study to relative rather than absolute effects because insect populations fluctuate considerably in response to climatic conditions. Hollier et al. (2005), however, give one example where the influence of year was less than other factors. To minimize the effect of climate during the year of the study, insects were sampled only on sunny days when the temperature exceeded 16°C and only between 0900 and 1900 hours. To avoid bias due to the time of day sampled, the first site sampled on any given day was altered between native prairie and restored sites, although both transects at a site were sampled consecutively. Sampling consisted of taking 400 sweeps, in 40

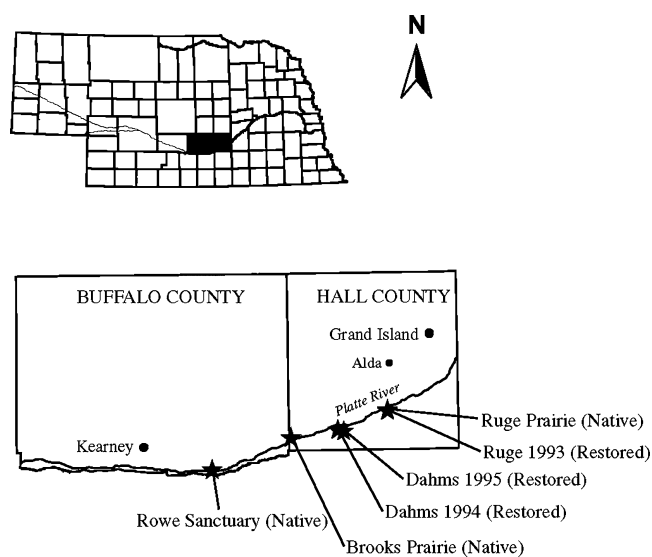


Figure 1. Study sites in central Nebraska.

sweep sets, using a 38-cm diameter, standard canvas sweep net. Each sweep consisted of a movement either from right to left or from left to right. This sampling protocol is widely used (e.g., Evans 1988) and was selected over a more comprehensive one in order to obtain as broad a cross-section of prairie invertebrates as could be sampled within the time available for the study. Results, therefore, represent the relative density of different insect taxonomic groups where, theoretically, those less suited to being sampled by sweep nets would be collected less frequently than those more suited to this sampling procedure. The proportion of each individual taxonomic group at either native or restored sites, however, would reflect the relative contribution of that group to the respective invertebrate communities as shown, for example, by Evans (1988) for Acrididae.

After each set of 40 sweeps, insects in the net were placed in a container filled with 70% ethyl alcohol. All 400 sweeps along a transect were placed in the same container. Once all sweeps for a transect had been completed, the content of the container was transferred to a 947-mL glass jar for storage and subsequent sorting. Specimens were separated into Cicadellidae, Fulgoroidea, and Membracidae (Order Hemiptera, Suborder Auchenorrhyncha) and Tettigoniidae or Acrididae (Order Orthoptera) which, together, make a good indicator assemblage because they are abundant and occupy a range of ecological niches (Brown 1991; Biedermann et al. 2005; Whiles & Charlton 2006). In addition, a high proportion of Cicadellidae are either remnant-dependent or found exclusively in high-quality prairie (Panzer et al. 1995). Dr. Andy Hamilton provided identifications of Cicadellidae and Fulgoroidea, Dr. Stephen Wilson of Fulgoroidea, Dr. Chris Dietrich of Membracidae, and Bradford Danner of Acrididae and Tettigoniidae. Specimens were preserved in 70% alcohol and stored in the Plant Ecology Lab at the University of Nebraska at Omaha.

**Plant Sampling.** Plant communities were sampled from 5–6 June and 14–18 August 2000 by Chris Helzer (The Nature Conservancy, Platte/Rainwater Basin Office). At each site, sampling was conducted in each of five, 1-m<sup>2</sup>-radius plots systematically placed 3 m apart along each of the 20-m transects used for insect sampling. The canopy cover of all plant species within each plot was recorded using procedures modified from Daubenmire (1959). Canopy cover categories used were as follows: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, 7 = 95–99%, and 8 = >99%. Category midpoints were used in data analyses. In addition, all plants observed to be flowering along each transect were listed.

#### Data Analysis

**Community-Level Analyses.** Because seasonal variation in the insect community was not the intent of this study, data from each sampling period were pooled during analy-

ses. Quantitative analyses were based on relative *insect density*, referred to throughout as “density” and defined as the number of individuals of each taxonomic group collected in each set of 400 sweeps (individuals/400 sweeps). Plant analysis was based on the mean percent canopy cover of each species from each transect. The standard error is the measure of variance used throughout the study.

Statistical differences among sites were determined using the analysis of variance (ANOVA) procedure (SAS Institute, Inc. 1999) calculated using (1) mean species richness values ( $S$  = the number of species) for each of six samples for each insect taxonomic group (2 transects per site  $\times$  3 sampling periods) and (2) mean canopy cover from each of four samples for plants (2 transects per site  $\times$  2 sampling periods). The ANOVA procedure was used because it is sufficiently robust to accommodate some considerable departures from its theoretical assumptions, particularly the expectation that sample size be equal (Zar 1999). ANOVA procedures were not applied when comparing Shannon diversity because of the low number of insect taxonomic groups collected during some sampling periods. The nonparametric Student–Newman–Keuls multiple comparison test was selected to detect differences between specific sites because other multiple comparison tests are sensitive to parametric assumptions.

Statistical differences between treatments (i.e., between combined native and combined restored prairies) were analyzed using a two-sample  $t$  test (SAS Institute, Inc. 1999) for species richness and a comparable  $t$  test described by Zar (1999) for Shannon–Weiner diversity indices ( $H'$ ) (Shannon 1948). Comparisons of diversity were based on the mean of 18 values per treatment for insects (3 sites per treatment  $\times$  2 transects per site  $\times$  3 sampling periods) and 12 values for plants (3 sites per treatment  $\times$  2 transects per site  $\times$  2 sampling periods). The highest canopy cover of each plant species from either the June or the August sampling period was used in plant analyses to accommodate different plant phenologies. Although sample size was small ( $n = 18$  or 12), the two-sample  $t$  test is sufficiently robust to accommodate such a departure from theoretical assumptions (Zar 1999). Results of  $t$  tests are shown parenthetically throughout the text.

Detrended correspondence analysis, commonly used in invertebrate studies (e.g., Evans 1988; Asteraki et al. 1995), was applied using PC-ORD (McCune & Mefford 1999) to detect trends in insect and plant communities. The ability to summarize community-level information was felt to outweigh concerns about the marginal number of samples available for ordination. Individual rather than combined transect data were used in order to maximize sample size. Insect density from the three insect sampling periods ( $n = 18$ ) was combined for analysis, as was plant canopy cover for the two plant sampling periods ( $n = 12$ ).

**Species-Level Analyses.** PC-ORD was used to conduct *indicator species analysis* which detects species most

closely associated with a particular habitat (Dufrene & Legendre 1997). In this analysis, insect density and plant canopy cover were used as the main data matrix, with treatment as the secondary matrix. The highest indicator value ( $IV_{max}$ ) for a species from either native or restored prairie was recorded as the overall indicator value for that species. Values ranged from 0 (not dependent) to 100 (highly dependent). Other measures indicating a close association with native or restored habitats were, for insects, classification as a remnant-dependent species or for plants, an average canopy cover more than 5% in either two native or two restored sites.

## Results

One hundred and twelve Hemiptera and Orthoptera species and 85 plant species were identified. Of the invertebrates, Cicadellidae were most numerous (71), followed by Acrididae (15), Fulgoroidea (15), Tettigoniidae, (8) and Membracidae (3) (Nemec 2003). Sixteen insect species (14% of the total insect species collected) and 26 plant species (31%) were found only at native prairies, whereas 35 insect species (31%) and 36 plant species (44%) were found only at restored prairies.

### Number of Species and Remnant-Dependent Species

Of the 89 Hemiptera species collected, Cicadellidae were the most species rich (71 species) (Nemec 2003). More Cicadellidae were collected at restored sites than at native prairies (63 vs. 49 species), although a greater proportion of those collected at the native prairies (24% of the 49 species) were highly remnant-dependent compared to those collected at restored sites (19% of the 63) (Table 1; Nemec 2003). Of the 15 highly remnant-dependent Cicadellidae species collected, the number at restored sites averaged higher than at native prairies ( $S = 3.5 \pm 0.33$  and  $2.8 \pm 0.25$  species/400 sweeps, respectively), although the difference was not significant ( $p = 0.0883$ , two-sample  $t$  test). The distribution of the 15, however, was not as remnant dependency would predict because species density was higher at native prairie than at restored sites for only 8 of the 15 species and because only 3 of the remnant-dependent species recorded were found exclusively at native prairies (Table 1).

Fulgoroidea was the next most species rich of the Hemiptera with 15 species (Nemec 2003). As with the Cicadellidae, a greater number of Fulgoroidea were collected at restored than at native prairies (12 vs. 9 species), with the one remnant-dependent species collected, *Delphacodes parvula*, found at both native and restored sites. The Membracidae, represented by only three species, were collected primarily at restored sites. No remnant-dependent Membracidae were collected.

Of the 23 Orthoptera collected, the Acrididae were most species rich (15 species) with Tettigoniidae least

common (8 species) (Nemec 2003). Like the Hemiptera, more Acrididae species were collected at restored sites than at native prairies (12 vs. 10 species). In contrast, Tettigoniidae was the only family of both Hemiptera and Orthoptera having greater numbers of species at native than at restored sites (8 vs. 7 species).

### Relative Density

Eighty-nine Hemiptera species were collected, of which Cicadellidae were the most numerous (3,067 individuals = 84.4% of the 3,633 Hemiptera collected). As with the number of species, mean relative density of Cicadellidae was higher for native prairies than for restored sites (mean relative density =  $95.2 \pm 14.36$  vs.  $75.2 \pm 6.57$  individuals/400 sweeps, respectively) although the difference was not significant ( $p = 0.2163$ , two-sample  $t$  test) (Table 2). Similar results were obtained when comparing remnant-dependent Cicadellidae density at restored and native sites (Table 1).

Fulgoroidea was the second most numerous Hemiptera (486 = 13.4% of the total collected) (Nemec 2003). Although Fulgoroidea density was higher at native than at restored sites (mean density =  $14.3 \pm 3.61$  vs.  $12.7 \pm 2.17$  individuals/400 sweeps, respectively) (Table 2), the opposite was found for remnant-dependent Fulgoroidea density which was higher at restored sites than at native prairies (mean density =  $2.6 \pm 1.14$  vs.  $1.2 \pm 0.42$  individuals/400 sweeps, respectively) (Table 1). Neither difference, however, was significant.

The Membracidae were lowest in number (80 individuals; 2.2% of the total Hemiptera collected) and lacking in any remnant-dependent species (Nemec 2003). In contrast to Cicadellidae and Fulgoroidea, Membracidae relative density averaged significantly higher at restored sites than at native prairies ( $4.2 \pm 1.71$  vs.  $0.2 \pm 0.22$  individuals/400 sweeps) ( $p = 0.0262$ , two-sample  $t$  test) (Table 2).

The most numerous of the Orthoptera collected were Tettigoniidae, making up 68% (1,128) of the 1,657 individuals collected of this family (Nemec 2003). The relative density of Tettigoniidae was higher on native than on restored sites ( $\bar{X} = 39.8 \pm 13.20$  vs.  $22.8 \pm 6.34$  individuals/400 sweeps, respectively) but the difference was not significant ( $p = 0.2568$ , two-sample  $t$  test) (Table 2). In contrast, the relative density of Acrididae, which made up the remaining 32% of Orthoptera collected, averaged higher at restored than at native prairies ( $\bar{X} = 18.7 \pm 4.21$  vs.  $10.7 \pm 2.50$  individuals/400 sweeps), although this difference was neither significant ( $p = 0.1114$ , two-sample  $t$  test) nor consistent for all species (Table 1). *Phoetaliotes nebrascensis* density, for example, was significantly higher at native than at restored sites ( $\bar{X} = 6.1$  vs. 1.3 individuals/400 sweeps) ( $p = 0.0177$ , two-sample  $t$  test).

### Diversity

In general, diversity averaged higher at restored sites than at native prairies for all three Hemiptera groups collected

**Table 1.** Insect and plant taxa most closely associated with native or restored habitats based on (1) significant ( $p \leq 0.05$ ) association with native or restored prairie from indicator species analysis, (2) for insects, classification as remnant-dependent, or (3) for plants, an average canopy cover greater than 5% in either two native or two restored sites.

Species	Insect Density (Mean No. of Individuals/400 Sweeps) or Plant Canopy Cover (%)				Indicator Values		
	Native		Restored		Habitat Type	$IV_{max}$	$p$
	$\bar{X}$	SE	$\bar{X}$	SE			
<b>Cicadellidae</b>							
<i>Amplicephalus inimicus</i>	0.94	0.29	3.83	0.80	Restored	80.3	0.005
<i>A. kansiensis</i> <sup>r</sup>	4.11	2.89	0.17	0.17	—	—	—
<i>Athysanus argentarius</i>	21.39	6.74	0	0	Native	99.0	0.005
<i>Chlorotettix spatulatus</i>	0.44	0.27	2.06	0.78	Restored	82.3	0.031
<i>Cicadula ciliata</i> <sup>r</sup>	0.11	0.11	0	0	—	—	—
<i>Commellus comma</i>	0	0	18.56	3.82	Restored	100.0	0.005
<i>Flexamia albida</i> <sup>r</sup>	0	0	0.06	0.06	—	—	—
<i>F. prairiana</i> <sup>r</sup>	4.50	1.42	1.22	0.48	—	—	—
<i>F. reflexa</i> <sup>r</sup>	0	0	0.11	0.11	—	—	—
<i>Graminella mohri</i> <sup>r</sup>	4.00	1.29	3.22	0.80	—	—	—
<i>Laevicephalus minimus</i> <sup>r</sup>	0.11	0.08	0.28	0.23	—	—	—
<i>L. unicoloratus</i> <sup>r</sup>	7.11	2.41	1.89	0.86	—	—	—
<i>Limotettix osborni</i>	0	0	2.22	0.95	Restored	100.0	0.005
<i>Mesamia straminea</i> <sup>r</sup>	0.06	0.06	1.28	0.55	—	—	—
<i>Paraphlepsius nebulosus</i> <sup>r</sup>	0	0	0.06	0.06	—	—	—
<i>Pendarus magnus</i> <sup>r</sup>	0.28	0.16	0.11	0.08	—	—	—
<i>Polyamia dilata</i> <sup>r</sup>	0.06	0.06	0	0	—	—	—
<i>Psammotettix lividellus</i>	7.17	2.32	1.39	0.56	Native	83.8	0.026
<i>Scaphytopius cinereus</i> <sup>r</sup>	0.11	0.08	3.22	0.81	Restored	96.7	0.008
<i>Xerophloea peltata</i> <sup>r</sup>	0.11	0.08	0	0	—	—	—
<b>Fulgoroidea</b>							
<i>Acanalonia bivittata</i>	0	0	1.39	0.58	Restored	83.3	0.020
<i>Delphacodes parvula</i> <sup>r</sup>	1.17	0.42	2.56	1.14	—	—	—
<i>Scolops sulcipes</i>	0.50	0.22	2.56	0.76	Restored	83.6	0.037
<b>Membracidae</b>							
<i>Campylenchia latipes</i>	0	0	3.17	1.51	Restored	100.0	0.003
<b>Acrididae</b>							
<i>Melanoplus bivittatus</i>	0.06	0.06	0.83	0.30	Restored	78.2	0.035
<i>M. femurrubrum</i>	1.06	0.44	14.60	4.03	Restored	93.2	0.002
<i>Phoetaliotes nebrascensis</i> <sup>r</sup>	6.11	1.78	1.33	0.47	—	—	—
<b>Tettigoniidae</b>							
<i>Conocephalus saltans</i> <sup>r</sup>	25.78	11.67	1.28	0.40	Native	95.1	0.002
<b>Plants</b>							
<i>Agrostis stolonifera</i>	6	10	0	0	Native	100.0	0.004
<i>Andropogon gerardii</i>	48	29	47	22	—	—	—
<i>Bromus inermis</i>	16	24	tr	—	—	—	—
<i>Calamagrostis</i> spp.	6	10	0	0	Native	100.0	0.004
<i>Carex</i> spp.	8	10	tr	—	Native	99.0	0.004
<i>Desmanthus illinoensis</i>	tr	—	16	13	Restored	81.9	0.014
<i>Eleocharis elliptica</i>	3	4	0	0	Native	100.0	0.004
<i>Elymus canadensis</i>	0	0	25	21	Restored	83.3	0.014
<i>Equisetum</i> spp.	tr	—	0	0	Native	100.0	0.004
<i>Sorghastrum nutans</i>	35	24	18	15	—	—	—
<i>Spartina pectinata</i>	17	17	tr	—	Native	81.5	0.034

$IV_{max}$  = indicator value where 0 = not dependent and 100 = highly dependent. Habitat type = the habitat to which the species is most closely associated. Highly remnant-dependent insects indicated by superscript letter r ( $x^r$ ). tr = canopy cover less than or equal to 0.5%. For full species lists, see Nemeč (2003). Selected plant species discussed in the text are also included.

(Table 2). For Cicadellidae, Shannon diversity ( $H' = 1.38$  for restored sites and 1.24 for native prairie) differed significantly ( $p < 0.0001$ , two-sample  $t$  test) ( $n = 18$ ) as did species richness of restored (mean  $S = 17.1 \pm 0.98$  species/

400 sweeps) and native sites (mean  $S = 13.6 \pm 0.75$  species/400 sweeps) ( $p = 0.0087$ , two-sample  $t$  test). As with Cicadellidae, Shannon diversity of Fulgoroidea was significantly higher at restored than at native prairies

**Table 2.** Insect diversity and density by site for the 2000 sampling season.

	Native			Restored			ANOVA <i>p</i> Value
	Brooks Prairie	Rowe Prairie	Ruge Prairie	Ruge 1993	Dahms 1994	Dahms 1995	
Size (ha)	3.4	93.1	6.5	4.9	3.0	4.9	
Last burn	Long unburned	1998	1999	1999	1998	1999	
<b>Cicadellidae</b>							
Shannon diversity ( $H'$ )	1.04	1.19	1.02	1.26	1.32	1.25	N/A
Species richness ( $S$ )							
Total	1.42 ± 1.58	14.3 ± 1.15	12.3 ± 1.23	16.0 ± 2.27	17.2 ± 0.79	18.0 ± 1.88	0.137
Remnant-dependent	2.7 ± 0.56	2.8 ± 0.48	2.8 ± 0.31	4.0 ± 0.77	3.3 ± 0.42	3.2 ± 0.48	0.512
Density							
Total	108.0 ± 21.37	76.3 ± 13.04	101.3 ± 36.93	51.3 ± 3.86	70.5 ± 7.21	103.5 ± 9.64	0.242
Remnant-dependent	24.0 ± 8.65	15.2 ± 2.36	24.3 ± 3.81	9.2 ± 1.89	15.7 ± 2.82	12.0 ± 2.99	0.105
<b>Fulgoroidea</b>							
Shannon diversity ( $H'$ )	0.779	0.549	0.443	0.649	0.642	0.618	N/A
Species richness ( $S$ )							
Total	2.3 ± 0.67	3.2 ± 0.48	1.7 ± 0.56	2.7 ± 0.61	3.3 ± 0.57	3.0 ± 0.82	0.446
Remnant-dependent	0.5 ± 0.22	0.5 ± 0.22	0.5 ± 0.22	0.5 ± 0.22	0.5 ± 0.22	0.67 ± 0.20	0.399
Density							
Total	4.3 ± 1.48 <sup>B</sup>	31.3 ± 5.66 <sup>A</sup>	7.3 ± 3.34 <sup>B</sup>	11.3 ± 4.26 <sup>B</sup>	13.7 ± 2.50 <sup>B</sup>	13.0 ± 4.80 <sup>B</sup>	<0.001*
Remnant-dependent	0.8 ± 0.48	1.0 ± 0.52	1.7 ± 1.12	1.5 ± 0.81	3.3 ± 2.75	5.7 ± 3.08	0.399
<b>Membracidae</b>							
Shannon diversity ( $H'$ )	0	0	0	0.369	0.0455	0.249	N/A
Species richness ( $S$ )							
Total	0.2 ± 0.17	0	0	0.5 ± 0.34	0.8 ± 0.31	0.7 ± 0.33	0.084
Remnant-dependent	0	0	0	0	0	0	N/A
Density							
Total	0.7 ± 0.67 <sup>B</sup>	0 <sup>B</sup>	0 <sup>B</sup>	1.2 ± 0.83 <sup>B</sup>	10.3 ± 4.17 <sup>A</sup>	1.2 ± 0.65 <sup>B</sup>	0.002
Remnant-dependent	0	0	0	0	0	0	N/A
<b>Acrididae</b>							
Shannon diversity ( $H'$ )	0.306	0.675	0.473	0.485	0.228	0.621	N/A
Species richness ( $S$ )							
Total	2.0 ± 0.52	1.8 ± 0.54	2.2 ± 0.40	3.2 ± 0.40	2.8 ± 0.48	3.0 ± 0.45	0.227
Remnant-dependent	0.8 ± 0.17 <sup>A</sup>	0 <sup>B</sup>	0.7 ± 0.21 <sup>A</sup>	0.5 ± 0.22 <sup>AB</sup>	0.2 ± 0.17 <sup>AB</sup>	0.8 ± 0.17 <sup>A</sup>	0.006*
Density							
Total	13.2 ± 4.34 <sup>B</sup>	3.7 ± 1.38 <sup>B</sup>	15.2 ± 5.30 <sup>B</sup>	12.0 ± 2.71 <sup>B</sup>	34.5 ± 9.57 <sup>A</sup>	9.7 ± 2.59 <sup>B</sup>	0.005*
Remnant-dependent	10.5 ± 3.39 <sup>A</sup>	0 <sup>B</sup>	7.8 ± 2.99 <sup>AB</sup>	0.8 ± 0.48 <sup>B</sup>	0.8 ± 0.83 <sup>B</sup>	2.3 ± 1.02 <sup>B</sup>	0.002*
<b>Tettigoniidae</b>							
Shannon diversity ( $H'$ )	0.491	0.512	0.357	0.453	0.120	0.474	N/A
Species richness ( $S$ )							
Total	2.5 ± 0.43	3.5 ± 0.72	3.2 ± 1.05	2.3 ± 0.67	1.7 ± 0.33	1.5 ± 0.50	0.234
Remnant-dependent	0.8 ± 0.17	0.7 ± 0.21	0.7 ± 0.21	0.2 ± 0.17	0.5 ± 0.22	0.7 ± 0.21	0.280
Density							
Total	18.2 ± 5.96	33.2 ± 10.60	68.2 ± 36.95	17.3 ± 5.53	45.5 ± 14.36	5.7 ± 2.46	0.149
Remnant-dependent	11.2 ± 5.39	13.8 ± 7.55	52.3 ± 33.02	0.2 ± 0.17	1.7 ± 0.84	2.0 ± 0.73	0.107

Species richness ( $S$ ) is shown as an  $\bar{X} \pm SE$  ( $n = 6$ ). Only values with significant differences among sites are indicated with superscript letters ( $p \leq 0.05$ ; Student–Newman–Keuls) and values with different superscripts differ significantly. ANOVA  $p$  values are results from single-factor ANOVA tests among sites, although ANOVA was not applied to Shannon diversity (see text). N/A = not applicable.

\*Significant differences among sites (ANOVA  $p \leq 0.05$ ).

( $H' = 0.796$  and  $0.659$ , respectively) ( $p = 0.0001$ , two-sample  $t$  test) ( $n = 18$ ). Species richness of Fulgoroidea also averaged higher at restored sites than at native prairies but, unlike Cicadellidae, the difference was neither large nor significant (mean  $S = 3.0 \pm 0.37$  and  $2.4 \pm 0.34$  species/400 sweeps, respectively) ( $p = 0.2353$ , two-sample  $t$  test). For Membracidae, species richness averaged significantly higher for restored than for native prairies for both species richness ( $S = 0.7 \pm 0.18$  and  $0.06 \pm 0.056$  species/400 sweeps) ( $p = 0.0027$ , two-sample  $t$  test) and Shannon

diversity ( $H' = 0.290$  vs.  $H' = 0$ ) ( $p < 0.0001$ , two-sample  $t$  test) ( $n = 18$ ).

As with Hemiptera, species richness of Orthoptera was higher at restored sites than at native prairies (mean  $S = 3.0 \pm 0.24$  species/400 sweeps for restored site vs.  $S = 2.0 \pm 0.27$  species/400 sweeps for native prairie) ( $p = 0.0091$ , two-sample  $t$  test), although the difference was small and probably not biologically significant (Table 2). Opposite results were observed for Shannon diversity of Acrididae, which was significantly higher at native prairie than at restored sites

( $H' = 0.560$  vs.  $H' = 0.420$ ) ( $p = 0.0033$ , two-sample  $t$  test) ( $n = 18$ ). Unlike Hemiptera, and somewhat unlike Acrididae, both species richness and Shannon diversity of Tettigoniidae were significantly higher at native prairies (mean  $S = 3.1 \pm 1.83$  species/400 sweeps;  $H' = 0.480$ ) than at restored sites (mean  $S = 1.8 \pm 1.25$  species/400 sweeps;  $H' = 0.364$ ) ( $p = 0.0261$ ;  $p < 0.0001$ ; two-sample  $t$  test) ( $n = 18$ ).

**Spatial Distribution**

Based on relative density, both Hemiptera and Orthoptera were separated into native and restored sites in ordination space (Fig. 2). Cicadellidae (1) were more distinctly separated by site than other Hemiptera collected, suggesting site specificity may be an important factor explaining their distribution, (2) differed more among native prairies

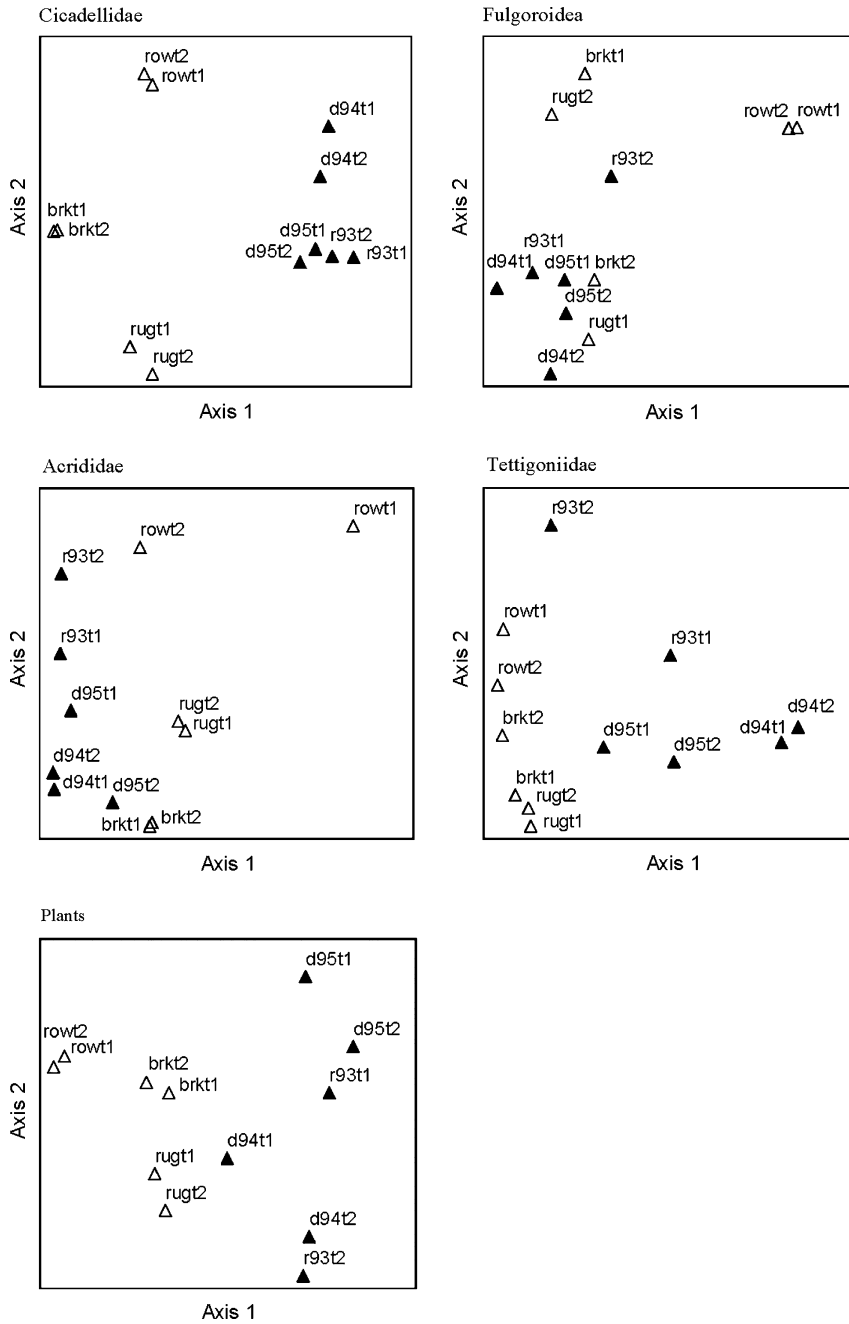


Figure 2. Detrended correspondence analysis ordination plots of Cicadellidae, Fulgoroidea, Acrididae, and Tettigoniidae relative density (number of individuals/400 sweeps) and plant mean canopy cover by transect for Brooks Prairie (brk), Rowe Sanctuary (row), Ruge Prairie (rug), Ruge 1993 Restoration (r93), Dahms 1994 Restoration (d94), and Dahms 1995 Restoration (d95). Open triangles are native prairie transects and shaded triangles are restored prairie transects: +1 = Transect 1, +2 = Transect 2. Transects that appear closer together are more similar in diversity than those farther apart.

than within any one prairie, suggesting a landscape-level patchiness but local homogeneity, and (3) were more heterogeneous within native than within restored sites, suggesting a greater patchiness of Cicadellidae niches in native communities. Fulgoroidea were not as clearly separated in ordination space as were Cicadellidae although, like Cicadellidae, their density appeared more heterogeneous among native prairies than among restored sites. Membracidae were too few in numbers for ordination to be carried out.

Like the Hemiptera, the relative densities of Orthoptera collected showed both Acrididae and Tettigoniidae to be separated in ordination space into native and restored sites (Fig. 2). As with the other taxonomic groups collected, Acrididae density appeared to be more heterogeneous among native than among restored sites. In contrast to all other Hemiptera and Orthoptera collected, the relative density of Tettigoniidae suggests a more homogeneous distribution among native than among restored sites (Fig. 2).

#### Significant Associations to Habitat

**Hemiptera.** Two of the 71 species of Cicadellidae (3% of 71) were significantly associated with native prairie and five species (7%) significantly associated with restored site ( $p \leq 0.05$ ) (Table 1). Although not calculated to be indicator species, eight Cicadellidae species (11%) were found only at native prairies. Twenty-two others (31%), including two indicator species, were observed only at restored sites. Large differences in Cicadellidae abundance were observed between native and restored sites for some species. For example, *Athysanus argentarius*, an introduced European species, was abundant at all three native prairies but scarce at the restored sites (mean density = 21.4 and 0.2 individuals/400 sweeps, respectively). In contrast, *Commellus comma*, a native of North American grasslands, was absent from native prairies but abundant at the restored sites (mean density = 18.6 individuals/400 sweeps).

*Delphacodes parvula* was the only highly remnant-dependent Fulgoroidea species collected, although it was found in low numbers in all native and restored sites. Indicator species analysis identified 2 of the 15 Fulgoroidea species, *Acanalonia bivittata* and *Scolops sulcipes*, as indicator species for restored sites (Table 1). Although not significantly associated with a particular habitat, three other species (20% of Fulgoroidea species collected) were collected only at the native prairies (Nemec 2003). Six species (40%), including the two indicator species, were collected only at restored sites.

None of the three Membracidae species were listed as remnant-dependent, although *Campylenchia latipes* was significantly associated with restored sites by indicator species analysis (Table 1). *Campylenchia latipes* and *Stictocephala bisonia* were found only at restored sites with the third species, *Micrualis*, collected at both native and restored sites (Nemec 2003). *Campylenchia latipes* does not

require a woody host for oviposition and is often collected in prairies. It is not considered a true prairie insect because of its abundance in old fields and forest edges. *Stictocephala bisonia* and *Micrualis* sp., however, both require woody hosts for oviposition and, thus, are not restricted to prairies (C. Dietrich 2001, Illinois Natural History Survey, Champaign, IL, personal communication).

**Orthoptera.** Of the 15 Acrididae species collected, *Phoetaliotes nebrascensis*, the only one described as highly remnant-dependent, was present in high numbers at two of the native prairies (Brooks and Ruge), absent from the third, but present in low numbers at all three restored sites (Nemec 2003, unpublished data). Two other species, *Melanoplus bivittatus* and *M. femurrubrum*, although not remnant-dependent, were significantly associated with restored sites based on indicator species analysis (Table 1). An additional three species (20% of Acrididae species collected) were collected only at native prairies, whereas five others (33%) were observed only at restored sites (Nemec 2003).

All but one Tettigoniidae species were found at both native and restored sites, *Orchelimum nigripes* being found exclusively at two native prairie sites (Nemec 2003). *Conocephalus saltans*, the only highly remnant-dependent species collected, was found in higher numbers at native than at restored sites ( $\bar{X} = 25.8$  vs. 1.3 individuals/400 sweeps), although the difference, while large, was not significant ( $p = 0.0511$ , two-sample  $t$  test) (Table 1). *Conocephalus saltans* was also determined to be significantly associated with native prairie based on indicator species analysis (Table 1).

#### Plant Community

**Community Level.** A total of 85 plant species were identified within plots (Nemec 2003). Native and restored prairies were separated in ordination space with restored prairie showing greater within-site heterogeneity (Fig. 2). As with Hemiptera, but not Orthoptera, species diversity of the plant communities was higher at restored than at native prairies for both species richness (mean  $S = 15.6 \pm 1.57$  vs.  $S = 14.3 \pm 1.27$ ) and Shannon diversity ( $H' = 1.07$  vs.  $H' = 1.04$ ), although in neither instance was the difference significant ( $p = 0.5420$  and  $0.5623$ , respectively; two-sample  $t$  test) ( $n = 12$ ) (Table 3). Significant differences in plant guild diversity were not consistent among prairie or among restored sites.

Six of the 85 plant species (7% of the total plant species collected) were significantly associated with native prairie with 2 (2%) significantly associated with restored prairie (Table 1; Nemec 2003). Twenty-six (31%) were observed only at native prairie and 36 (42%) only at restored sites (Nemec 2003). Other plant species were found to be ubiquitous. For example, Big bluestem (*Andropogon gerardii*) and Indiangrass (*Sorghastrum nutans*) dominated the canopy cover at both native and restored prairies



**Table 3.** Plant diversity ( $H'$  and  $S$ ) by site and guild.

	Native			Restored			ANOVA $p$ Value
	Brooks Prairie	Rowe Prairie	Ruge Prairie	Ruge 1993	Dahms 1994	Dahms 1995	
Size (ha)	3.4	93.1	6.5	4.9	3.0	4.9	
Last burn	Long unburned	1998	1999	1999	1998	1999	
Shannon diversity ( $H'$ )	0.916	0.939	0.817	0.944	0.954	0.966	N/A
Total species richness	1.75 ± 1.55	16.0 ± 0.71	10.0 ± 1.58	19.8 ± 3.90	13.8 ± 1.55	15.8 ± 4.03	0.1853
Species richness by guild							
Native C4 grasses	4.00 ± 0.41 <sup>A</sup>	4.50 ± 0.29 <sup>A</sup>	2.50 ± 0.87 <sup>A</sup>	2.20 ± 0.48 <sup>A</sup>	3.00 ± 0.41 <sup>A</sup>	3.00 ± 0.41 <sup>A</sup>	0.0421*
Native C3 grasses	1.20 ± 0.63	1.00 ± 0.41	0.50 ± 0.29	1.20 ± 0.25	1.20 ± 0.25	1.00 ± 0	0.6548
Exotic C3 grasses	1.80 ± 0.25 <sup>A</sup>	0.50 ± 0.29 <sup>B</sup>	1.80 ± 0.25 <sup>A</sup>	1.00 ± 0.41 <sup>AB</sup>	0.25 ± 0.25 <sup>B</sup>	0 <sup>B</sup>	0.0005*
Sedges and rushes	1.20 ± 0.25 <sup>B</sup>	4.50 ± 0.50 <sup>A</sup>	1.50 ± 0.65 <sup>B</sup>	0.75 ± 0.75 <sup>B</sup>	0.50 ± 0.50 <sup>B</sup>	0.500 ± 0.29 <sup>B</sup>	0.0003*
Native forbs	8.80 ± 1.11	5.50 ± 0.29	3.80 ± 0.85	11.20 ± 3.01	8.20 ± 1.03	10.20 ± 3.17	0.1008
Exotic forbs	0.50 ± 0.29	0	0	1.00 ± 0.41	0	0.75 ± 0.48	0.0755
Woody plants	0 <sup>B</sup>	0 <sup>B</sup>	0 <sup>B</sup>	2.20 ± 0.63 <sup>A</sup>	0.50 ± 0.29 <sup>B</sup>	0.25 ± 0.25 <sup>B</sup>	0.0003*

Species richness ( $S$ ) is shown as an  $\bar{X} \pm SE$  ( $n = 4$ ). Only those guilds with significant differences among sites include superscript letters where different letters indicate statistically different values ( $p \leq 0.05$ ; Student–Newman–Keuls). N/A = not applicable.

\*Significant difference among sites based on results from single-factor ANOVA tests among sites (ANOVA  $p$  values).

(Table 1). These are important host plants for Acrididae and Cicadellidae, especially generalist species (Mulkern et al. 1969; Whitcomb et al. 1987b).

## Discussion

In general, this study shows a direct relationship between insect and plant diversity based on both community and species data. The relationship remained irrespective of whether a site was native or restored. For example, at the community level, Shannon diversity of Hemiptera and Orthoptera differed significantly between native and restored sites for all five insect taxonomic groups. Similarly, species richness differed significantly for four of the five insect taxonomic groups. These results were paralleled by significantly higher insect diversity at restored sites for all groups sampled except Tettigoniidae. Although individual species may vary, these results are consistent with results of studies conducted in grasslands and other ecosystems where invertebrate community composition is related to plant community composition. At least in part, this relationship is due to structural changes in the plant community at different stages of postdisturbance development (e.g., Lawton & Schroder 1977). In the jarrah forests of Australia, for example, invertebrate composition followed a similar trajectory to that of the plant community—from generalists to specialists—after mining ceased (Moir et al. 2005). Similarly, in limestone quarries at Derbyshire, United Kingdom, time since establishment and the resulting increasing plant cover was associated with a greater number of both invertebrate orders and individuals of each order present (Wheater & Cullen 1997).

Data from individual species further support a direct relationship between plant and insect diversity through (1) host specificity, (2) plant community structure, and (3)

other modifying factors, such as proximity of restored sites to native prairies.

## Host Specificity

Host specificity suggests a direct relationship between the distribution of insects and that of their host plants (Mulkern et al. 1969; Gwynne 2001; Biedermann 2002). Results from this study suggest several such relationships. For restored sites, examples include the common occurrence of the Cicadellidae *Driotura gammaroides* and its host plant, Goldenrod (*Solidago*) and the Cicadellidae *Commellus comma* and its host plant, Wild rye (*Elymus*), the latter also reported by Whitcomb et al. (1987b). Membracidae density also was higher at restored sites where woody plant density was highest. Membracidae use woody and herbaceous plants for oviposition or feeding (Dietrich et al. 1999). For native sites, a high density of the Fulgoroidea specialist *Prokelisia crocea* was accompanied by a high cover of its host plant Prairie cordgrass (*Spartina pectinata*). Similarly, the cicadellid *Athysanus argentarius* was most common in native prairie where its host plant, Smooth brome (*Bromus inermis*), was highest, results also noted by Hamilton (1983). We also found native prairies, where grass cover was higher than restored sites, to support a higher density of *Conocephalus fasciatus*, a tettigoniid that feeds on flowers of grasses (Vickery & Kevan 1985).

## Plant Structure

In addition to species-specific relationships, other elements affecting insect distribution may be plant community structure. For example, some insects prefer structural complexity such as would occur where forb cover was high because forbs provide desirable sites for insect feeding,

resting, over wintering, and oviposition (Lawton & Schroder 1977). Other insects, however, may prefer structurally simple communities (Joern 1982). For example, in our study, the grammivorous acridids *Orphulella speciosa* and *Phoetaliotes nebrascensis* were noticeably more abundant at native prairies where grass cover was higher than at restored prairies. This difference also could be a function of Acrididae preference for vertical lines that characterize grass-dominated communities (Mulkern 1969).

### Modifying Factors

An additional factor affecting the distribution of species, particularly remnant-dependent species, may be related to geographic location. For example, Panzer et al. (1995) proposed that remnant-dependent species would comprise a greater proportion of the invertebrate community in areas surrounded by pastures and hay meadows than in areas surrounded by highly developed and paved landscapes. In our study, the close proximity of restored sites to native, albeit often degraded, prairie may account for the high number of remnant-dependent species collected in restored sites. These patterns of remnant-dependent insects, however, should be interpreted with caution because the determination of a species' remnant-dependence was developed for insects in the vicinity of Chicago, Illinois (Panzer et al. 1995). Further studies are needed to determine if remnant-dependent classifications of insects in Illinois are applicable to other locations.

### Conclusions

For central Nebraska mesic tallgrass prairies, Cicadellidae, Fulgoroidea, and Membracidae diversity, and often their density, generally was higher at restored sites than at native prairies. In contrast, Acrididae and Tettigoniidae diversity generally was higher at native sites. The high diversity, and often high density, of insect communities at restored sites appears to be explained by a close relationship between the distribution of these taxonomic groups and the distribution of their host plants rather than whether a site is native or restored or whether the plant species present are native or introduced.

Because insect populations can fluctuate widely from year to year, this study must be extrapolated to other locations with care, preferably supported with additional data from other studies. Long-term monitoring of the insect and plant communities of the sites used in this study will provide valuable information on the responses of insects to various management strategies, to successional changes in the plant community, and to different climatic conditions. From a broader perspective, the difficulties, expenses, and uncertainties associated with restoring prairie should place a high priority on the preservation and management of existing prairie remnants where biotic diversity is an important objective.

### Implications for Practice

- High diversity insect communities at restored sites are best explained by the diversity of their extant plant community rather than by whether a site is native or restored.
- Prairie restored sites intended to include maximizing invertebrate diversity should include seeding a diversity of plants.
- Whether restored or native, tallgrass prairie intended to maximize invertebrate diversity should be managed to encourage maintenance of high plant diversity.

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