Management implications for invertebrate assemblages in the Midwest American agricultural landscape

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Chapter 5

Arthropod Recovery After a Wildfire: A Case Study

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Abstract

Summer wildfires are infrequent and rarely documented in the American Midwest. Historically, fires were set by indigenous people for various reasons while today prescribed fire in the dormant season with carefully controlled conditions is most often used as a tool for vegetation management. Here we document the acute and chronic impacts of an accidental wildfire on invertebrate populations in a 20 ha grassland restoration in central Illinois, USA. Samples were collected in burned and nearby unburned areas using sticky boards and pitfall traps each month of the growing season immediately following the fire and the first and third growing seasons post-fire. Our study found that in the third growing season post-fire; some taxa did still not have the same taxonomic richness, diversity and abundance as the neighboring unburned area. Common measures of taxonomic richness, diversity and abundance did not represent the changes in invertebrate assemblages that occurred three growing seasons post-fire. We provide information for fire management decisions.

Keywords: wildfire, invertebrates, grassland, Conservation Reserve Program, CRP, mid-season fire, taxonomic richness, diversity, abundance

Introduction

Fire has long-term repercussions on invertebrates. Prescribed burns have been used for decades to mimic historic fires that were instrumental in the development of the tall-grass prairie ecosystem. It is believed that fire kept forests from encroaching on the grasslands. Current practice is to use prescribed burning, generally in the spring, for vegetation control. Increasingly, concern is being expressed about the impact of prescribed burns, their timing, interval, and intensity on other inhabitants of the prairie, specifically invertebrates (Jacobs *et al.,* 2015). Common population metrics may not tell the entire story.

Fire is frequently used a tool for gross vegetative control in grassland habitats in the Midwest (Knapp *et al.,* 2009). The benefits include fuel load reduction, seed release, and invasive species control (Warren *et al.*, 1987; Ryan *et al.,* 2013). Fires are usually conducted by trained personnel under narrowly prescribed conditions including relative humidity, wind speed and direction, soil moisture levels, and temperatures (Weir, 2009). Prescribed fire is usually conducted during the dormant season while many species are inactive and in a generally protected environment (Ryan *et al.,* 2013). There is a litter layer of dried vegetation to provide fuel for the fire (Knapp *et al.,* 2009). Often there is considerable soil moisture which keeps the soil and its plant and animal inhabitants from drying (Warren *et al.,* 1987; Gagnon *et al.,* 2015). Lack of canopy vegetation keeps the fire low on the ground and lessens impact on larger trees. Spring burns provide a flush of ash that acts as fertilizer (Sharrow and Wright, 1977). Removal of the litter layer allows increased insolation and early greening of the nascent vegetation (Sharrow and Wright, 1977; Swengel, 2001).

There are some negative aspects of dormant season burns. The window when all conditions are good is very small. Some species overwinter in the litter layer and are consumed by the fire (Ryan *et al.,* 2013). The effects of fire are additive and repeated dormant season burns may affect some species disproportionately. Consequently, there is an effort by some land managers to incorporate timing and interval of fires from historical data to mimic the evolutionary conditions of prehistoric prairies (Ryan *et al.,* 2013).

The acute and chronic impacts of fire on biodiversity can be divided into four phases: 1) fuel development phase; 2) combustion phase; 3) shock phase; and 4) recovery phase (Warren *et al.,* 1987). Acute impacts include mortality from the combustion and continue indirectly until new vegetative regrowth begins. Chronic impacts include immigration and emigration, changed botanical composition and physical structure, and altered invertebrate assemblages and trophic structures (Warren *et al.,* 1987). Invertebrate response is variable, dependent on which specific invertebrate group is being studied and the timing of the burn (Harper *et al.,* 2000; Swengel, 2001). Species below ground, protected by aboveground structure (e.g., unburned wood or rocks), or highly mobile species that can escape have little or no decline during the combustion or shock phases. For less mobile individuals, those in a flightless life stage or with slow dispersal propensity the impact is greater during each of the combustion, shock and recovery phases. There is also evidence that some species in a variety of families (mostly Coleoptera: Buprestidae, Cerambycidae, Silphidae; Diptera: Empididae, Platypezidae) are attracted to fire or smoke (Warren *et al.,* 1987; Reed, 1997; Schmitz *et al.,* 2016).

There are numerous studies focusing on the impact of fire on grasslands both short and long-term on single species (Morris, 1975; Bargmann *et al.,* 2015). There are also studies comparing impacts from a variety of vegetation control methods (Callaham *et al.,* 2003; Benson *et al.,* 2007). There are fewer studies looking at the long-term impacts on prescribed burns with various fire intervals (Evans, 1988; Enright *et al.,* 2015; Moore *et al.,* 2015). There is a lack of information about the impacts of fire that is not prescribed during the growing season in the Midwest agricultural landscape. Examination of these unusual conditions will allow us to develop general recommendations to benefit invertebrate assemblages rather than focus on survival of a single species of interest during the growing season.

In Illinois, wildfire is an uncommon event. In 2012, an unplanned wildfire burned a 100 ha area that included a 20 ha field enrolled as part of a larger area enrolled in the Conservation Reserve Program (CRP). A study of the invertebrate assemblage immediately following the wildfire found in increase in lepidopteran larva associated with the spring-like growth of vegetation 70 days post-fire (Evans *et al.,* 2013). This paper examines both acute and chronic impacts of the wildfire on invertebrate populations until new vegetation was established three growing seasons post-fire. Our study documented three population metrics, taxonomic richness, diversity, and abundance during the shock phase (ten days to the end of the vegetation growing season three months post-fire), the recovery phase (first complete vegetation growing season post-fire), and new vegetation establishment (third complete vegetation growing season post-fire).

In light of the ongoing discussions about the impact of fire on invertebrate communities, we took the unique opportunity of a mid-growing season wildfire to show long-term effects on the invertebrate assemblages. We used hypotheses testing with Kullback-Leibler information theory as a basis, to infer the impact of time post-fire through vegetation recovery phases on each of the population metrics (Warren *et al.,* 1987; Burnham and Anderson, 1998, Burnham and Anderson, 2001). After selecting the model that best fit our data, we then examined the impact on invertebrate abundance within taxonomic units and trophic guilds. We show how studies that report no change in population metrics such as taxonomic richness, diversity and abundance may be missing “the rest of the story” (Aurandt, 1977).

Methods

Study Area. The study area is located in Sangamon County, Illinois, USA (39°45’09.18N, 89°28’16.98W). This area was historically part of the tall-grass prairie within the Grand Prairie Natural Division (Schwegman, 1973) and more recently converted to agriculture. The research area was a 20 ha segment of a larger parcel of land enrolled in the Conservation Reserve Program (CRP). The field was seeded in native warm season grasses and mixed forbs in 2000. The landowners managed the field with hand removal of brush and trees and cut-stump herbicide applications.

Illinois climate is typically continental with cold winter temperatures (mean −3.8 °C), warm summers (24.6 °C), and frequently fluctuating temperature, humidity, cloudiness and wind conditions. Precipitation averages 895 mm per year and temperatures average 11.2°C. The growing season is ~185 days. During the first year of the study (2012) precipitation was 300-400 mm below average and ambient temperatures were 2.4 °C higher than average (Midwestern Regional Climate Center 2009; Springfield, Illinois http:/mrcc.isws.illinois.edu\CLIMATE –accessed December 4, 2015).

On July 27, 2012, an unplanned wildfire burned more than 100 ha which included the 20 ha field of study (Figure 1). Ambient weather conditions were extremely hot and dry with high winds. High fuel loads caused by the drought made the fire intensely hot. The fire was allowed to burn to the natural firebreak provided by a creek. The fire consumed most of the above ground vegetation that included young trees, grasses and litter layer. The fire was followed by new growth resembling spring conditions (Evans *et al.,* 2013). We used the opportunity to compare post-fire invertebrate populations with an unburned portion of the same field.

Sampling. We sampled invertebrates using sticky boards and pitfall traps placed on 80 m transects in the unburned and burned prairie restoration. We used nine sampling points 10 m apart on each transect. The ends of the transects were 50 m apart, 25 m from the burn boundary (Figure 1). Pitfall traps were 150 ml plastic cups with a water and vinegar solution and detergent added to break the surface tension of the water (Eymann, 2010). We retrieved pitfall contents seven days after placement, strained and stored in isopropyl alcohol.

We placed one sticky board (Sensor ~ 8 cm x 13 cm Yellow Monitoring Cards, GrowSmart), attached to a flag (~ 6 cm X 9 cm X 76 cm LimeGlo, Forestry Suppliers) adjacent to each pitfall trap. We placed sticky boards with a minimum of half the board above the vegetation. We retrieved sticky boards after two days, placed them in a clear plastic cover and saved them for future identification.

We conducted sampling to include the shock phase (ten days to the end of the vegetation growing season three months post-fire), the recovery phase (first complete vegetation growing season post-fire), and new vegetation establishment (third complete vegetation growing season post-fire) (Warren *et al.* 1987). In 2012, we collected invertebrate samples on 11 August, 9 September, and 5 October. In 2013 and 2015, collections were made on five dates, 1 May, 9 June, 9 July, 5 August, and 3 September 2013, and 12 May, 16 June, 21 July, 25 August, and 29 September 2015. We terminated the collections after the first hard freeze that seriously damaged or killed seasonal vegetation. The small area (~ 2 ha) of unburned prairie limited the number of replicates (Figure 1). A botanist characterized the vegetation, both in the burned unburned areas, on July 12, 2013 and again on August 26, 2015. Plant nomenclature follows Mohlenbrock (1986).

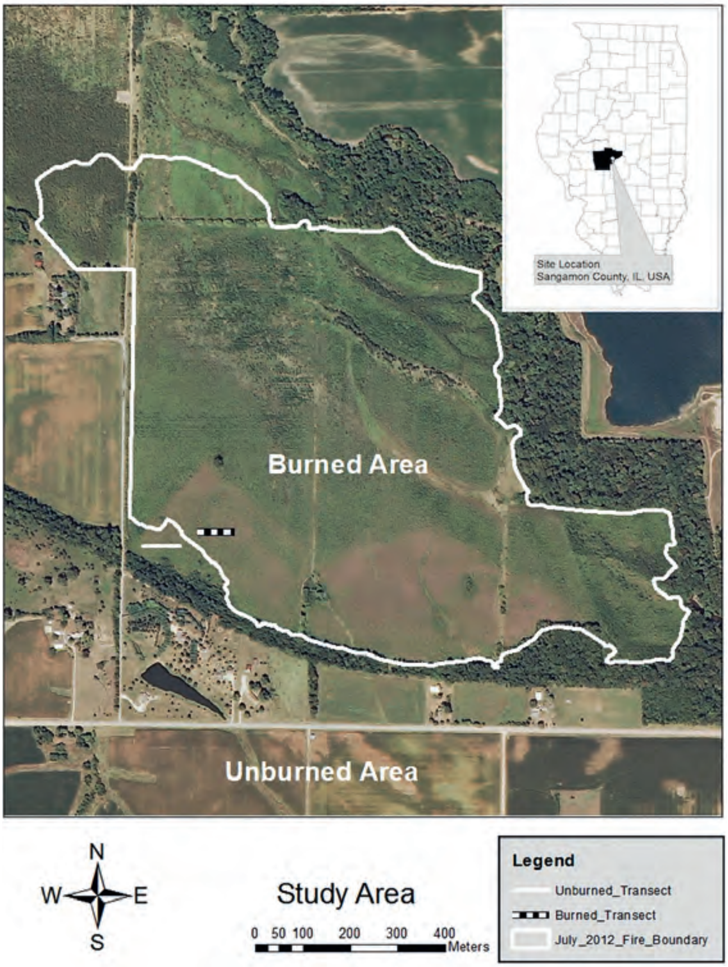


Figure 1. Map of study site and extent of wildfire 27 July, 2012.

We examined arthropods under a binocular microscope for identification. We re-examined ten percent of the samples as quality control. An independent expert adjudicated conflicting identifications. We estimated numbers of arthropods smaller than 2 mm. We used taxonomic keys (Triplehorn and Johnson, 2005) and reference collections housed at the Illinois State Museum Research and Collections Center (ISM RCC) to identify invertebrates larger than 2 mm. We made identifications to the lowest operational taxonomic unit (OTU) possible that in most cases was family. We characterized all OTUs to trophic guild, i.e., herbivores, detritivores, flower visitors, omnivores, predators, parasites and parasitoids, and non-feeding adults.

Data Analysis. We performed statistical analysis using R software 3.1.2 (R Development Core Team 2014). For analysis we used a Linear Mixed Model (LMM) [lmer () of the package lme4 (Bates *et al.* 2014). Treatment, month and year of collection, and method of collection were our independent variables that could also be used as random effect variables. All our models were maximum random effect models, i.e., including the effects on both the intercept and the regression coefficient in order to achieve conservative testing of the fixed effects (Barr *et al.* 2013). Our dependent variables were Taxonomic Richness (TR), i.e., the number of OTUs per sample, Taxonomic Diversity (TD) per sample, i.e., the exponentially transformed Shannon Wiener H', making it Hill numbers of order 1 (Hill, 1973; Spellerberg and Fedor, 2003; Jost, 2007), and Absolute Abundance (AA), i.e., the number of individuals per sample. TR is a measure giving equal weight to both rare and common species; TD as a measure of the evenness of distribution giving more weight to common species and less to rare species; and AA gives a measure of the difference in population size before and after the fire. Residuals were visually assessed in all analyses and were normally distributed for TR and TD. AA in the complete study area was not normally distributed and was log transformed for LRT analysis. Data is reported as $\bar{x}\pm$ SE. Impact of the fixed variables was tested with a Likelihood Ratio Test (LRT).

We used mathematical models to represent the various hypotheses of impact of fire on TR, TD, and AA (Burnham and Anderson, 1998; Burnham *et al.,* 2011). We developed four hypotheses about invertebrate assemblages being dependent on time post-fire. H_1 says that after 3 seasons, there is still an impact on the burned area; H_2 says that there was an impact the first two seasons but the burned area recovered in 2015; H_3 says there was an initial difference but had recovered in both 2013 and 2015; and H_4 says there was normal variation between years and no difference between burned and unburned areas after the fire. Each of the hypotheses was applied to TR, TD, and AA.

We used Akaike's information criterion corrected for sample size (AIC_c) to compare models (Burnham *et al.* 2011). Models having a difference in AIC_c scores within 1–2 of the best model have substantial support. Models within about 4–7 of the best model have considerably less support, while models with $\Delta AIC_c > 10$ have essentially no support.

We tested the impact of fire, year and month on AA within the trophic guilds (detritivores, flower visitors, herbivores, omnivores, parasites and parasitoids, and predators) with an LRT. While there are some species in each family that are exceptions, we classified each family as fitting a specific trophic guild. We then determined the percentage of individuals for each trophic guild as representative of energy transfer within the food chain. We tested the impact of fire and year on abundance within Orders that were greater than 4% of the total population with an LRT.

Results

Vegetative response. The pre-fire vegetation was rather homogenous, dominated by early successional native and non-native species typical of sites formerly in row crop agriculture. The dominant species was the highly rhizomaceous tall goldenrod (*Solidago altimissima*). The apparently lighter soils were dominated by annual species such as mule tail (*Erigeron canadensis*), daisy fleabane (*Erigeron strigosus*), pigweed (*Amaranthus* spp), as well as dense stands of Indian grass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardi*). Other grasses present in the unburned area were Hungarian brome (*Bromus inermis*) and Kentucky blue grass (*Poa pratensis).* Among invading woody species were cottonwood (*Populus deltoides*), mulberry (*Morus rubra),* Amur honeysuckle (*Lonicera maackii*), black cherry (*Prunus serotina*), and an abundance of blackberry (*Rubus alleghenensis*) in the sub-canopy.

Post-fire vegetation had a similar compositional matrix of big blue stem (*A. gerardii*) and Indian grass (*S. nutans*), and was also was dominated by Canada goldenrod (*S. altissima*). The burned area had more flowering stems and vegetative biomass with as well as less vigorous woody growth in the understory. The fire seemed to benefit the C_4 grasses and not the C_3 grasses. Effects of the fire on the vegetation species composition were still visually evident three years post-fire in large part by the absence of many of the annual and biennial species. Invading woody species had been top-killed in the fire but were beginning to re-grow.

Invertebrate response. There were 119 OTUs sampled from both the burned and unburned transects (Appendix) over the three sampling periods. The pattern of invertebrate richness, diversity and abundance in the unburned area and was used as a comparison to the area burned in the wildfire. In both areas combined there were 34018 individuals sampled over the 3-year study period. Taxonomic richness (TR) in the complete study area averaged 8.07 ± 0.17 (1-22) per sample. Overall TR did not differ in the burned and unburned areas (7.32 vs 8.82; LRT: $\chi^2 = 2.4054$; df = 1; $P = 0.1209$: random variables: month, year, and method, n = 468). Overall TD in the complete study area averaged 4.26 ± 0.08 (1-13.45) per sample and differed in the burned and unburned areas (3.95 vs. 4.57; LRT: $\chi^2 = 4.3654$; df = 1; $P = 0.03668$; random variables: month, year, and method, n = 468). Overall AA in the complete study area averaged 72.69 ± 4.53 (2 – 635) per sample and did not differ in the burned and unburned areas (60.29 vs. 85.09; LRT: $\chi^2 = 0.9604$; df = 1; $P = 0.3271$; random variables: month, year, and method, n = 468).

We used model-based inference based on Kullback-Leibler information using maximized log-likelihood to test the impact of the fire in each of three growing seasons post-fire for each of the population metrics: TR, TD, and AA (Burnham and Anderson, 1998; Anderson, 2007). For all three population metrics, the fire had an impact each growing season surveyed post-fire (Tables 1-2, Figures 2-4).

Table 1. Average taxonomic richness, diversity and abundance ± SE in the burned and unburned areas in each of the three growing seasons post fire.

Population metric	Location	2012	2013	2015
Taxonomic Richness	Burned	7.94 ± 0.49	6.54 ± 0.38	7.71 ± 0.26
	Unburned	6.76 ± 0.42	8.63 ± 0.47	10.23 ± 0.34
Taxonomic Diversity	Burned	3.49 ± 0.16	3.67 ± 0.16	4.51 ± 0.19
	Unburned	3.79 ± 0.17	3.94 ± 0.16	5.67 ± 0.23
Absolute Abundance	Burned	81.22 ± 10.82	52.39 ± 7.2	55.63 ± 7.45
	Unburned	61.09 ± 11.18	121.07 ± 16.31	63.50 ± 7.99

Table 2. Comparison of the four models for (a) taxonomic richness (TR), (b) diversity (TD) and (c) abundance (AA). H_1 says that after 3 seasons, there is still an impact on the burned area; H_2 says that there was an impact the first two seasons but the burned area recovered in 2015; H_3 says there was an initial difference but had recovered in both 2013 and 2015; and H_4 says there was normal variation between years and no difference between burned and unburned areas after the fire. Df: degrees of freedom of the model; AICc: corrected AIC; Delta AICc: difference in AICc between the model and the model with the smallest AICc; AICcWt: model weight according to delta AICc; Cum.Wt: cumulative model weights; LL: Log Likelihood.

(a) Comparison of the four models for TR.

Hypothesis	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	51	2125.64	0	1	1	-1005.4
H_2	41	2143.65	18.01	0	1	-1026.8
H_3	31	2168.36	42.72	0	1	-1050.9
H_4	25	2175.11	49.48	0	1	-1061.1

(b) Comparison of the four models for TD

Hypothesis	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	39	500.24	0	0.99	0.99	-207.48
H_2	29	508.77	8.53	0.01	1	-223.40
H_3	19	554.91	54.67	0	1	-257.61
H_4	13	557.14	56.90	0	1	-265.17

(c) Comparison of the four models for AA.

Hypothesis	Df	AICc	Delta AICc	AICcWt	Cum.Wt	LL
H_1	39	1009.54	0	1	1	-462.12
H_2	29	1081.28	71.74	0	1	-509.66
H_3	19	1139.90	130.36	0	1	-550.10
H_4	13	1202.70	193.16	0	1	-587.95

Invertebrates were identified to trophic guild. Although there are species with different feeding habits within families, we generalized from the most common species in our samples (Appendix). We tested abundance for each trophic guild with a LRT (Table 3). We analyzed invertebrate abundance as percentage of the total population in each of the trophic guilds to determine the ecological impact on population structure (Table 4, Figures 11-28). All trophic guilds differed between years, however, parasites did not differ between the burned and unburned areas. During the shock phase, the abundance of detritivores increased and flower visitors, omnivores, and predators declined in the burned area. During the recovery phase detritivores and predators decreased in the burned areas and flower visitors and omnivores increased. After the recovery phase omnivore abundance declined in the burned area while detritivores, flower visitors, and predators increased in the burned area.

Figure 2. **Graphs showing taxonomic richness in 2012, 2013, and 2015.**

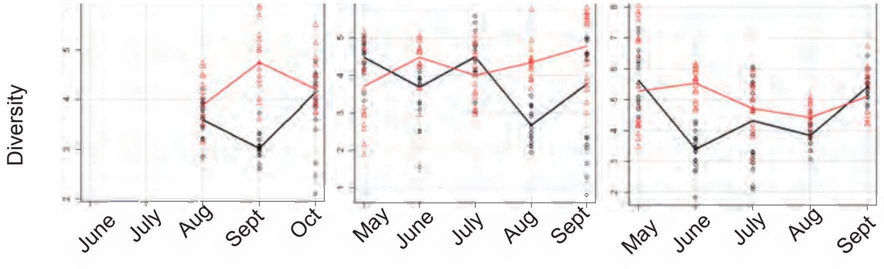


Figure 3. **Graphs showing taxonomic diversity in 2012, 2013, and 2015.**

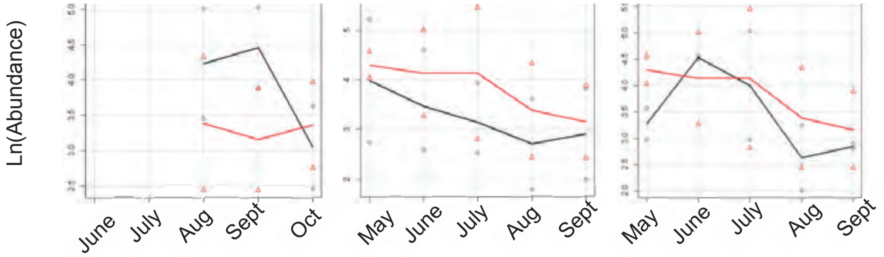


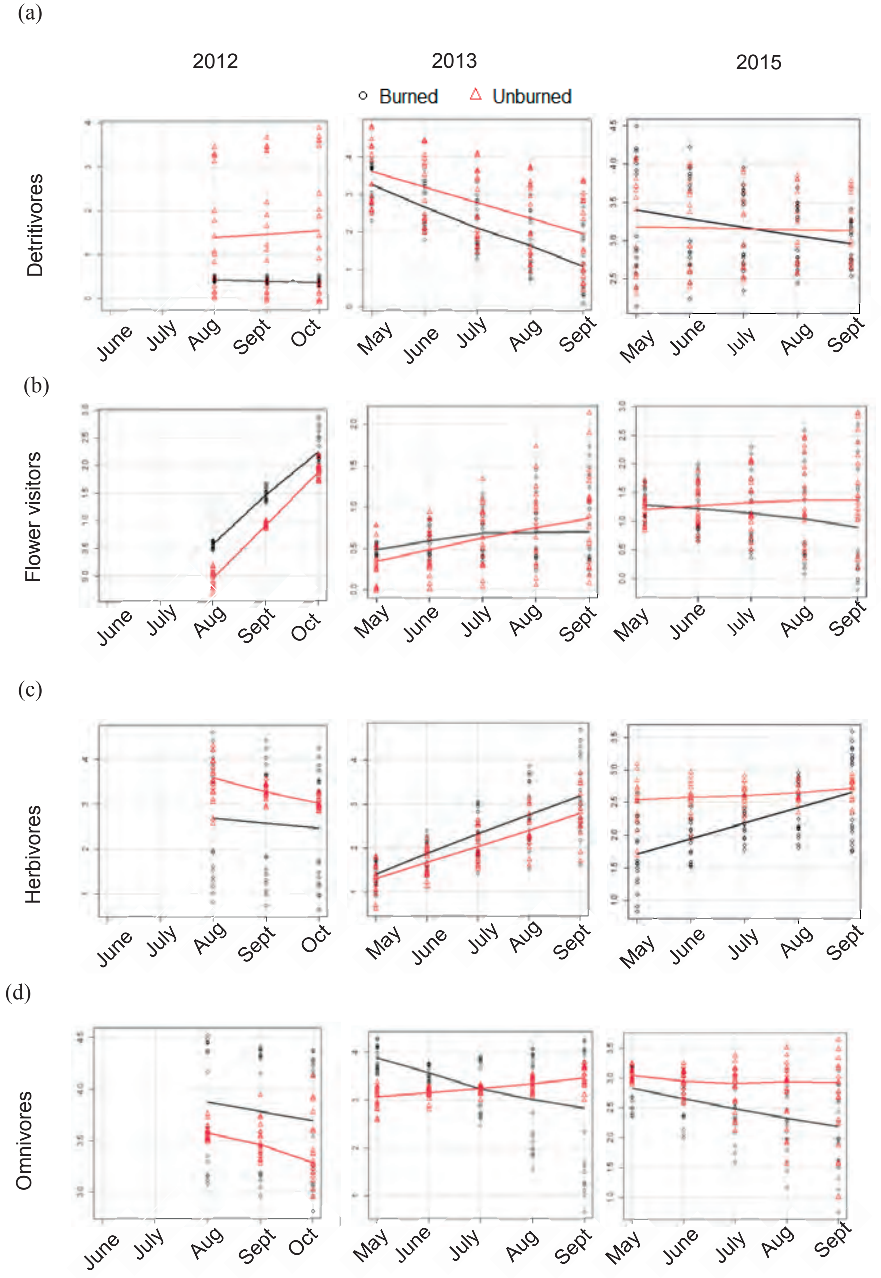
Figure 4. **Graphs showing abundance in 2012, 2013, and 2015.**

Table 3. Summary table of the impact of the fire on abundance within trophic guilds. Main Effects: T=Treatment (burned or unburned), M=Month of Collection; Y=Year of Collection; Interaction effects; T*M, T*Y, M*Y, T*M*Y; Det = Detritivores, Flower = Flower Visiting Insects, Herb = Herbivores, Omni = Omnivore, Par = Parasites and Parasitoids, Pred = Predators. Signif. Codes: “.”:$P < 0.1$; *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$); NS: not significant. Method of collection was a random variable.

Effect	Det	Flower	Herb	Omni	Par	Pred
T	.	*	NS	*	NS	**
M	***	*	***	NS	*	**
Y	***	*	*	***	**	**
T*M	NS	*	NS	NS	NS	***
T*Y	*	*	**	NS	NS	NS
M*Y	***	*	***	NS	*	NS
T*M*Y	NS	*	NS	NS	NS	NS

Table 4. Percentages of total abundance in each of the trophic guilds ± SE in the burned and unburned areas in each of the three years post-fire.

Guild	Treatment	2012	2013	2015
Detritivore	Burned	1.60 ± 0.88	21.58 ± 2.48	36.98 ± 3.15
	Unburned	17.82 ± 3.63	35.48 ± 3.32	33.60 ± 2.51
Flower	Burned	7.23 ± 1.24	3.36 ± 0.87	5.27 ± 0.93
	Unburned	3.12 ± 0.63	2.57 ± 0.60	5.24 ± 0.76
Herbivore	Burned	30.23 ± 4.16	20.52 ± 2.63	12.82 ± 1.52
	Unburned	34.03 ± 3.27	13.07 ± 1.58	15.00 ± 1.25
Omnivore	Burned	54.57 ± 4.44	39.56 ± 2.71	18.13 ± 1.73
	Unburned	39.46 ± 3.34	32.64 ± 2.24	24.03 ± 2.21
Parasite	Burned	4.02 ± 0.75	11.26 ± 1.97	11.81 ± 1.72
	Unburned	4.55 ± 1.01	11.22 ± 1.60	9.82 ± 1.06
Predator	Burned	2.34 ± 0.40	3.72 ± 0.52	14.99 ± 1.57
	Unburned	1.01 ± 0.32	5.01 ± 0.83	12.31 ± 1.59


(a)
2012
2013
2015
○ Burned
△ Unburned
Detritivores
June
July
Aug
Sept
Oct
May
June
July
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Flower visitors
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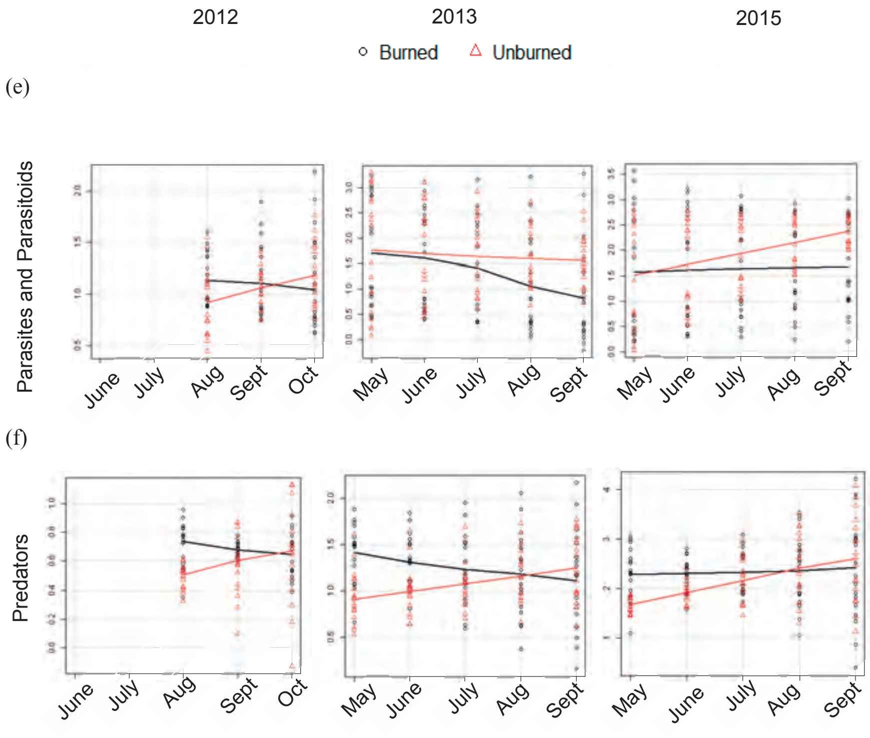

Figure 5. Graphs showing feeding guilds in 2012, 2013, and 2015.

Table 5. Summary of impacts on orders. Main Effects: Treatment (burned or unburned), Year of Collection; Interaction effects; treatment*year; Signif. Codes: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$); NS: not significant. Method of collection was a random variable.

	Treatment	Year	Interaction
Aranae	NS	***	NS
Coleoptera	**	***	**
Collembola	NS	***	NS
Diptera	**	**	**
Hemiptera	*	***	*
Hymenoptera	*	*	*
Isopod	**	**	***

Table 6. Percentages of total abundance in each of the orders ± SE in the burned and unburned areas in each of the three years of the study.

Order	Treatment	2012	2013	2015
Aranae	Burned	0.30 ± 0.17	3.26 ± 0.67	6.69 ± 1.04
	Unburned	0.75 ± 0.31	5.27 ± 0.94	4.73 ± 0.77
Coleoptera	Burned	5.47 ± 1.01	4.35 ± 0.85	7.75 ± 1.09
	Unburned	3.22 ± 0.77	4.65 ± 0.78	6.63 ± 0.75
Collembola	Burned	0.38 ± 0.17	3.26 ± 0.67	6.69 ± 1.04
	Unburned	0.75 ± 0.31	5.27 ± 0.94	4.73 ± 0.77
Diptera	Burned	39.59 ± 4.08	27.09 ± 3.33	17.7 ± 2.38
	Unburned	39.81 ± 3.63	35.59 ± 3.62	27.09 ± 3.63
Hemiptera	Burned	29.78 ± 4.35	19.27 ± 2.66	6.75 ± 0.97
	Unburned	39.01 ± 3.12	13.21 ± 1.62	11.87 ± 1.32
Hymenoptera	Burned	28.95 ± 3.96	34.28 ± 3.02	15.79 ± 1.78
	Unburned	17.38 ± 2.66	16.36 ± 1.82	14.22 ± 1.54
Isopod	Burned	13.52 ± 2.91	5.68 ± 1.42	4.69 ± 1.15
	Unburned	8.80 ± 2.36	13.81 ± 2.07	9.00 ± 1.72

We examined orders that represented more than 4 % of the total sample to see how composition changed taxonomically each year of the study. Significance of the burned area compared to the unburned area, natural variation in invertebrate abundance each year and their interactions are tested using LRT (Table 5). The abundance of Aranae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, and Isopods all differed between years; however, Aranae, and Collembola did not differ between burned and unburned areas. During the shock phase Coleoptera, Hymenoptera, and Isopods were greater in the burned area and abundance was down in Diptera and Hemiptera. During the recovery phase, Hemiptera and Hymenoptera were more abundant in the burned area and abundance of Coleoptera, Diptera and Isopods were decreased in the burned area. After the recovery phase, abundance of Coleoptera, and Hymenoptera were greater in the burned area. The abundance of Diptera, Hemiptera and Isopods was down in the burned area compared to the unburned area. Mean percent of the total population ± SE in each of the burned and unburned areas in each year (Table 6).

Discussion

General Discussion. Invertebrate taxonomic richness and abundance in the burned area in the three growing seasons of our study appeared to completely recover (Table 1, Figures 2-4). These abundance measures are somewhat misleading in that they do not tell us how the composition of species has changed (Warren *et al.,* 1987). All trophic guilds except herbivores and parasites differed between the burned and unburned areas three vegetative growing season post-fire (Table 3). Abundance of all orders with more than 4% of the total except spiders and springtails differed between the burned and unburned area (Table 5). Taxonomic diversity tells us that the mix of taxa is not significantly different in the burned and unburned areas. However, the fluctuation in taxonomic diversity was greater and continued three growing seasons post-fire (Table 1, Figures 5-7).

New vegetation and lush spring-like growth drew invertebrates to the burned area in the shock phase post-fire. This is visible in the higher TR and AA in the burned area. This attraction may have applied to generalist species since it was not reflected in the TD. In the recovery phase, all three metrics TR, TD, and AA had lower levels in the burned than in the unburned area that continued within the third season. More nutritious vegetative growth and earlier emergence due to elevated post-burn soil temperature have been cited to account for increased metrics following the initial burn (Swengel, 2001; Evans *et al.,* 2013). Our two transects were relatively close. Differences were probably due to the local effects of burning such as changes in vegetation, litter layer, and topsoil, and not to different species pools or isolation. The close proximity of the unburned area provided a source of recolonization. However, the vegetation shift may have made the new habitat inappropriate for recolonization. Additionally, there may be cascade effects e.g., the increase in herbivores of the new vegetation may draw an increase in predators followed by an increase in parasites and parasitoids.

Detritivores largely disappeared in the burned areas during the shock phase of recovery (Table 3, Figures 11-13). They increased the following spring presumably in response to increased soil detritus which accompanied enhanced vegetation growth following the fire (Lussenhop, 1981). Springtails live in the soil and feed on decaying organic material. They are considered sensitive to soil moisture levels that could explain the difference found in the second growing season. It is not until there was a vegetative litter layer that the springtails approached abundances in the unburned area. This is consistent with other research in Illinois (Rice, 1932).

Flower visitors were trapped in the burned area but almost non-existent in the unburned area immediately post-fire (Table 3, Figures 14-16). Butterfly and moth larvae are phytophagous but the adults are beneficial plant pollinators. Adult butterflies and moths are strong fliers and responded to the flush of new growth for oviposition (Evans *et al,*. 2013). Adult Lepidoptera were not common in either the burned or unburned areas the second growing season post-fire. It was not surprising that early growth drew flower visitors as the vegetation first appeared immediately after the fire. The following spring, the charred soil allowed for early green-up and the fertilizing effect of the ash created good conditions for vegetative growth when the spring rains broke the drought. Differing responses between the final sampling period in the recovery phase and the following growing season may reflect a lack of overwinter survival as the litter layer began to accumulate.

Phytophagous invertebrates (herbivores) had a varied response to the fire. Beetles found in our study may have adaptations to fire conditions (Warren *et al.,* 1987; Reed, 1997; Schmitz *et al.,* 2016). Hemiptera in our study were dominated by Cicadellidae: leafhoppers, and Aphidae: aphids. The shift in leafhopper numbers may have been related to the shift in vegetation. There was a large difference in aphids that were possibly being drawn to the new vegetation. Abundance seems to have stabilized three growing seasons post-fire. Many phytophagous invertebrates fly well and were not impacted by the fire. Herbivores may have had difficulty overwintering in the burned area due to lack of a litter layer (Table 3, Figures 17-19).

Omnivores were initially drawn to the burned area but may have not responded well to the lack of litter layer and increased insolation of the recovery phase (Table 3, Figures 20-22). The most abundant Diptera taxa were not impacted by the fire. This is consistent with research following a winter fire in Illinois (Rice, 1932). Isopods (pillbugs) are moisture dependent. Because they are nocturnal and live mostly underground, they may have survived the combustion phase and migrated out of the burned area to the unburned area. Ants were more abundant in the burned than the unburned area. Their tolerance of dry soil makes them well adapted to arid conditions following a fire. They are known as rapid colonizers due to their social structure (Swengel, 2001).

Parasites and parasitoids were not different in abundance between burned and unburned areas (Table 3, Figures 23-25). Predators had greater abundance in the early part of each growing season and overall had a complex reaction to the fire with significant impacts of period of the growing season, phase post-fire, and impacts of the fire itself (Table 3, Figures 26-28). Carabid beetles increased in both the burned and unburned areas of our study. Other studies have documented an increase in numbers of predators following fire (e.g., (Rice 1932, Warren *et al.* 1987). Spiders make up a large proportion of predators. They survive the combustion phase by seeking refuge in the soil. Taxa active on the surface at the time of burning were probably eliminated, while those occupying subsurface burrows or sacs under rocks or in clumps of dense vegetation may have escaped thermal damage (Riechen and Reeder, 1972). Survival at this point is dependent on numerous factors. In addition, spiders are among the quickest invertebrates to colonize new sites due to their ballooning behavior (Weyman, 1995). Movement between the unburned and burned areas may have been dependent on prey availability.

Opportunism is widespread in fire ecology studies, with data on insects and other biota being obtained from wildfires or other unanticipated events contributing to the wider pool of knowledge and experience (Buddle *et al.,* 2006; Jackson *et al.,* 2012). While it might be considered desirable to study numerous mid-summer fires, it is our contention that every fire is unique. Studies of numerous fires bring with them the inevitable differences in weather, fuel load and other undetermined factors. A myriad of other factors includes the fire characteristics and timing of the burn related to phenology of the invertebrates being studied. Our study is limited but has the benefit of invertebrates being exposed to similar conditions at a single location. An interesting variable we were not able to study was the possibility that because of the severe drought conditions some invertebrates may have been in diapause similar to overwintering conditions. Thus, they may have survived the fire and not come out of diapause until the following year spring rains. This would explain why some groups did not differ between burned and unburned areas. An alternative explanation of the absence of some invertebrate groups in 2012 is life history. Some groups are active in the spring and less active late July and August. An additional limitation to our study and others is the introduction of sampling bias based on ease or difficulty of capture with the shift in vegetative cover.

Our study examines the response to fire through the four phase sequence of fire impact: fuel development, combustion, shock and ecosystem recovery (Warren *et al.,* 1987). The non-burned portion of the field represents the fuel development phase. The combustion phase was not documented due to the unplanned nature of the wildfire. Monitoring the shock and recovery phases began ten days post-fire and continued from the remainder of the season post-fire through the third complete growing season. The shock phase of this fire was complicated by the interaction of the fire with the effects of drought (Evans *et al.,* 2013). The vegetative response of spring-like growth was in distinct contrast to the dried dormant vegetation in the unburned area. The shock phase continued overwinter due to lack of litter layer, microclimate conditions, and continued drought. The first full growing season post-fire allowed the vegetation to shift composition based on the new soil and insolation conditions. During the growing season and following dormant period, a litter layer became established. The third growing season showed that vegetation in the burned area was well established and, as in other studies, fire seemed to simplify the plant community and favor warm-season C_4 grasses (Gibson *et al.,* 1993; Callaham *et al.,* 2003).

Management implications. The shift from positive taxonomic richness of that of the unburned area post-fire to negative in the first growing season post-fire indicates possible issues with overwintering or lack of appropriate habitat due to loss of the litter layer. We continued to see an overall 25% decrease in taxonomic richness the third growing season post-fire. At this time, the structure of the burned area was similar to the unburned areas and, therefore, reasons for the difference in taxonomic richness are probably not related to depletion of the litter layer (i.e., catchability of the invertebrates, increased insolation, lack of cover etc.). Reasons for this decrease are probably related to the change in vegetation. Vegetative changes in our study seemed to favor the C_4 grasses and prairie forbs. The suitable invertebrate assemblages for this mix of vegetation have to come from somewhere. Unless there is an appropriate habitat in the vicinity it may take some time, if ever, for the correctly matched invertebrates to populate the burned area. Historical burns would probably have been patchy with large spaces left unburned providing refugia for existing invertebrates to survive and repopulate the area. The burned area in our study did not have either refugia or nearby intact prairies to repopulate the site.

Fire is considered the most important tool in the management of vegetation in the Midwest (Kelly *et al.,* 2015). It is believed to be historically present and an important factor in the evolution of the American prairie (McClain and Elzinga, 1994). To land managers, it is a technique preferable to the use of chemical treatments, at the very least, used in conjunction with chemical application to undesirable vegetation (Warren *et al.,* 1987). The timing and intensity of the wildfire in our study was probably similar to conditions of fire before European settlement. We know that fire was responsible for keeping the forest from encroaching on the prairie (Briggs *et al.,* 1998). There is however, a degree of uncertainty about the interval and landscape scale of the burns. There is also some controversy about whether some prairie plants are fire dependent or fire tolerant.

The impacts of fire vary across taxa. Characteristics of the fire associated with invertebrate responses relate to the direct exposure to fire and amount of subsequent stress post-fire, suitability of post-fire vegetation to meet life history requirements, and availability of colonizing populations (Warren *et al.,* 1987; Swengel, 2001). It should also be noted that vegetation survival of fire is also dependent on the same fire characteristics (Frost, 1984). Information on invertebrate life history and ecology serve as a starting point and may allow one to predict their responses to fire. Yet the response of a species with a known life history and ecology may be confounded by the unknown effect of the fire on its predators, parasitoids, pathologies, and host plant (Harper *et al.,* 2000).

Prescribed fire has been proposed for control of insect pests (Vermeire *et al.,* 2004; Iglay *et al.* 2012). We suggest caution in implementing fire for manipulating arthropod populations for this purpose. While fire can control for some pests it may effectively open the door to other pests (McCullough *et al.,* 1998; Iglay *et al.,* 2012; Evans *et al.,* 2013). Moreover, this study shows that there may also be multi-year post-fire effects on invertebrates.

Here we show that while fire may be a desirable tool for vegetation management, it should be used with caution and an understanding that fire can have consequences with lasting effects for the invertebrate assemblages inhabiting the same space. Alternating timing or season of the burn may effectively decimate a species by destroying eggs, larva and adult forms. Burning on a short rotation may locally extirpate a species by not allowing a complete recovery. Using alternative forms of vegetation control such as mowing or grazing has a negative impact on invertebrates (Callaham *et al.,* 2003; Benson *et al.,* 2007). Alternating methods of vegetation control (grazing, mowing, and fire) also impacts invertebrates (Swengel, 2001). The argument that prairie dependent invertebrates evolved in tandem with fire dependent prairie vegetation is misleading because we may be mistaking fire tolerance for fire dependence (Anderson, 2006). We believe methods of vegetation control should be implemented to lengthen the fire rotation particularly in areas where we wish to maintain threatened species. To minimize the impact of prescribed fire on invertebrate taxa we recommend the use of fire exclosures, an extended fire rotation, and creating refugia that are representative of the entire grassland within the burn area. These management strategies add a layer of complication to an already intricate preparation period, but probably necessary to protect invertebrate assemblages.

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Appendix

Invertebrate taxa sampled post-fire during the remainder of the 2012 vegetation growing season, and the 2013 and 2015 growing seasons. Guilds: detritivores (D), flower visitors (F), herbivores (H), not feeding as an adult (NA), omnivores (O), parasites and parasitoids (PA), and predators (PR). B = burned area, U = unburned area.

Taxa	Guild	2012		2013		2015	
		B	U	B	U	B	U
Class Oligochaeta: Earthworms	D	1	17	19	133	8	26
Class Gastropoda							
Snails	H	0	5	1	45	11	30
Slugs	H	0	0	4	5	41	37
Order Araneae: Spiders							
Linyphiidae: Sheet Web Spiders	PR	6	7	19	24	17	31
Lycosidae: Wolf Spiders	PR	11	15	113	98	136	59
Gnaphosidae: Parson Spiders	PR	0	1	1	6	0	0
Thomisidae: Crab Spiders	PR	0	1	2	26	0	0
Salticidae: Jumping Spiders	PR	4	2	1	5	2	2
Spider hatchlings	PR	0	0	220	310	27	23
Spider ssp.	PR	0	0	0	72	0	2
Order Opiliones: Harvestmen	PR	6	4	7	40	10	11
Order Acari: Ticks	PA	0	0	4	14	1	3
Order Isopoda: Isopods							
Armadillidiidae: Common Pillbugs	O	1334	451	225	1126	104	768
Order Diplopoda: Millipedes	D	15	6	18	63	6	20
Order Chilopoda: Centipedes	PR	0	0	3	7	0	7
Order Collembola: Springtails	D	62	1253	1754	6367	2279	1847
Order Orthoptera							
Acrididae: Grasshoppers	H	28	23	40	34	65	62
Tettigoniidae: Katydids	H	0	0	0	0	0	1
Gryllidae: Crickets	H	4	3	27	7	27	23
Order Phasmatodea: Walkingsticks							
Heteronemiidae: Stick Bugs	H	0	0	0	0	1	0
Order Plecoptera: Stoneflies	NA	0	0	1	0	0	0
Order Blattaria: Cockroaches							
Blattidae: Cockroaches	O	0	0	0	0	0	3

Taxa	Guild	2012		2013		2015	
Order Hemiptera:True Bugs							
Gerridae: Water Striders	PR	0	0	0	2	0	0
Miridae: Plant Bugs	H	0	0	2	1	2	0
Nabidae: Damsel Bugs	PR						
Anthocoridae: Minute Pirate Bugs	PR	14	6	1	2	0	0
Reduviidae: Assassin Bugs	PR	2	0	1	1	0	1
Lygaeidae: Seed Bugs	H	6	0	0	1	0	1
Blissidae: Cinch Bugs	H	0	0	0	0	1	0
Coreidae: Leaf-footed Bugs	H	0	0	0	0	2	5
Cydnidae: Burrower Bugs	H	0	0	0	0	0	2
Thyreocoridae: Ebony Bugs	H	0	0	0	3	0	0
Pentatomidae: Stink Bugs	H	1	0	0	0	0	1
Membracidae: Treehoppers	H	0	0	0	1	1	3
Cercopidae: Spittlebugs	H	0	0	0	0	0	1
Cicadellidae: Leafhoppers	H	109	694	368	323	85	282
Fulgoroidea: Planthoppers	H	0	0	4	1	0	0
Aphidae: Aphids	H	507	77	67	17	130	135
Order Thysanoptera: Thrips	H	0	0	0	0	2	11
Order Coleoptera: Beetles							
Cicindelidae: Tiger Beetles	PR	12	0	11	0	9	2
Cicindela punctulata: Punctured Tiger Beetle	PR	0	0	9	0	0	0
Carabidae: Ground Beetles	PR	19	11	38	64	55	61
Carabidae: *Notiophilis ssp.*	PR	0	0	2	2	4	1
Calosoma sycophanta: Caterpillar hunter	PR	0	0	1	1	0	0
Histeridae: Hister Beetles	PR	0	0	4	5	0	0
Silphidae: Carrion Beetles	D	0	3	4	45	15	36
Scaphidiidae: Shining Fungus Beetles	H	0	0	0	0	0	1
Staphylinidae: Rove Beetles	PR	24	5	30	22	11	18
Trogidae: Trox Beetles	D	1	4	8	7	14	5
Scarabaeidae: Scarab Beetles	D	3	0	21	59	4	3
Popillia japonica: Japanese Beetle	H	1	0	0	0	0	0
Buprestidae: Jewel Beetles	D	1	0	0	2	0	0
Elateridae: Click Beetles	H	2	0	0	1	4	2
Lampyridae: Fireflies	PR	0	0	0	0	0	3
Cantharidae: Soldier Beetles	PR	2	0	2	0	4	7
Cleridae: Checkered Beetles	PR	10	3	0	1	2	3
Melyridae: Soft-winged Flower Beetles	D	0	0	0	0	0	1
Erotylidae: Pleasing Fungus Beetles	D	2	1	1	1	0	0
Coccinellidae: Lady Beetles	PR	0	0	1	1	1	0
Latridiidae: Minute Brown Scavenger Beetle	PR	0	0	0	0	2	3
Mordellidae: Tumbling Flower Beetles	F	35	12	16	20	30	66

Taxa	Guild	2012		2013		2015	
Tenebrionidae: Darkling Beetles	H	0	0	0	3	4	0
Meloidae: Blister Beetles	H	16	3	5	1	0	0
Chrysomelidae: Leaf Beetles	H	3	0	4	4	2	20
Microrhopala vittata: Goldenrod Leaf Miner	H	0	0	9	5	2	4
Curculionidae: Weevils	H	6	1	8	8	3	9
Coleoptera larva ssp	H	5	2	7	4	4	6
Order Neuroptera: Antlions, Lacewings	NA	1	0	3	0	2	1
Order Hymenoptera: Wasps, Bees, Ants							
Symphyta: Sawfly ssp	H	0	0	1	0	0	1
Siricidae: Horntails	H	0	0	0	3	0	0
Ichneumonidae: Ichneumon Wasps	PA	0	7	4	5	5	10
Ichneumonidae: *Ophion ssp*	PA	0	1	0	0	3	0
Braconidae: Parasitic Wasps	PA	28	36	75	64	45	38
Chrysididae : Cuckoo Wasps	PA	3	0	2	3	0	1
Megachilidae: Resin Bees	F	1	0	0	0	0	0
Sphecidae: Thread-Waisted Wasps	PR	4	3	2	2	0	1
Halictidae: Sweat Bees	PA	32	20	21	13	46	14
Andrenidae: Mining Bees	F	18	14	3	1	0	0
Apidae: Honey Bees	F	3	0	17	10	5	4
Bombus pensylvanicus: Bumble Bee	F	1	8	0	0	0	0
Tiphiidae: Flower Wasps	PA	1	4	0	0	0	0
Mutillidae: Velvet Ants	PA	1	0	0	1	0	0
Vespidae: Hornets, Wasps	PA	1	2	2	4	1	1
Formicidae: Ants	O	1677	402	1431	910	323	462
Trichoptera: Caddisflies	PR	0	0	0	1	0	4
Lepidoptera: Butterflies and Moths							
Micro-lepidoptera[1]	F	4	1	0	5	2	9
Hesperiidae: Skippers	F	7	6	0	0	2	5
Papilioninidae: Swallowtails	F	7	6	0	0	0	0
Papilio polyxenes anterius: Black Swallowtail	F	1	0	0	0	0	0
Pieridae: Sulfurs	F	6	5	3	0	0	1
Pieris rapae: Cabbage Butterfly	F	6	5	3	0	2	1
Nymphalidae: Brush-footed Butterflies	F	2	0	0	0	0	0
Geometridae: Geometer Moths	F	3	7	0	0	0	1
Noctuidae: Owlet Moths	F	0	0	0	1	7	3
Lepidoptera larva ssp	H	68	5	2	0	30	21

Taxa	Guild	2012		2013		2015	
Order Diptera: Flies							
Tipulidae: Crane Flies	D	1	10	1	2	2	5
Chironomidae: Midges	D	10	8	53	379	6	13
Culicidae: Mosquitoes	PA	22	2	47	144	209	240
Mycetophilidae: Fungus Gnats	D	3	0	9	44	640	390
Stratiomyidae: Soldier Flies	F	0	0	0	0	1	0
Tabanidae: Horse Flies, Deer Flies	PA	0	0	0	0	0	22
Apeioceridae: Flower-Loving Flies	PR	0	0	0	0	1	0
Bombyliidae: Bee Flies	F	0	0	0	0	0	2
Dolichopodidae: Long-legged Flies	PR	1	5	13	28	251	196
Phoridae: Hump-backed Flies	O	1	0	0	0	2	3
Pipunculidae: Big-headed Flies	PA	0	0	0	0	0	2
Syrphidae: Flower Flies	F	34	9	17	17	31	24
Calliphoridae: Blow Flies	D	0	0	0	0	1	1
Muscidae: House Flies	O	32	69	166	80	209	488
Sarcophagidae: Flesh Flies	O	66	75	0	0	0	0
Tephritidae: Fruit Flies	F	0	0	0	0	1	1
Ulidiidae: Picture-winged Flies	F	7	2	2	0	49	46
Diptera ssp	O	185	134	273	463	25	49
Diptera larva ssp	O	0	0	4	4	4	6

[1] Small Lepidoptera of the Super Families Gelechioidea, Pyraloidea, Tiniodea, Gracillarioidea, Incurvarioidea, and Families Tortricidae and Pterophoridae.

Guilds are mostly detritivores (D), flower visitors (F), herbivores (H), omnivores (O), parasites and parasitoids (PA), predators (PR), or not feeding as adults (NA)

- Other species not identified due to damage of features or difficulty in identification