

A cross-taxonomic comparison of insect responses to grassland management and land-use legacies

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Citation: Debinski, D. D., R. A. Moranz, J. T. Delaney, J. R. Miller, D. M. Engle, L. B. Winkler, D. A. McGranahan, R. J. Barney, J. C. Trager, A. L. Stephenson, and M. K. Gillespie. 2011. A cross-taxonomic comparison of insect responses to grassland management and land-use legacies. *Ecosphere* 2(12):131. doi: 10.1890/ES11-00226.1

Abstract. Many species of plants and animals associated with grasslands are rare or declining due to habitat loss and degradation. Although grassland plants and insects evolved in the context of both grazing and fire, the appropriate use of grazing and fire has been debated among those concerned with protecting insect communities. We established an experiment to test insect responses to three grassland management treatments: (1) patch-burn graze (burning of spatially distinct patches and free access by cattle), (2) graze-and-burn (burning of entire tract with free access by cattle), and (3) burn-only. Because we expected that land-use legacies could also affect insect abundance and diversity, we evaluated effects of time since fire, grazing history, remnant history (remnant or reconstructed grassland) and pre-treatment vegetation characteristics, which were assumed to be a legacy of prior land-use. Butterflies (Lepidoptera), ants (Hymenoptera: Formicidae), and leaf beetles (Coleoptera: Chrysomelidae) were surveyed for three years to compare their responses to each of these treatments as measured by abundance, richness and species diversity. Each of these taxa is relatively diverse and was expected to have the potential to have strong negative responses to grazing and burning, but we predicted more positive responses to patch-burn grazing. Our results showed that land-use legacies affected insect abundance, richness and diversity, but treatments did not. Ant abundance was lower in tracts with a history of heavy grazing. Ant species richness was positively associated with pre-treatment time since fire and vegetation height and negatively associated with pre-treatment proportion native plant cover. Butterfly abundance was positively associated with pre-treatment litter cover. Leaf beetle diversity was positively associated with pre-treatment native plant cover, and leaf beetle abundance was negatively associated with time since fire. Our results indicate that land-use legacies can exert more influence on grassland insect community composition than current management, but the particular aspects of these land-use legacies that are important vary across insect taxa. The implications of these findings are that (1) land-use legacies should garner more attention in grassland management and (2) conservation of grassland insect communities will be improved by taxon-specific analysis of land-use legacy variables.

Key words: burning; butterflies; Chrysomelidae; Formicidae; grassland; grazing; insect diversity; Iowa; land-use legacy; Lepidoptera; Missouri; tallgrass prairie.

Received 6 August 2011; revised and accepted 11 November 2011; **published** 12 December 2011. Corresponding Editor: D. P. C. Peters.

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INTRODUCTION

Managing and restoring grassland ecosystems for insect communities has been a topic of heated debate for the past few decades, and this is particularly true in the tallgrass prairie ecoregion of the U.S. The use of fire is contested among those concerned with protecting insect communities (Swengel 1998, Panzer and Schwartz 2000, Cook and Holt 2006), and concerns have been raised as to the compatibility of burning smaller grassland tracts relative to the conservation of insect populations within these tracts (Panzer 2002). Burning can greatly influence the presence-absence of arthropod species on a particular grassland tract, and species differ in their tolerances for fire (Warren et al. 1987, Swengel 1996). In addition, the time since fire can influence the species present (Reed 1997). Many insect species decline immediately after a burn (Swengel 2001) while other species increase (Gibson et al. 1993, Larsen and Work 2003, Moran 2010), and the trajectory of abundance relative to time since burn can vary among species even within the same taxonomic group (Vogel et al. 2010).

Grazing, like fire, can affect the species abundance and diversity of grassland fauna (Andresen et al. 1990, Sutter and Ritchison 2005, Warui et al. 2005) and flora (Towne et al. 2005), and controversies have ensued regarding the potential impacts on insects. Grazing sometimes reduces grassland insect diversity (e.g., Stoner and Joern 2004), even in areas where it has little effect on the plant community (Milchunas et al. 1998), yet in other locations increases insect species richness and Shannon diversity (Joern 2005). The intensity of grazing can influence the direction of the insect response. For example, insect species richness was greater in grasslands with low-intensity grazing than those with high-intensity grazing (Kruess and Tscharntke 2002). Ants have been less extensively studied in grasslands, but in Argentine subtropical forest, ant community composition varied along a gradient of grazing intensity (Bestelmeyer and

Wiens 1996). Ant species were distributed based on their preference for litter versus bare ground; both of these variables were affected by grazing, but can also be altered by burning.

Patch-burn grazing is a management approach that combines both fire and grazing and has potential for insect conservation because it creates heterogeneity in both the spatial and temporal patterns of grazing and burning (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Whereas uniform application of either grazing or fire can simplify the landscape, different levels of grazing creates habitat heterogeneity which can support a more diverse set of invertebrate species (Tscharntke and Greiler 1995, Swengel 2001). Patch-burn grazing involves subdividing a pasture into sections which are burned sequentially over multiple years. Large ungulates focus their grazing on the recently burned patches (Coppedge and Shaw 1998, Vermeire et al. 2004), creating a mosaic of (1) heavily grazed/recently burned patches, (2) patches that were burned six to 18 months earlier and are dominated by forbs after the ungulates have moved on to more recently burned patches, and (3) patches dominated by grass and senesced vegetation. Engle et al. (2008) found that the increased habitat heterogeneity generated by patch-burn grazing was reflected in increased heterogeneity of insect biomass compared to pastures under traditional homogeneity management.

However, in addition to current management, many grasslands are influenced by legacies of prior land-use (Burke et al. 1989, Trimble 1999). Plowing, grazing, and fire can leave immediate effects as well as enduring consequences on ecosystem structure and function for centuries after the processes have been operative (Foster et al. 2003). Land-use legacies can be measured via abiotic properties of the ecosystem (e.g., soil carbon, nitrogen content, soil compaction), as well as biotic components (e.g., current plant or animal community composition). It is often difficult to determine the history of land use, but this history can be important when evaluating grassland restoration success.

To better understand the responses of invertebrate communities to fire and/or grazing, a variety of investigators have quantified invertebrate community responses before and after disturbances (Nekola 2002, Larsen and Work 2003, Engle et al. 2008, Doxon et al. 2011). Due to taxonomic challenges, these responses are often quantified at the order or family level. Although these assessments provide important information, the interpretation of the results can be challenging because of the diversity of life history traits within a family (which may include herbivores, predators, or decomposers and species with life stages that include belowground as well as aboveground activity). Alternatively, much of the research that has been done at the species level to assess responses has focused on a single family or order.

Here we describe the results of an experimental grassland management project that compared abundance, species richness, and diversity responses of ants (Order Hymenoptera, Family Formicidae), butterflies (Order Lepidoptera), and leaf beetles (Order Coleoptera, Family Chrysomelidae) to three grassland treatments: burn-only, graze-and-burn, and patch-burn graze. These taxa are relatively diverse in grassland ecosystems and were expected to respond strongly to grazing, burning, or the combination thereof. Trager (1998) argues that the sheer biomass of ants compared with other insect families justifies research concerning ants. Additionally, ants often serve as ecosystem engineers by altering habitat through burrowing and foraging (Jones et al. 1994, Wagner et al. 2004) and have been shown to respond to anthropogenic change across a wide range of habitats (e.g., Majer and Nichols 1998, Bestelmeyer and Wiens 2001). Butterflies are excellent subjects for ecological management studies because they are relatively easy to identify in the field and can be highly responsive to disturbance via direct as well as indirect effects (Waltz and Covington 2004, Nelson 2007). Chrysomelid (leaf) beetles have been less extensively examined in grassland ecosystems, but are a diverse group of herbivores, and, like butterflies, many species have specialized associations with host plants (Clark et al. 2004, Barney and Hall 2011).

All three of these insect taxa could be expected to have strong responses to burning, grazing, and

vegetative composition and structure due to their dependence on vegetation for food and habitat as well as the importance of bare ground or litter for nesting and overwintering habitat. In addition, there is value in cross-taxonomic comparison of these responses to determine whether a broader group of insects is responding similarly to disturbance patterns and/or habitat characteristics. With that in mind, we tested for effects of treatment (burn-only, graze-and-burn, and patch-burn graze) on abundance, richness, and diversity of each taxon, while simultaneously testing for effects of pre-treatment covariates, including land-use history variables (grazing history, remnant history [i.e. remnant versus reconstructed grassland]), fire history, and pre-treatment vegetation variables (i.e., composition and structure). The vegetation present at the beginning of our study is in fact the legacy of prior land use (McGranahan 2008, McGranahan 2011) and was expected to affect insect community richness and diversity patterns. We made the following predictions:

1. Patch-burn grazed tracts will have higher species richness and diversity compared to tracts managed using more traditional techniques (i.e., graze-and-burn and burn-only tracts) due to non-burned refugia, spatial heterogeneity of grazing pressure, and increased structural heterogeneity of the vegetation.
2. Prior land use (plowing, heavy grazing by cattle, and burning) will have left legacies that affect abundance, richness, and diversity of each of the three taxa (ants, leaf beetles and butterflies). Specifically, tracts that were plowed and later reconstructed, and tracts with a history of heavy grazing will have lower richness and diversity than grassland remnants and those that lacked a history of heavy grazing. Tracts with longer pre-treatment time since fire will have higher diversity and abundance of all three insect taxa.
3. Variation in pre-treatment vegetation characteristics (e.g., proportion native plant cover) that are legacies of land-use history will affect abundance and diversity of each of the three insect taxa, but these patterns may vary across the taxonomic groups

based upon habitat preferences for nest sites (ants), overwintering sites (butterflies), and species-specific plant use (all three taxa).

METHODS

Study tracts

In 2006, we selected 12 tracts for a controlled experiment to test the effects of fire and grazing treatments on vegetation structure, plant community composition, and terrestrial insect community composition in the Grand River Grasslands of southern Iowa and northern Missouri, USA (Appendix A). The tracts, which ranged in size from 15 to 34 ha, occurred within a mixture of private and public grasslands. They were allocated to one of three treatments: (1) patch-burn graze (burning of spatially distinct patches and free access by cattle, $N = 4$), (2) graze-and-burn (burning of entire tract with free access by cattle, $N = 4$), and (3) burn-only (burning of entire tract with no grazing, $N = 4$). From 2007 through 2009, tracts receiving the first two treatments were stocked with cattle at about 3.4 animal unit months per ha between May 1 and October 1. Each tract was divided into three patches of approximate equal area. In patch-burn graze tracts, natural topographic features such as waterways, drainages, and ridgetops were used as patch boundaries to the extent possible. Each year, a different patch within each patch-burn graze tract was burned in early spring (mid-March). Tracts in the burn-only and graze-and-burn treatments were burned in their entirety in spring 2009, except for one burn-only tract, which was burned in spring 2008. Thus, the fire-return interval was the same across all three treatments.

Land-use history was classified in terms of remnant history as well as fire and grazing history. Remnants were defined as grassland tracts that had never been plowed, whereas reconstructed grasslands were planted from seed in bare soil. Pre-treatment time since fire denoted the number of years since fire had been applied to each tract as of 2006 (values ranged from 0 to 15 years). Grazing history was classified as either having a history of severe grazing or not. Although some of the tracts had long histories of severe grazing, we defined our pre-treatment legacies in terms of the previous three years

(2003–2005) for consistency in this analysis. The land-use history of each tract was determined by interviewing landowners and governmental land managers who owned/managed the tracts.

Vegetation sampling

Pre-treatment vegetation variables were used as covariates to enable us to separate treatment from legacy effects. Pre-treatment vegetation data were collected in 2006 at the transect-level to describe plant community composition, and at the patch-level to describe plant composition and structure. Plant community composition was sampled twice during the summer season and measured at the species level in two permanently-marked Whittaker plots (Stohlgren et al. 1995) per patch (i.e., $N = 6$ Whittaker plots per tract) as described in McGranahan (2011). The canopy cover value for each species was the maximum canopy cover value observed. From Whittaker plot data, we calculated the proportion of native plant canopy cover in each patch, using the following equation: $\text{proportion native plant cover} = \text{total native plant canopy cover} / (\text{total native plant canopy cover} + \text{total exotic plant canopy cover})$.

During July of 2006 we measured pre-treatment plant functional group composition and vegetation structure in thirty 0.5-m² quadrats that were placed systematically within each patch as described in Pillsbury et al. (2011). Variables measured included Robel vegetation height (Robel et al. 1970), percent cover of litter and bare ground, and canopy cover of warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, woody plants and *Lolium arundinaceum* (Schreb.) S.J. Darbyshire (tall fescue). Cover measurements used the following cover classes: 0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100% (Daubenmire 1959). Center points of each cover class were averaged within each patch ($N = 30$ quadrats/patch) and tract ($N = 90$ quadrats/tract).

Sweep net sampling

Sweep net surveys of terrestrial invertebrates were conducted in each tract twice per year during the periods of major emergence (June to early July and mid-July to early August) from 2007–2009. Surveys were conducted along 50-m transects parallel to the eastern edge of each

Whittaker plot with a starting point 10 m east of the north-center coordinate of each plot, resulting in 12 samples per tract per year (2 transects per patch \times 3 patches per tract \times 2 sampling periods per year). Surveys were conducted between 0930–1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/hr, and the sun was not obscured by clouds. Surveys were conducted by a single individual walking south along each transect at a constant pace, holding a net with both hands with the net handle directed forward and the net opening pointed sideways. The net was swept at a constant pace from side to side 40 times, where one sweep includes the complete back and forth swing in both directions, as the individual traveled the transect. Completing 40 sweeps was preferred to traveling exactly 50 m to maintain constant effort. Insects were carefully transferred from the net to a plastic zip lock bag at the completion of each transect and frozen until they could be sorted. Due to the greater than expected labor costs of identifying insects, only samples from each patch's northern transect were identified, resulting in six identified samples per tract per year. Samples from each patch's southern transect remain frozen for future processing if funding permits.

Sweep net samples were sorted to family level, preserved in ethanol in vials categorized by tract, replicate, and date, and stored until they could be later identified to species. L. Winkler, with the assistance of J. Trager, identified ant species. R. Barney identified the chrysomelid leaf beetles.

Butterfly sampling

Butterflies were sampled via Pollard walk transects (Pollard and Yates 1993) twice per year from 2007–2009. Sampling was spaced temporally to cover the major emergence periods (June to early July and mid-July to early August). One 100 \times 5-m transect was established parallel to the west side of each Whittaker vegetation sampling plot, with a starting point 10 m west of the north-center coordinate of the plot, resulting in 12 samples per tract per year (2 transects per patch \times 3 patches per tract \times 2 sampling periods per year). During butterfly sampling, an observer walked the transect at a steady pace (\sim 10 m/min) and recorded data on butterflies seen within the 5 m \times 5 m area in front of the observer (extending

2.5 m to each side of the transect, and 5 m forward). Each butterfly was identified to the species level. Specimens that could not be identified in the field were captured and identified in our lab. Surveys were conducted between 0930–1830 h when temperatures were between 21°C and 35°C, sustained winds were below 16 km/hr, and the sun was not obscured by clouds.

Data analysis

Insect count data from the June and July sampling periods were added together, so that a single value of each response variable was obtained for each transect each year. For each of three major taxa, we calculated four response variables: abundance, species richness, Shannon diversity, and Simpson diversity. Abundance was defined here as the total number of individuals of each taxonomic group (butterflies, ants, or leaf beetles) found per transect. Species richness was calculated as the number of unique species found per transect. Shannon diversity was calculated as $H = -\sum(p_i \ln(p_i))$ and Simpson diversity was calculated as $D = 1 / \sum p_i^2$, where p_i is the percentage of i th species and \ln is the natural log. Shannon diversity is a measure of species evenness, while Simpson diversity is a measure of species dominance (Magurran 2004). Due to the difference in total samples available, for butterflies, response variables were calculated for two transects per patch per year, whereas for ants and leaf beetles, response variables were calculated for one transect per patch per year.

Univariate data analysis.—We performed mixed model analysis of covariance using the statistical software package SAS version 9.2 (SAS Institute 2008) to test for effects of treatment and year on response variables for our three focal taxa after accounting for the influence of pre-treatment covariates. We viewed plots of residuals versus fitted values. If residuals failed to exhibit an approximately normal distribution, analyses were re-run with transformed response variables. Values of pre-treatment covariates were obtained in 2006. Before performing analysis of covariance, we reviewed the grassland insect literature to select a list of potential variables to serve as covariates. Then, we tested for correlations among those vegetation variables; when correlation coefficients were 0.70 or greater, the variable more likely to be associated with insect density (based

on our literature review) was retained as a covariate whereas the other was excluded to reduce multicollinearity. Pre-treatment covariates entered in all analyses of covariance included: grazing history, remnant history, time since fire, proportion of native plant cover, forb cover, Robel vegetation height, litter cover, and the cover of bare ground. Backward elimination was performed to remove insignificant covariates from each analysis of covariance, with $\alpha = 0.05$ used as criterion for retaining each covariate. When analysis of covariance indicated a significant effect of treatment, or a significant treatment by year interaction, we used differences of least squares means as our multiple comparison procedure.

Multivariate data analysis.—We used nonmetric multidimensional scaling (NMDS) to describe separately the structure of the ant, butterfly, and leaf beetle communities. NMDS is an unconstrained, distance-based ordination technique in which the distance between samples in ordination space corresponds to the similarity in community structure among samples. Ordinations were performed using VEGAN (Oksanen 2009), a package of community analysis functions for the statistical software R (R Development Core Team 2010). In order to avoid spurious results, species occurring in only one transect were not included in the ordinations. Bray-Curtis distance was used as the measure of dissimilarity among grassland transects.

For all ordinations, transect-level abundance data from 2007–2009 were plotted together, i.e., each point on the ordination represents community composition of a transect in a particular year. Thus, the vectors that describe the insect responses to vegetation variables represent the composite response across all three years. Subsequently, we tested for correlations between ordination axis scores and values of 11 pre-treatment vegetation variables derived from the same Whittaker plot locations: proportion of native plant cover, plant species richness, Robel vegetation height, percent cover of litter and bare ground, and canopy cover of warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, woody plants and *Lolium arundinaceum*. Vegetation variables significantly correlated with one or more ordination axes at $\alpha \leq 0.05$ were plotted as vectors.

RESULTS

Over three years, the numbers of species and total individuals collected were as follows: ants: 14 species and 5101 individuals; butterflies: 33 species and 2048 individuals; leaf beetles: 44 species and 1189 individuals. Fig. 1 presents tract-level patterns of abundance (Fig. 1A), richness (Fig. 1B), Shannon diversity (Fig. 1C), and Simpson diversity (Fig. 1D) for each treatment, whereas Fig. 2 represents tract-level patterns of abundance and richness relative to grazing history and remnant history (with graphs of diversity indices omitted for simplicity's sake). However, the statistical results we wish to emphasize are those of Table 1 because the ANCOVA results evaluate responses of transect-level abundance, richness, and diversity after accounting for the influence of covariates, which is a more accurate representation of the responses. Grassland management treatments had no main effects on any of the four response variables (abundance, species richness, Shannon diversity and Simpson diversity) measured for each taxon, and had interactive effects (with year) only on butterfly abundance (Table 1). Because treatment showed no significant main effects, we present ordinations of each of the communities superimposed with vectors defining significant pre-treatment vegetation variables relative to species distributions but without designation of treatment type. Year affected response variables for each of the three taxa. Regarding significant year effects, we refer the reader to Table 1 and save further mention of this for the discussion.

Ants

Grasslands with a recent history (2003–2005) of grazing had fewer ants ($F = 7.75$, $df = 1, 10$, $P = 0.019$), than grasslands without such a history (Table 1, Fig. 2A). No other factors, including remnant history (Fig. 2C) affected ant abundance (Table 1). Ant species richness was influenced by three pre-treatment covariates (Table 1, Fig. 2B, D): remnant history (with remnants having greater species richness than reconstructed grasslands), proportion native cover (negative correlation), and Robel vegetation height (positive correlation). Remnant grasslands had greater Shannon diversity of ants than reconstructed

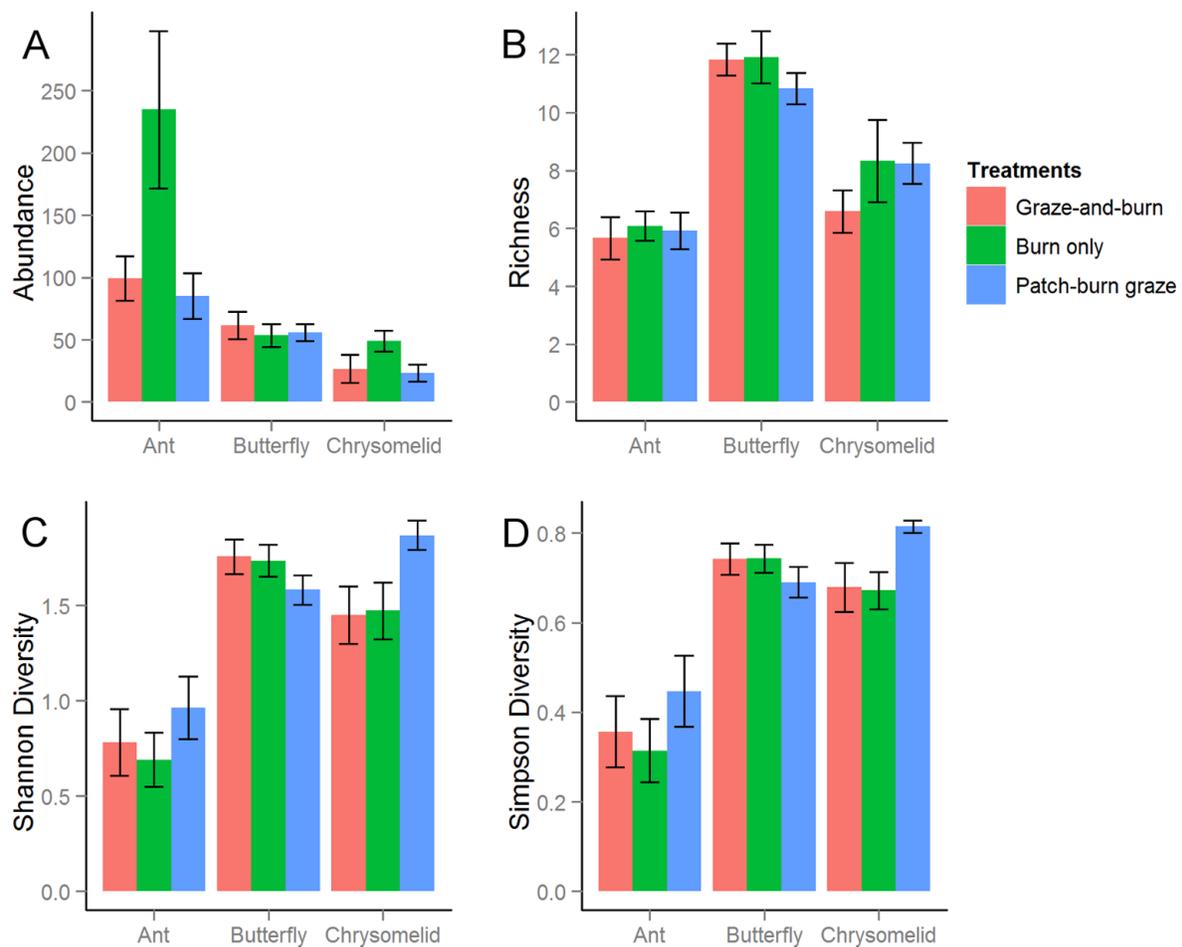


Fig. 1. Treatments compared for (A) abundance, (B) species richness, (C) Shannon diversity, and (D) Simpson diversity of three taxa (ants, butterflies, and leaf beetles). Means and standard errors are based on tract-level values from 2007 through 2009.

grasslands ($P = 0.002$, Table 1). Three pre-treatment covariates were positively correlated with Shannon diversity: cover of bare ground, Robel vegetation height, and time since fire (Table 1). Several findings on Simpson diversity were consistent with those obtained on Shannon diversity: (1) ant diversity did not differ among treatments, (2) remnants had greater ant diversity than reconstructions ($P < 0.001$), and (3) Robel vegetation height was positively correlated with ant diversity ($P < 0.001$). However, two unique results were obtained using Simpson diversity. Tracts having a recent history of heavy grazing had lower ant diversity than tracts without that history ($P = 0.027$), and proportion of native cover was negatively correlated with ant diver-

sity ($P = 0.002$).

Ordination of ant data (Fig. 3) showed that grasslands dominated by *Formica montana*, the most abundant ant species in our study (representing 81% of all ants captured), separated from grasslands with several less dominant species (*Camponotus americanus*, *Formica subsericea*, *F. exsectoides* and *Lasius alienus*). The ant community ordination was correlated with one vegetation variable: pre-treatment Robel vegetation height ($r^2 = 0.06$, $P = 0.025$).

Butterflies

Treatment and year interacted to affect butterfly abundance ($P = 0.029$) (Table 1); both grazing treatments exhibited high interannual variation

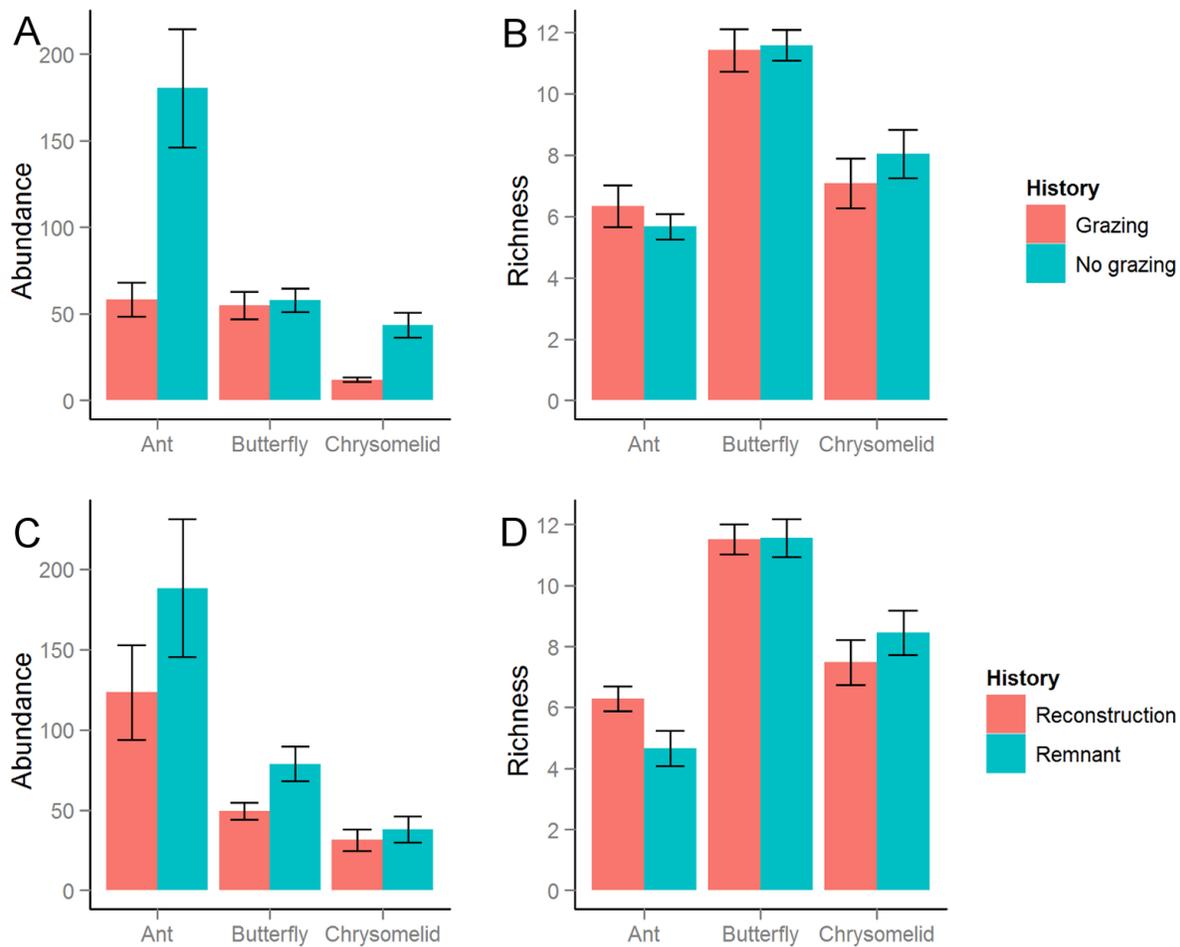


Fig. 2. Effects of grazing history on (A) abundance and (B) species richness, and effects of remnant history on (C) abundance and (D) species richness of three taxa (ants, butterflies, and leaf beetles). Means and standard errors are based on tract-level values from 2007 through 2009.

in butterfly abundance ($P < 0.001$ for each treatment), whereas abundance did not vary among years in the burn-only treatment. Pre-treatment litter cover was positively associated with butterfly abundance ($P = 0.011$, Table 1). No pre-treatment covariates were associated with butterfly species richness, or with either diversity index (Shannon or Simpson) (Table 1, Fig. 2A–D). Ordination of butterfly community structure (Fig. 4) showed that three habitat specialists (*Cercyonis pegala*, *Lycaena hylus* and *Speyeria idalia*) and one habitat generalist (*Danaus plexippus*) were associated with grasslands having greater pre-treatment proportion native cover ($r^2 = 0.41$, $P = 0.002$), forb cover ($r^2 = 0.20$, $P = 0.008$), and woody cover ($r^2 = 0.07$, $P = 0.012$). Species at

the opposite end of the primary ordination axis included two exotic, habitat-generalist species (*Thymelicus lineola* and *Pieris rapae*) and three native, habitat-generalist species (*Cupido comyntas*, *Colias philodice*, and *Papilio polyxenes*) that were associated with pre-treatment values of cool season grass cover ($r^2 = 0.07$, $P = 0.06$) (Fig. 4).

Leaf beetles

Pre-treatment values of time since fire were negatively associated with leaf beetle abundance ($P = 0.01$) (Table 1). Pre-treatment values of proportion native cover were positively associated with leaf beetle species richness ($P = 0.018$) and Shannon diversity ($P = 0.022$), whereas no covariates were significant predictors of Simpson

Table 1. Associations between independent variables and insect response variables.

Independent variables	Ants				Butterflies				Leaf beetles			
	AB	RIC	SHA	SIM	AB	RIC	SHA	SIM	AB	RIC	SHA	SIM
Experimental variables												
Treatment												
Year			**	***	***	**			**	*	**	*
Treatment × Year					*							
Legacy variables												
Grazing history	−*			−*								
Remnant history		+	+	+								
Time since fire			+						−**			
Proportion native cover		−*		−**						+	+	
Forb cover												
Bare ground cover			+									
Litter cover					+							
Robel vegetation height		+	+	+								

Notes: Legacy variables are covariate data from 2006. Response variables are based on data from 2007, 2008 and 2009, and are abbreviated as follows: AB = abundance, RIC = species richness, SHA = Shannon diversity, SIM = Simpson diversity. Blank cell indicates that independent variable was not a significant predictor of response variable. Asterisks indicate that independent variable was a significant predictor of response variable: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Plus and minus signs indicate whether the relationship between variables was positive or negative. For the independent variable “grazing history” a minus sign indicates that grasslands with a recent history of grazing had lower values of response variable than grasslands without a recent history of grazing. For the independent variable “remnant history” a plus sign indicates that remnant grasslands had higher values of response variable than grassland reconstructions.

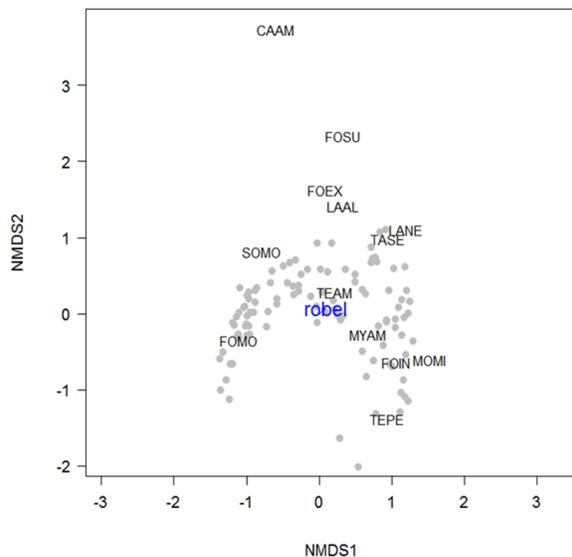


Fig. 3. Ant community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet, see Appendix B). Pre-treatment Robel vegetation height (robel) is significantly correlated with the ordination and is plotted as a vector to demonstrate its relationship to ant community composition.

diversity. Leaf beetle community structure (Fig. 5) was correlated with pre-treatment variables including proportion native plant cover ($r^2 = 0.50$, $P = 0.013$), warm season grass cover ($r^2 = 0.40$, $P = 0.024$), cool season grass cover ($r^2 = 0.26$, $P = 0.038$), and legume cover ($r^2 = 0.17$, $P = 0.025$). Some of the more common species of leaf beetles (e.g., *Zygogramma suturalis*, *Epitrix* spp., *Paria thoracica*, *Diabrotica barberi* and *D. undecimpunctata*) were widely separated in ordination space.

DISCUSSION

The results of this research show that land-use legacies had far more influence on insect distribution and abundance patterns than currently imposed management treatments, even after three years of treatment implementation. Our prediction that patch-burn grazed tracts would have higher species richness and diversity of ants, butterflies, and leaf beetles than tracts managed for homogeneity was not supported by our results. In fact, this experiment showed few effects of burning and grazing treatments on invertebrate abundance, richness and diversity measures. These results contrast strongly with responses observed for grassland birds within the same tracts (Pillsbury et al. 2011).

We propose two hypotheses to explain this

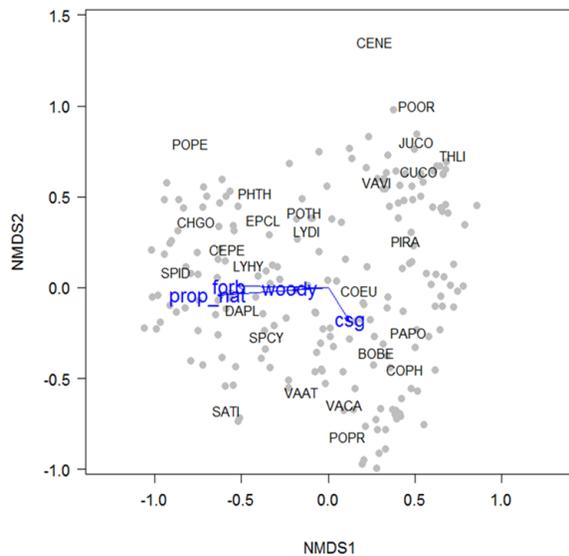


Fig. 4. Butterfly community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet; see Appendix C). Four pre-treatment vegetation variables significantly correlated with the ordination are plotted as vectors to demonstrate their relationships with butterfly community composition: cool season grass cover (csg) woody plant cover (woody), forb cover (forb), and proportion of native plant cover (prop_nat).

unexpected outcome. First, for some taxa, particularly ants, legacies of previous land-use appear to have had significant impacts on determining local distribution and abundance. These legacies may have diminished our ability to observe treatment effects, and three years of these treatments are not enough to alter differences in abundance, diversity and composition that were established by heavy grazing. This might be especially so for ants, whose colonies are perennial, often taking three or more years to reach maturity, and thus having a longer lag time. Heavy grazing might also have more of an impact on ants, as colony-founding queens often seek areas of loose, bare soil rather than compacted soil in which to dig their incipient nests (J. C. Trager, *personal observation*).

Second, patch-burn grazing failed to generate

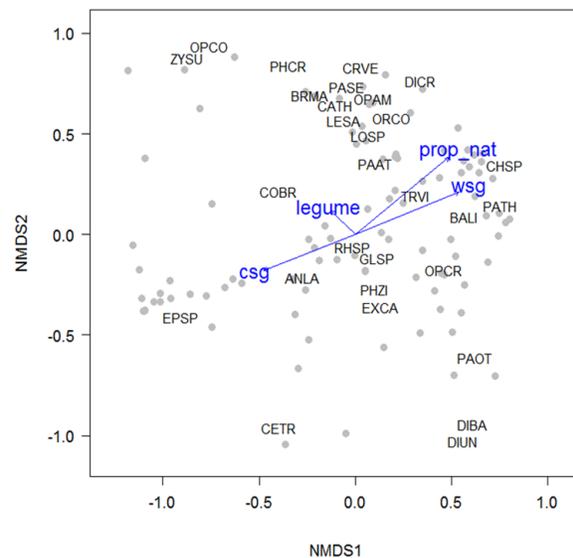


Fig. 5. Chrysomelid community ordination plot showing the results of nonmetric multidimensional scaling analysis (NMDS) of abundance data from 2007 through 2009. The position of each species in ordination space is indicated by a four letter abbreviation of its scientific name (first two letters of genus followed by first two letters of specific epithet; see Appendix D). Four pre-treatment vegetation variables that are significantly correlated with the ordination are plotted as vectors to demonstrate their relationships with chrysomelid community composition. These variables are cool season grass cover (csg), legume cover (legume), proportion of native plant cover (prop_nat) and warm season grass cover (wsg).

among-patch heterogeneity in vegetation structure, thus vegetation structure of patch-burn graze tracts did not differ from that of graze-and-burn tracts (McGranahan 2011). Without the structural heterogeneity that is so important to insect diversity (Tscharntke and Greiler 1995), our implementation of patch-burn grazing failed to deliver the anticipated increase in diversity. Elsewhere, patch-burn grazing under moderate stocking has generated structural variation among patches (Fuhlendorf and Engle 2004, Winter et al., *in press*). In our patch-burn graze tracts, stocking rate may have been excessive, so that cattle were obliged to forage intensively on all patch-types, rather than focusing on the recently burned patches.

Our prediction that land-use legacies would

have significant effects on insect abundance and diversity was supported, but the patterns of response varied across the three insect groups. Land-use legacy variables such as grazing history, remnant history, fire history, and pre-treatment vegetation characteristics had numerous significant effects on ants, but fewer effects on butterfly or leaf beetle diversity or richness. In addition, the pre-treatment vegetation variables that were significantly correlated with insect abundance, richness, and diversity varied across taxonomic groups.

Ants exhibited higher richness and diversity in remnants and tracts with higher vegetation as compared to reconstructed grasslands and tracts with shorter vegetation. They also had lower Simpson diversity in tracts with a history of grazing. We speculate that ants were more affected by legacies in part because of the lower complexity of the ant dataset. Over 80% of the ants captured were *Formica montana*, therefore responses of ants to predictor variables were due in large part to a response of *F. montana*. *F. montana* is behaviorally dominant (Henderson et al. 1989), defending their above-ground nests from cows as well as other ant species. They are also numerically dominant (Trager 1998, Henderson et al. 1989) in prairies of central North America. We hypothesize that the lower richness and diversity of ants in grassland reconstructions is due to *F. montana* dominance. A lower abundance of *F. montana* in 2009 may have led to increased survival and fecundity of other ant species, particularly opportunist species, and thus an increase in ant diversity that year. As grassland reconstructions age, and habitat conditions become less suitable for *F. montana*, we predict that ant species richness will increase as other species colonize the reconstructions.

In contrast to ants, which are predacious and respond to prey availability, butterfly and leaf beetle communities of central North American grasslands have no analogous social hierarchy of species (and have no species that is numerically dominant), so we expected that their responses would be driven more by pre-treatment vegetation structure and diversity. A number of studies have found positive correlations between invertebrate diversity and plant diversity (Crisp et al. 1998, Stoner and Joern 2004), and Collinge et al. (2003) found differences in butterfly species

richness among grassland types. In our system, butterfly abundance and diversity showed few significant responses to treatment or to land-use legacies beyond the positive association with pre-treatment litter cover. This legacy effect makes sense given that litter is an especially important habitat component for butterflies (Vogel et al. 2010). However, ordination provided additional insights by showing a clear separation between habitat-specialist species and habitat-generalist species. Of the four species (*Cercyonis pegala*, *Danaus plexippus*, *Lycaena hyllus*, and *Speyeria idalia*) associated with tracts having higher pre-treatment proportion of native cover and forb cover, all except *D. plexippus* have been designated as habitat specialists (i.e., grassland specialists) in prior studies (e.g., Panzer et al. 1995, Shepherd and Debinski 2005, Vogel et al. 2010). And although *D. plexippus* uses a wide variety of habitats when considering its entire range, we suspect its association with higher pre-treatment proportion of native plant cover is due to its dependence on native forbs (*Asclepias* spp.) as hosts.

Leaf beetles showed what might be the most predictable response of a group of host plant specialist insects to grassland characteristics. In contrast to ants, leaf beetles responded positively in terms of species richness and Shannon diversity to the pre-treatment proportion of native plant cover. We were surprised that leaf beetle richness and diversity did not respond to pre-treatment time since fire, but Hall and Barney (2011) found no significant effect of prescribed burns on species richness of leaf beetles or vegetation in several state nature preserves in Kentucky. Leaf beetle abundance did respond negatively to increased time since fire. This may be linked to the beneficial effects of fire in reducing dead plant biomass and promoting new plant growth (Glenn-Lewin et al. 1990) which can enhance food quality and availability for herbivorous insects (Tscharntke and Greiler 1995).

There were strong effects of year on all three taxa, which is not surprising, as populations of many insect species fluctuate widely from year to year (Andrewartha and Birch 1954). However, the three taxa were not synchronous in their fluctuations in abundance, richness and diversity (e.g., while butterfly abundance was high in 2008,

leaf beetle abundance was quite low). Some of the common butterfly species (*Colias philodice* and *Cupido comyntas*) suffered large population declines in 2009 (R. A. Moranz, *personal observation*). Initially, we suspected that fire was the cause, as most of our burn-only tracts and all of our graze-and-burn tracts were burned spring 2009. However, *C. philodice* and *C. comyntas* declined irrespective of treatment, including responses in tracts that were patch-burn grazed (thus receive approximately the same amount of prescribed fire each year). This suggests that some other factor (bad winter weather, disease outbreak, etc.) operating at the regional level was the cause of the declines.

In summary, land-use legacies and their associated pre-treatment vegetation conditions had significant effects on ants, butterflies and leaf beetles, but they did not have equivalent effects across taxa as measured by abundance, richness, or diversity. This is an important finding because managers might otherwise assume that all insects would respond in similar ways to land-use legacies. Others have found that cross-taxonomic comparisons can reveal disparities in richness patterns relative to habitat types or locations of diversity hotspots, meaning that one taxon cannot serve as a surrogate for another (e.g., Prendergast et al. 1993, Su et al. 2004, Davis et al. 2008). If our goal is conservation of all of these taxa, it is imperative to know that ants, butterflies, and leaf beetles are each responding to different components of land-use legacies. Virtually all grassland restoration projects are influenced by some type of land-use legacy, yet rarely are such legacies taken into consideration when evaluating restoration success. Whether these legacies are acknowledged or not, they may be having significant effects—even more significant than the current management being applied.

ACKNOWLEDGMENTS

Funding for this project was through the Iowa State Wildlife Grants program grant T-1-R-15 in cooperation with the U. S. Fish and Wildlife Service, Wildlife and Sport Fish Restoration Program. The authors acknowledge the support of the Iowa Agriculture and Home Economics Experiment Station and the Oklahoma Agricultural Experiment Station. We thank Megan Kirkwood, Matt Nielsen, Jessica Orlofske, Michael Rausch, Shannon Rusk, and Laura Winkler for their

dedicated work in the field and Mary Jane Hatfield, Jenny Hopwood, Laura Merrick, Jessica Orlofske, Michael Rausch, and others for their assistance in sorting and identification in the laboratory. We thank Karl Pazdernik, Dennis Lock, and Dr. Philip Dixon of the Agriculture Experiment Station Consulting Group of Iowa State University for their assistance with statistical analyses. Special thanks go to research associate Ryan Harr for his efforts in managing almost every aspect of our research project. Finally, we pay our respects to the late Sheri Svehla for initiating our work in the field and the lab.

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SUPPLEMENTAL MATERIAL
APPENDIX A

Table A1. Characteristics of study tracts in the Grand River Grasslands of Iowa and Missouri.

Treatment	Tract name	Remnant history	Grazing history (2003–2005)	Previous pre-treatment fire	Tract area (ha)
Burn-only	Kellerton Tauke	Prairie restoration†	None	2003	32.4
Burn-only	Pawnee	Prairie remnant	None	2005	21.8
Burn-only	Richardson	Prairie remnant	None	1994 or earlier	15.6
Burn-only	Ringgold North	Prairie remnant	None	2004	15.4
Graze-and-burn	Gilleland	Prairie remnant	Cattle grazing	1994 or earlier	31.2
Graze-and-burn	Lee Trail Road	Prairie remnant	None	2004	34.0
Graze-and-burn	Pyland West	Prairie remnant	Cattle grazing	1994 or earlier	17.8
Graze-and-burn	Sterner	Prairie restoration†	None	1994 or earlier	32.4
Patch-burn graze	Ringgold South	Prairie remnant	Cattle grazing	2003	32.4
Patch-burn graze	Kellerton North	Prairie restoration†	None	2004	32.4
Patch-burn graze	Pyland North	Prairie remnant	Cattle grazing	1994 or earlier	25.3
Patch-burn graze	Pyland South	Prairie remnant	Cattle grazing	1994 or earlier	22.7

† Prairie restorations were restored from croplands between 1980 and 2004.

APPENDIX B

Table B1. Codes for ant scientific names used in community ordination (Fig. 3).

Code	Scientific name
CAAM	<i>Camponotus americanus</i>
FOEX	<i>Formica exsectoides</i>
FOIN	<i>Formica incerta</i>
FOMO	<i>Formica montana</i>
FOSU	<i>Formica subsericea</i>
LAAL	<i>Lasius alienus</i>
LANE	<i>Lasius neoniger</i>
MOMI	<i>Monomorium minimum</i>
MYAM	<i>Myrmica americana</i>
SOMO	<i>Solenopsis molesta</i>
TASE	<i>Tapinoma sessile</i>
TEAM	<i>Temnothorax ambiguus</i>
TEPE	<i>Temnothorax pergandei</i>

APPENDIX C

Table C1. Codes for butterfly scientific names used in community ordination (Fig. 4).

Code	Scientific name
BOBE	<i>Boloria bellona</i>
CENE	<i>Celastrina neglecta</i>
CEPE	<i>Cercyonis pegala</i>
CHGO	<i>Chlosyne gorgone</i>
COEU	<i>Colias eurytheme</i>
COPH	<i>Colias philodice</i>
CUCO	<i>Cupido comyntas</i>
DAPL	<i>Danaus plexippus</i>
EPCL	<i>Epargyreus clarus</i>
JUCO	<i>Junonia coenia</i>
LYDI	<i>Lycaena dione</i>
LYHY	<i>Lycaena hyllus</i>
PAPO	<i>Papilio polyxenes</i>
PHTH	<i>Phyciodes tharos</i>
PIRA	<i>Pieris rapae</i>
POOR	<i>Polites origenes</i>
POPE	<i>Polites peckius</i>
POTH	<i>Polites themistocles</i>
POPR	<i>Pontia protodice</i>
SATI	<i>Satyrium titus</i>
SPCY	<i>Speyeria cybele</i>
SPID	<i>Speyeria idalia</i>
THLI	<i>Thymelicus lineola</i>
VAAT	<i>Vanessa atalanta</i>
VACA	<i>Vanessa cardui</i>
VAVI	<i>Vanessa virginiensis</i>

APPENDIX D

Table D1. Codes for leaf beetle scientific names used in leaf beetle community ordination (Fig. 5).

Code	Scientific name
ANLA	<i>Anomoea laticlavia</i>
BALI	<i>Bassareus lituratus</i>
BRMA	<i>Brachynoea margaretae</i>
CATH	<i>Capraita thyamoides</i>
CETR	<i>Cerotoma trifurcata</i>
CHSP	<i>Chaetocnema</i> spp.
COBR	<i>Colaspis brunnea</i>
CRVE	<i>Cryptocephalus venustus</i>
DIBA	<i>Diabrotica barberi</i>
DICR	<i>Diabrotica cristata</i>
DIUN	<i>Diabrotica undecimpunctata</i>
EPSP	<i>Epitrix</i> spp.
EXCA	<i>Exema canadensis</i>
GLSP	<i>Glyptina spuria</i>
LESA	<i>Lexiphanes saponatus</i>
LOSP	<i>Longitarsus</i> sp.
OPAM	<i>Ophraella americana</i>
OPCO	<i>Ophraella communis</i>
OPCR	<i>Ophraella cribrata</i>
ORCO	<i>Orthaltica copalina</i>
PAAT	<i>Pachybrachis atomarius</i>
PAOT	<i>Pachybrachis othonus</i>
PASE	<i>Paria sexnotata</i>
PATH	<i>Paria thoracica</i>
PHCR	<i>Phyllotreta cruciferae</i>
PHZI	<i>Phyllotreta zimmermani</i>
RHSP	<i>Rhabdopterus</i> sp.
TRVI	<i>Trirhabda virgata</i>
ZYSU	<i>Zygogramma suturalis</i>