

Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities

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Abstract Many grassland ecosystems are disturbance-dependent, having evolved under the pressures of fire and grazing. Restoring these disturbances can be controversial, particularly when valued resources are thought to be disturbance-sensitive. We tested the effects of fire and grazing on butterfly species richness and population density in an economically productive grassland landscape of the central U.S. Three management treatments were applied: (1) *patch-burn graze*—rotational burning of three spatially distinct patches within a pasture, and moderately-stocked cattle grazing ($N = 5$); (2) *graze-and-burn*—burning entire pasture every 3 years, and moderately-stocked cattle grazing ($N = 4$); and (3) *burn-only*—burning entire pasture every 3 years, but no cattle grazing ($N = 4$). Butterfly abundance was sampled using line transect distance sampling in 2008 and 2009, with six 100-m transects per pasture. Butterfly species richness did not respond to management treatment, but was positively associated with pre-treatment proportion of native plant cover. Population density of two prairie specialists (*Cercyonis pegala* and *Speyeria idalia*) and one habitat generalist (*Danaus plexippus*) was highest in the burn-only treatment, whereas density of one habitat generalist (*Cupido comyntas*) was highest in the patch-burn graze treatment. Treatment application affected habitat structural characteristics including vegetation height and cover of bare ground. Historic land uses have reduced native plant cover and permitted exotic plant invasion; for some butterfly species, these

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legacies had a greater influence than management treatments on butterfly density. Conservation of native insect communities in altered grasslands might require native plant restoration in addition to restoration of disturbance processes.

Keywords Butterflies · Grazing · Habitat management · Invasive species · Prairie · Prescribed burning

Abbreviations

AICc Akaike information criterion, corrected for finite sample sizes
NMDS Nonmetric multidimensional scaling

Introduction

Like many grasslands across the globe, North American prairies and their associated flora and fauna evolved with fire and grazing (Axelrod 1985; Anderson 2006; Bond 2008). Since Europeans arrived in North America, most prairie has been converted to other land cover types, and much of the prairie that remains has suffered from altered grazing and burning practices (Samson and Knopf 1994). Recent research on prairie conservation has focused on examining prehistoric patterns of fire and grazing, particularly the spatial and temporal interaction of these disturbances which may benefit native prairie species (Fuhlendorf and Engle 2001; Brudvig et al. 2007). However, understanding how these processes affect prairie insect distribution and abundance is a topic that has generated much controversy over the past several decades, particularly with respect to the effects of burning (Swengel 1996; Panzer and Schwartz 2000; Cook and Holt 2006; Swengel et al. 2011). For instance, fire is useful for maintaining prairie vegetation and preventing the spread of woody species (Collins and Steinauer 1998; Anderson 2006), but at some scales and fire return intervals, burning can reduce insect abundance directly by incinerating immatures and/or adults (Reed 1997; Branson et al. 2006) and can reduce insect abundance indirectly by altering habitat features such as litter cover and vegetation structure (Vogel et al. 2010). Grazing also has the potential to harm grassland insect populations, depending upon grazing intensity (Kruess and Tscharntke 2002; Poyry et al. 2005) and whether grazing is coupled with fire (Moranz 2010).

One approach to grassland restoration that also has potential to protect vulnerable insect taxa from disturbance processes is to apply management heterogeneously across the landscape. By burning and/or grazing only a portion of a grassland landscape, one might prevent local extirpation of disturbance-sensitive species. Applying disturbance heterogeneously can also increase habitat heterogeneity of grasslands (Fuhlendorf and Engle 2001) which in turn can increase taxonomic diversity (Christensen 1997; Kubo et al. 2009; WallisDeVries et al. 2007; Wiens 1974). Patch-burn grazing has been used increasingly as a management technique to increase grassland structural heterogeneity, particularly in larger grasslands (>300 ha) of the Great Plains (Fuhlendorf and Engle 2001; Helzer and Steuter 2005; Fuhlendorf et al. 2009) and Africa (Archibald et al. 2005), and is thought to more closely emulate the pre-historic interaction of fire and grazing (Fuhlendorf et al. 2009). Patch-burn grazing involves dividing an actively grazed pasture into patches of approximate equal area and then burning a different patch each year. It has shown promise in restoring diverse grassland bird communities when compared to traditional grazing

management practices (Fuhlendorf et al. 2006). Patch-burn grazing provides a revenue source (beef production) that is more lucrative than some alternative land-uses (e.g., leaving ground fallow or haying), particularly on highly erodible land, thus providing landowners with an economic incentive to conserve native grasslands instead of converting them to row-crop agriculture (Curtin and Western 2008).

Responses of insects to patch-burn grazing have been examined at the order level, with patch-burn grazed pastures having greater biomass of Orthoptera and Hemiptera than pastures managed under traditional homogeneity-based management regimes (Fuhlendorf and Engle 2004; Engle et al. 2008). However, the merits of patch-burn grazing for butterfly communities have not been assessed. Most butterflies are larval host specialists (Munguira et al. 2009), and many are nectar source specialists as well (Erhardt and Mevi-Schutz 2009). This high degree of host specialization suggests that the distributions and population dynamics of many butterfly taxa might be more influenced by changes in plant community composition than changes in vegetation structure caused by patch-burn grazing. Because plant community composition, litter cover, vegetation height, nectar source availability and other components of grassland butterfly habitat can be affected by fire and grazing (Oates 1995; Poyry et al. 2006; Vogel et al. 2007; Moranz 2010), we sought to assess the responses of these habitat variables and butterfly communities to alternative combinations of these disturbances. We were particularly interested in the responses of prairie specialist butterflies which occur primarily on prairies because they rely on native prairie plants as food for larvae and/or adults (Vogel et al. 2007).

Prairie restoration efforts should account for legacies of past land uses (Foster et al. 2003), as agricultural practices such as plowing, logging, and grazing have been found to have long-lasting effects on the composition of grassland plant communities and landscapes (Motzkin et al. 1996; Coppedge et al. 2001). These effects in turn can influence species richness and population density of present-day insect communities (Bergman et al. 2004; Ockinger and Smith 2006; Shepherd and Debinski 2005). Our objective was to tease apart the effects of management treatments we imposed from pre-existing differences in habitat and landscape characteristics. We predicted that (1) prescribed fire would reduce the population density of prairie specialist butterflies, but that (2) the heterogeneous application of fire (in patch-burn graze pastures) would result in higher density of prairie specialist butterflies compared to fire alone, or fire and grazing without the spatiotemporal interaction. We also predicted that habitat heterogeneity resulting from patch-burn grazing would result in higher butterfly species richness. Lastly, we sought to examine the links between vegetation, management treatments, and butterfly density.

Methods

Study area

We tested the effects of fire and grazing treatments on butterfly abundance and community composition, and on salient plant community and ecosystem characteristics at pastures ($n = 13$) in the Grand River Grasslands region of southern Iowa and northern Missouri, USA (Fig. 1). Concurrently, the same experimental design was used by colleagues to study the effects of treatments on avian communities (Pillsbury et al. 2011) and on the entire plant community (McGranahan 2011). The pastures occurred within a mixture of private and public grasslands, ranged in size from 15 to 31 ha, with 20 km the greatest distance separating them. All pastures were tallgrass prairies that had been invaded to varying

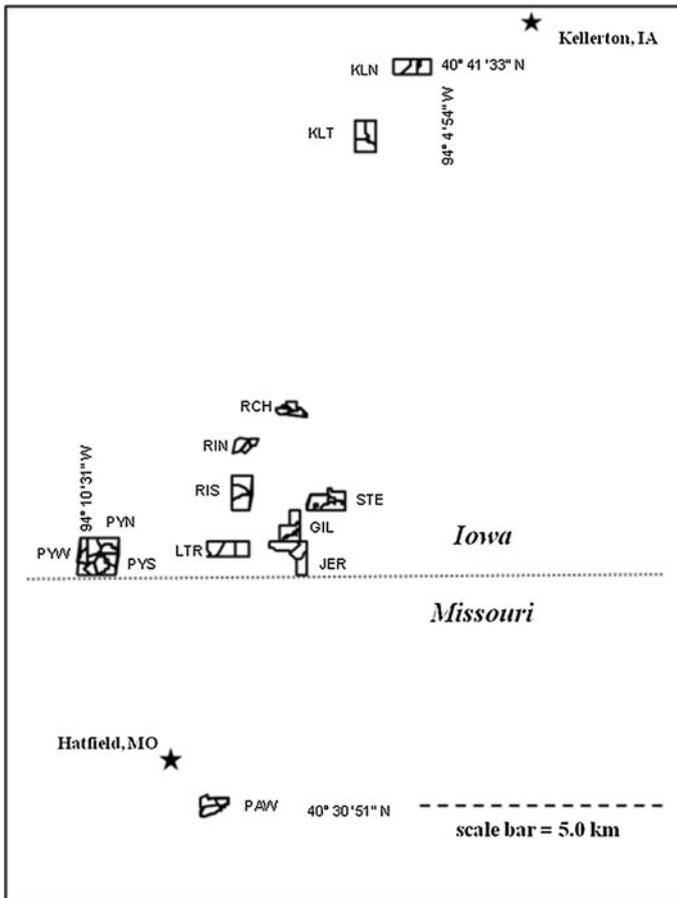


Fig. 1 Map showing locations of 12 experimental pastures in southern Iowa and one in northern Missouri. Boundaries of the three patches within each pasture are also shown. Note that the three western-most pastures are adjacent to one another, and form a square. *Three-letter codes* correspond to pasture names: *GIL* Gilleland, *JER* Jerome, *KLN* Kellerton North, *KLT* Kellerton Tauke, *LTR* Lee Trail Road, *PAW* Pawnee, *PYN* Pyland North, *PYS* Pyland South, *PYW* Pyland West, *RCH* Richardson, *RIN* Ringgold North, *RIS* Ringgold South, and *STE* Sterner. The treatment applied to each pasture is indicated in Appendix Table 3

degrees by Eurasian grasses (especially *Festuca arundinacea* and *Bromus inermis*) and legumes (*Lotus corniculatus*, *Trifolium repens*, *Trifolium pratense*). Each pasture was allocated to one of three treatments in a systematic random fashion, in order to distribute similar pastures across the different treatments (e.g. three pastures were prairie restorations, thus one prairie restoration was allocated to each treatment).

The three treatments were: (1) *burn-only* (burning of entire pasture with no grazing, $N = 4$), (2) *graze-and-burn* (burning of entire pasture with free access by cattle, $N = 4$), and (3) *patch-burn graze* (burning of spatially distinct patches and free access by cattle, $N = 5$). The burn-only treatment has long been the dominant habitat management regime on grassland preserves in Iowa and Missouri. In contrast, it is private cattlemen who have practiced graze-and-burn for decades, particularly in the southern tallgrass prairie region (Fuhlendorf et al. 2006). Grassland conservationists in the central United States have

recently taken interest in the patch-burn graze treatment, as it shows promise of providing private landowners with sufficient economic returns while enhancing biodiversity. Studying the effects of a fourth treatment, grazing with long-term absence of fire, might have generated interesting findings. However, we considered grazing in the absence of fire a non-viable approach to conservation management in the Grand River Grasslands, as grazing by cattle or bison without fire results in conversion of grasslands to woodlands in this region (Anderson 1990). Using sheep or goats to reduce woody plant encroachment was deemed socially non-transferable given the traditional “cowboy culture” of the region.

All 13 pastures were divided into three patches of approximate equal area for purposes of equivalent sampling across treatments; in grazed treatments cattle had open access to all portions of the pastures. Natural topographic features such as waterways, drainages, and ridgetops were used as patch boundaries where possible. From 2007 to 2009, a different patch within each patch-burn graze pasture was burned in spring, except for Jerome pasture, where patch-burn grazing was initiated in 2008. Pastures in the burn-only and graze-and-burn treatments were burned in their entirety in spring 2009, except for Pawnee pasture, which was burned in spring 2008. The fire-return interval was 3 years across all three treatments, so that by late spring 2009, every patch had been burned once during the study except for one unburned patch in Jerome pasture. From 2007 to 2009, pastures receiving either the patch-burn graze or the graze-and-burn treatments were stocked with cattle at 3.4 Animal Unit Months per ha between May 1 and October 1, where standard stocking density for private ranches in the Grand River Grasslands is approximately 5.0 Animal Unit Months per ha.

Butterfly and nectar plant surveys

Butterflies populations were surveyed in 2008 and 2009. Each year, sampling was split into two rounds (June and July) to include the peak emergence periods of most butterfly species that occur in the Grand River Grasslands, including all of the local species of conservation concern. Within each round of sampling, we alternated visits among the three management treatments to minimize temporal bias. So that we could assess the association of plant community composition with butterfly community composition, each 100 m butterfly transect was established parallel to the west side of a Whittaker vegetation sampling plot, with a starting point 10 m west of the north-center coordinate of the plot. Each patch had two randomly-placed Whittaker plots, thus each pasture had six Whittaker plots and six butterfly transects.

We used line-transect distance sampling, because this technique permits one to (1) generate estimates of butterfly density rather than indices of abundance (Powell et al. 2007), (2) correct for differences in butterfly detectability (Brown and Boyce 1998), and (3) attain higher sampling efficiency (Pocewicz et al. 2009) by counting butterflies that occur outside of the more traditional, fixed-width Pollard-walk transects (Pollard and Yates 1993). Line-transect distance sampling requires recording the distance of each study organism from the transect line at the moment the organism is first seen (Buckland et al. 2001). These distances are used to model the declining probability of detecting an organism as its distance from the transect line increases. The resulting mathematical model, known as a detection function, is then be used to develop robust estimates of population density.

During line-transect distance sampling, an observer walked the transect at a steady pace (10 m/min) scanning for butterflies in the 180° field of view spanning from the observer’s left to right. Upon seeing a butterfly, the observer halted, stopped the stopwatch, and

recorded data. Most butterflies were identified to species with the help of binoculars; when this was not possible, the observer would make a brief attempt to net the butterfly and identify it in the field if the butterfly was near the transect line. Distant butterflies of uncertain identity were classified as unknowns; their data were not included in our analyses. When butterflies were within 5 m (on either side) of the transect line, we visually estimated the perpendicular distance between the butterfly's location and the transect. For butterflies ≥ 5 m from the transect line, we used a Bushnell Yardage Pro[®] laser rangefinder to measure the perpendicular distance between the butterfly's location and the transect. These rangefinders measure distances from 5 to 200 m with accuracy of ± 1.0 m (Bushnell Performance Optics [®] 2004). Surveys were conducted between 0930 and 1830 h when temperatures were between 21 and 35 °C, sustained winds were below 16 km/h, and the sun was not obscured by clouds. Nectar source density was sampled during each round of butterfly sampling by a direct count of flowering ramets of each nectar-producing plant species occurring in the 1×100 m² strip on the east side of each butterfly transect line (Reeder et al. 2005).

Vegetation and landscape characteristics

We collected transect-level plant community composition data, and patch level composition and structure data each year from 2006 to 2009. The cover of each plant species was assessed in permanently-marked Whittaker plots (Stohlgren et al. 1995) adjacent to each butterfly transect, as described in McGranahan (2008). From Whittaker plot data, we calculated the proportion of native plant cover in each patch as total native plant cover / (total native plant cover + total exotic plant cover).

Each July we measured vegetation composition and structure in thirty 0.5-m² quadrats that were placed systematically within each patch as described in Pillsbury et al. (2011). Variables measured included vegetation height (obtained by assessing visual obstruction of a Robel pole) (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 *F. arundinacea* [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).

Because landscape characteristics have been shown to affect butterfly species richness and population density (Bergman et al. 2004; Davis et al. 2007; Ockinger and Smith 2006), we used landscape data collected from our study sites in 2006 by Pillsbury et al. (2011). The four landscape characteristics used were percent cover of three land cover types (cropland, grassland, forest) in a 300 m-wide zone around each of our study pastures, and within-pasture edge density, defined as:

$$([\text{wooded perimeter}] + [\text{length of linear features}]) / \text{pasture area.}$$

Landscape data were obtained using remote sensing and ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA), as described in Pillsbury et al. (2011).

Univariate data analysis

Each year, butterfly species richness was calculated for each transect by counting the species seen in either of the two rounds of sampling. Previous analysis has shown that this is an efficient method of estimating species richness in Iowa grasslands (Davis et al. 2008). We used the Conventional Distance Sampling analysis engine of Program Distance 6.0,

release 2 (Thomas et al. 2010) to estimate population density of each native species observed at least 25 times during each year of the study. Density estimates were generated from each transect in each round, then averaged over the two rounds to be used for statistical analyses.

Mixed-effect modelling is an effective method of analyzing data from subsamples (Pinheiro and Bates 2000). We performed repeated measures, mixed-effect model analysis of covariance using the statistical software package SAS version 9.2 (SAS Institute Inc., 2008) to test for effects of treatment and year on butterfly species richness, butterfly density, and nectar plant density (defined as the density of all nectar-producing plant species) after accounting for the influence of pre-treatment vegetation and landscape covariates. For these and other univariate analyses described in this paper, response variables were square-root transformed as needed to normalize the distribution of residuals (Crawley 2007). Values of pre-treatment vegetation covariates were obtained in 2006 at 12 pastures, and in 2007 at Jerome. Before performing analysis of covariance, we reviewed the grassland butterfly literature to select a list of potential variables to serve as covariates. Then, we tested for correlations among those covariates; when correlation coefficients were 0.70 or greater, the variable more likely to be associated with butterfly density (based on our literature review) was retained as a covariate whereas the other was excluded. Pre-treatment covariates entered in all analyses of covariance included: time since fire, proportion of native plant cover, plant species richness, forb cover, legume cover, vegetation height, litter cover, cover of bare ground, within-pasture edge density, and percent cover of the three land cover types between 0 and 300 m from each pasture's perimeter. When analysis of covariance indicated a significant treatment effect, we used differences of least squares means as our multiple comparison procedure.

We sought to compare the associations of pre-treatment habitat variables and butterfly response variables with the associations of post-treatment habitat variables and butterfly response variables. To do this, we performed two mixed model multiple regressions for each response variable using the statistical software package SAS version 9.2 (SAS Institute Inc., 2008). The first tested for the effects of *pre-treatment* vegetation and landscape variables (the same variables used in the analysis of covariance described in the previous paragraph) on response variable data collected during 2008, the first year of post-treatment butterfly density data. The second tested for the effects of *post-treatment* vegetation variables on response variable data in 2008 and 2009. For both sets of tests, we used backward elimination as our model selection procedure, with $\alpha = 0.05$ for retention of each independent variable in the model. This was done in conjunction with review of corrected values of Akaike information criterion (AIC_c). In most instances, backward elimination resulted in the regression model that was also AIC_c best, or within 2.0 of the AIC_c best model.

We performed paired t tests using SPSS version 17.0 (SPSS Inc., 2010) to test for patch-level effects of prescribed burning on population density of *Cercyonis pegala* (common wood nymph), *Speyeria cybele* (great spangled fritillary), *S. idalia* (regal fritillary), and *Danaus plexippus* (monarch) by comparing pre-fire data from 2008 with post-fire data from 2009. The first three are prairie specialists (Vogel et al. 2007), whereas *D. plexippus* is a habitat generalist, but also a species of conservation concern due to its endangered migratory phenomenon in North America and Mexico (Brower and Malcolm 1991). To be included in this analysis, a patch had to meet two criteria: (1) the patch had been burned in early spring 2009 and not in 2008 (thus, excluding data from Pawnee Prairie from the analysis); and (2) at least one individual of the focal species was observed in the patch during 2008 or 2009.

Lastly, we used SAS version 9.2 (SAS Institute Inc., 2008) to perform repeated measures analysis of variance that tested for effects of treatment and year on five habitat variables. These included two variables we had expected would be important components of butterfly habitat (proportion native cover and vegetation height) as well as three variables found post hoc to be important predictors of butterfly density. Data were from 2006 to 2009, thus data from Jerome pasture were omitted ($n = 12$).

Multivariate data analysis

We used nonmetric multidimensional scaling (NMDS) to produce two ordination plots, with the first visually describing patch-level patterns of plant community composition, and the second patch-level patterns of butterfly community composition. 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)]. Bray-Curtis distance was used as the measure of dissimilarity among grassland patches, and all patch-level samples for each treatment were connected via a spider plot.

Data included in the plant community ordination consisted of patch-level values of percent canopy cover of the following plant functional groups: warm-season grasses, cool-season grasses, non-leguminous forbs, leguminous forbs, and *F. arundinacea*. Data from 2008 to 2009 were plotted together in the same ordination (note that data were not averaged across years, but combined to create one data set). We tested for correlations between the plant community ordination and three vegetation structure variables (vegetation height, cover of bare ground and litter).

Butterfly community ordination used patch-level abundance data from all butterfly species observed in 2008 and 2009. As with the plant community ordination, data from the 2 years were combined and plotted together in the same ordination. Subsequently, to assess the influence of vegetation variables on butterfly community composition, we tested for correlations between the butterfly ordination and data collected on 12 vegetation variables in 2008 and 2009: proportion native vegetation, plant species richness, nectar plant density, 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 *F. arundinacea*. Vegetation variables significantly correlated with the ordination at $\alpha \leq 0.05$ were plotted as vectors.

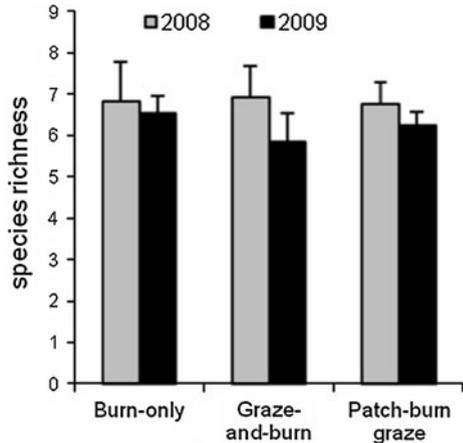
Results

Butterfly responses to treatment and year

We observed 2842 individuals representing 36 butterfly species across 2008 and 2009 (Appendices Tables 3, 4), with butterfly nomenclature following that of (Opler et al. 2012). The two most-commonly observed butterflies were habitat generalists: *Cupido comyntas* (eastern tailed-blue) with 702 individuals and *Colias philodice* (clouded sulphur) with 329. However, two prairie specialists ranked third and fourth in number of individuals observed: *S. idalia* with 296 and *C. pegala* with 287.

Butterfly species richness was not affected by treatment (Fig. 2). Eight species were observed at least 25 times each year, and thus were the response variables for analyses of

Fig. 2 Butterfly species richness at the transect level compared among treatments and years. Values are response variable averaged across pastures \pm standard error



covariance. Four of those eight species did respond to treatments (Fig. 3); three of the four species responded to an interaction of treatment and year. In 2009 only, burn-only pastures had higher densities of *C. pegala* (a habitat specialist) and *D. plexippus* (a habitat generalist) than either graze-and-burn or patch-burn graze pastures (*C. pegala*: $p = 0.004$ and 0.002 respectively; *D. plexippus*: $p = 0.018$ and 0.014 respectively) (Fig. 3a, b). Density of another habitat generalist (*Cupido comyntas*) also exhibited a treatment by year interaction, with greater density in patch-burn graze pastures than burn-only pastures in 2008 ($p = 0.028$) but no differences in 2009. Over the 2 years, density of *S. idalia* (a habitat specialist) was greater in burn-only pastures than graze-and-burn ($p = 0.040$) and patch-burn graze ($p = 0.011$) pastures (Fig. 3a).

All butterfly response variables except one (*Phyciodes tharos* density) were associated with at least one pre-treatment variable (Table 1). Conversely, all pre-treatment variables but two (forb cover and plant species richness) were associated with at least one butterfly response variable. Proportion native cover and grass cover within 300 m of the perimeter were particularly important. Proportion native cover was positively associated with butterfly species richness, *C. pegala* density, and *D. plexippus* density. Grass cover within 300 m of each pasture was positively associated with butterfly species richness, and density of two habitat-composition specialists (*S. cybele* and *S. idalia*) (Table 1).

All post-treatment vegetation variables except one (legume cover) were associated with at least one butterfly response variable (Table 2). Vegetation height was positively associated with butterfly species richness and the density of four species (*C. pegala*, *D. plexippus*, *S. cybele* and *S. idalia*). Proportion native cover was positively associated with *C. pegala* density, and negatively associated with density of two habitat generalists (*C. eurytheme* and *C. philodice*). Litter cover was negatively associated with two habitat generalists (*C. philodice* and *C. comyntas*) and one prairie specialist (*S. cybele*).

Burning did not have the expected negative effects on prairie specialists; post-fire density of *C. pegala* ($p = 0.04$) and *S. cybele* ($p = 0.001$) was higher than pre-fire density, and *S. idalia* density did not differ significantly from pre-fire density (Fig. 4). One pasture (Pawnee) was burned in 2008 rather than 2009, thus omitted from the analysis, but its post-fire density of *S. idalia* was 34 % higher than pre-fire. *Danaus plexippus*, which uses a great variety of habitats in the New World, appears to have responded positively to fire: post-fire density of *D. plexippus* was about twice that of the pre-fire summer ($p = 0.001$).

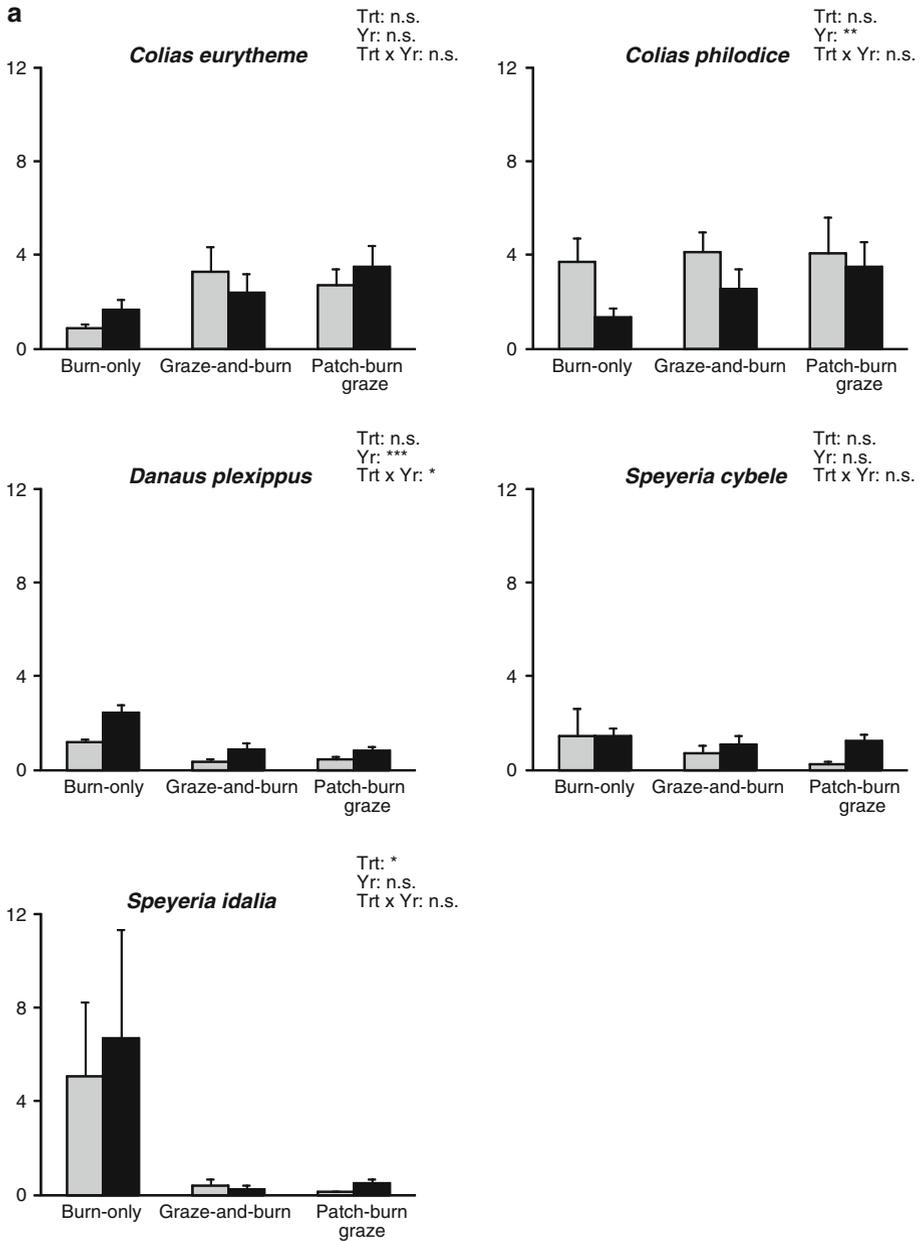


Fig. 3 Butterfly population density compared among treatments and years. Species are grouped into **a** low (<10 butterflies ha⁻¹), **b** medium (<50 butterflies ha⁻¹), and **c** high density (<150 butterflies ha⁻¹) categories. *Gray bars* denote 2008 means and *black bars* denote 2009 means. *Error bars* indicate standard errors among pastures managed with the same treatment. Asterisks indicate significant differences: **p* < 0.05, ***p* < 0.01, ****p* ≤ 0.001. *Trt* treatment, *Yr* year, *Trt* × *Yr* treatment by year interaction

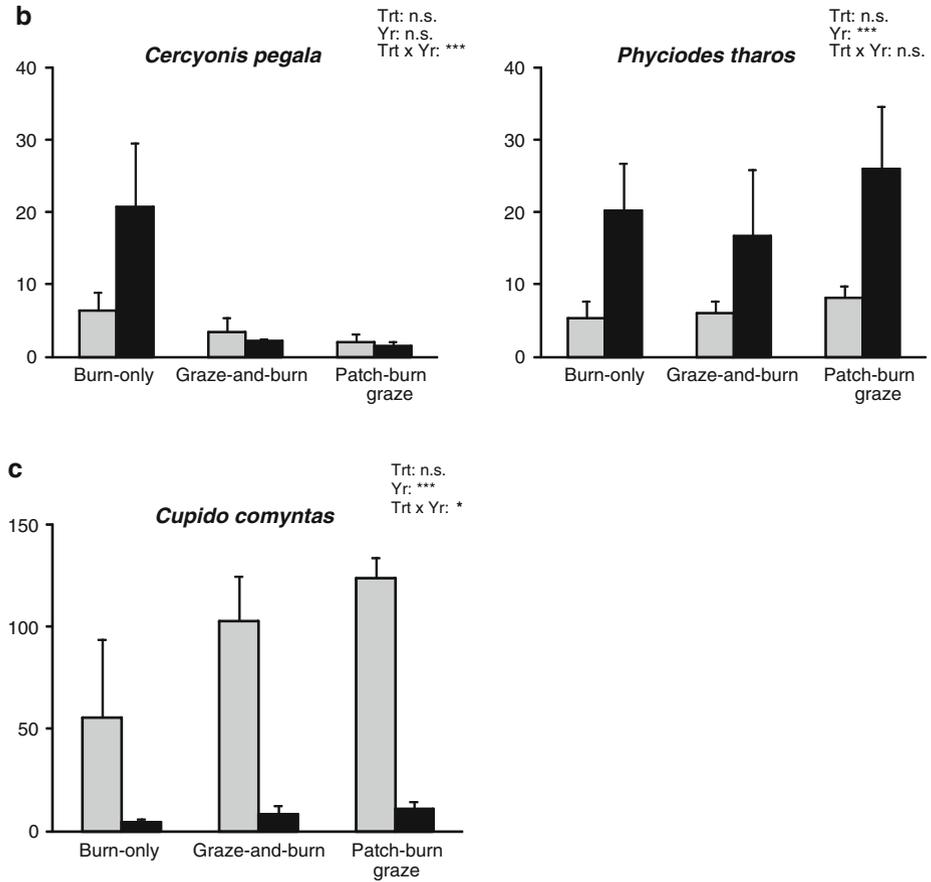


Fig. 3 continued

Nectar plant flowering ramet density

We observed 88 species of nectar sources across 2008 and 2009, with plant nomenclature following that of USDA, NRCS (2012). The two most abundant nectar sources [*Trifolium repens* (white clover) and *Lotus corniculatus* (bird’s-foot trefoil)] are exotic species, and comprised 57 % of all flowering ramets. The 10 most abundant nectar sources represented 95.5 % of the cumulative total (Appendix Table 5). Some nectar sources [*Echinacea pallida* (pale purple coneflower), *Asclepias tuberosa* (butterfly milkweed), *Asclepias syriaca* (common milkweed), and *Liatris pycnostachya* (prairie blazing star)] preferred by prairie-specialist butterflies [Moranz 2010] occurred at very low densities (an average of <1 flowering ramet per 100 m²). Total nectar plant density (Fig. 5) was affected by the interaction of treatment and year ($p = 0.014$), with patch-burn graze pastures having significantly higher flowering ramet densities than burn-only pastures in 2009, but not in 2008. Pre-treatment values of proportion native cover and time since fire were negatively associated with nectar plant density (Table 1).

Table 1 Results from mixed model multiple regression, using butterfly response variables from 2008 and pre-treatment habitat and landscape data from 2006

	Butterfly species richness	<i>Cercyonis pegala</i>	<i>Colias eurytheme</i>	<i>Colias philodice</i>	<i>Cupido comyntas</i>	<i>Danaus plexippus</i>	<i>Phyciodes tharos</i>	<i>Speyeria cybele</i>	<i>Speyeria idalia</i>	Nectar plant density
Proportion native cover '06	+****	+***				+*				-**
Forb cover '06										
Plant species richness '06			+*							
Legume cover '06	+***				+***					
Bare ground cover '06										
Litter cover '06	+*		+***							
Vegetation height '06							-*			
Time since fire '06							-*			-*
Within-pasture edge density							-*			
Crop cover within 300 m	+***			+*						
Grass cover within 300 m	+***							+*		+***
Tree cover within 300 m	+***								-*	

Asterisks indicate significant predictors: * $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$. Plus and minus signs indicate whether the relationship was positive or negative

Table 2 Results from mixed model multiple regression, using butterfly response variables and habitat data from 2008 and 2009

	Butterfly species richness	<i>Cercyonis pegala</i>	<i>Colias eurytheme</i>	<i>Colias philodice</i>	<i>Cupido comyntas</i>	<i>Danaus plexippus</i>	<i>Phyciodes tharos</i>	<i>Speyeria cybele</i>	<i>Speyeria idalia</i>	Nectar plant density
Proportion native cover	+*	-***	-**	-**						
Forb cover			-*	-*	-*					-*
Plant species richness								+*	+*	
Legume cover						+***				+***
Bare ground cover				-*						-*
Litter cover				-**	-*			-**		
Vegetation height	+**	+***				+***		+***	+***	
Time since fire				-*					-*	-*

Asterisks indicate significant predictors: * $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$. Plus and minus signs indicate whether the relationship was positive or negative

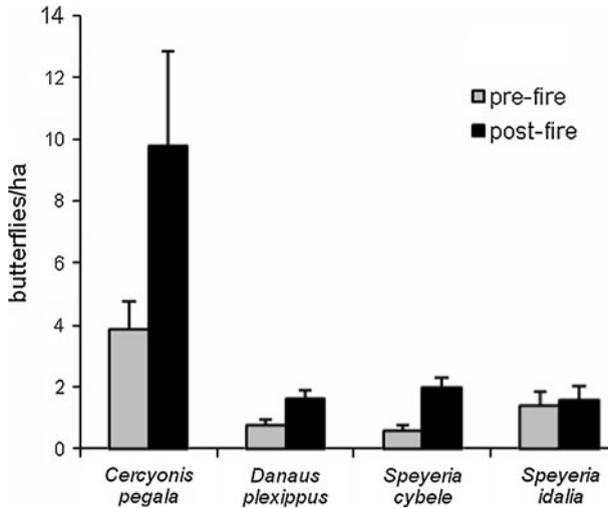
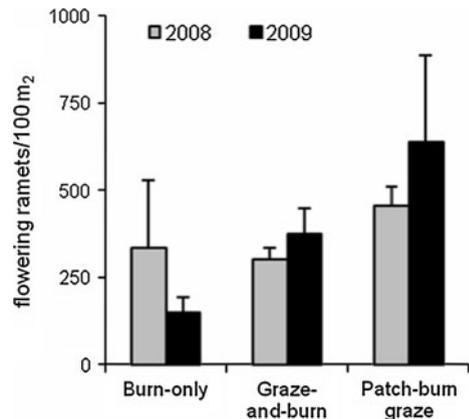


Fig. 4 Comparison of pre-fire and post-fire mean density of *Cercyonis pegala*, *Danaus plexippus*, and *Speyeria idalia*. Values are pasture-level mean \pm standard error

Fig. 5 Nectar plant flowering ramet density compared among treatments and years. Values are pasture-level mean \pm standard error



Vegetation responses to treatment and year

Implementation of treatments from 2007 to 2009 affected two habitat structure variables: cover of bare ground and vegetation height. Though cover of bare ground did not differ among treatments, cover of bare ground increased in 2009 ($p = 0.007$), the year that all graze-and-burn pastures and three of four burn-only pastures were burned (as well as a patch within each patch-burn graze pasture). In addition to exhibiting a strong year effect ($p < 0.001$), vegetation height responded to an interaction of treatment and year ($p = 0.034$), with burn-only pastures having higher vegetation than graze-and-burn pastures and patch-burn graze pastures in 2008 and 2009 but not in 2006 or 2007 (Fig. 6). In the pre-treatment year (2006), proportion native cover was greater in burn-only pastures

Fig. 6 Vegetation height compared among treatments and years. Values are pasture-level mean \pm standard error

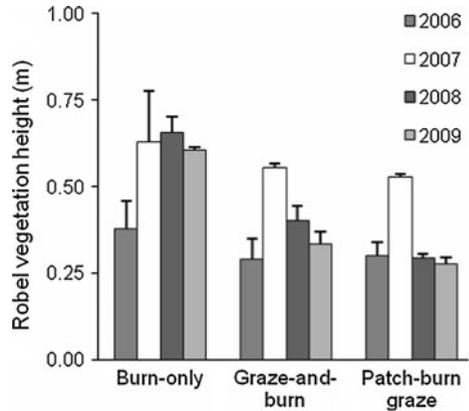
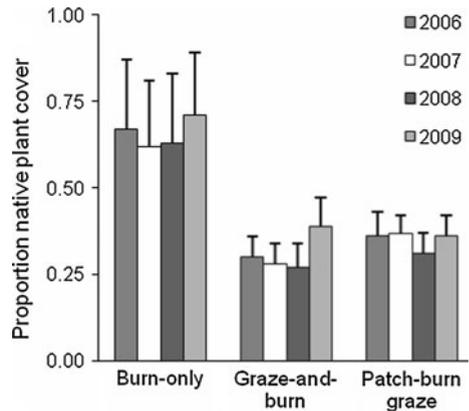


Fig. 7 Proportion native plant cover compared among treatments and years. Values are pasture-level mean \pm standard error



than in the other treatments ($p < 0.001$), even though variance was high (proportion native cover ranged from 0.14 to 0.99 in burn-only pastures). This pattern remained the same through 2009, implying that it was not altered by treatment implementation (Fig. 7). Similarly, forb cover was higher in burn-only pastures than in the two grazed treatments ($p < 0.001$). Forb cover also showed dramatic annual variation ($p < 0.001$). Lastly, legume cover showed the opposite pattern, as it was lower in burn-only pastures than in graze-and-burn or patch-burn graze pastures overall ($p < 0.001$), and during each year of the study, including the pre-treatment year.

Plant and butterfly community structure

Ordination of both plant functional group and butterfly community data revealed that the two grazing treatments hosted similar plant and butterfly communities, and that these biotic communities differed from those that received the burn-only treatment. Grasslands managed with either the graze-and-burn or patch-burn graze treatments were characterized by short vegetation, low cover of warm-season grasses and litter, and high cover of legumes and *Festuca arundinacea* (Fig. 8). Butterfly community composition in pastures managed

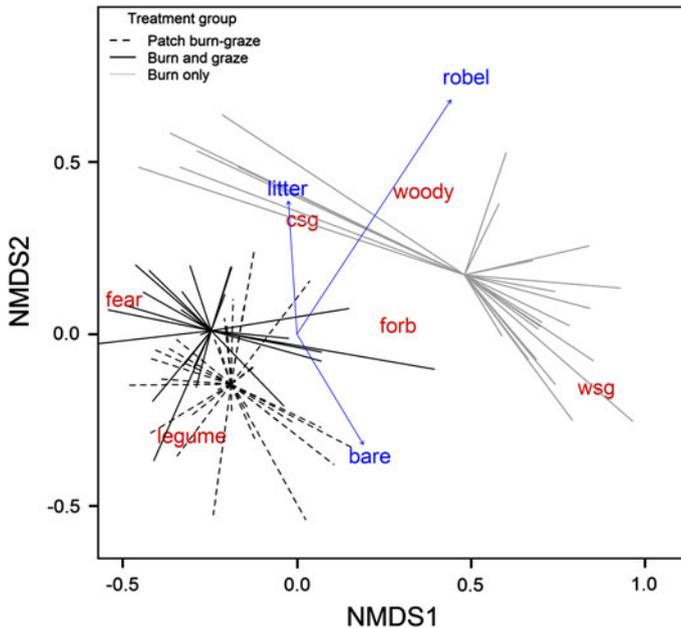


Fig. 8 Plant community ordination plot showing the results of NMDS analysis (NMDS) of plant functional group cover data from 2008 to 2009. Each treatment group is represented by its own spider plot, in which the terminus of each ray represents the position of a grassland patch in plant community ordination space, and the centroid represents the mean position of patches in that treatment group. The position of each plant functional group in ordination space is indicated by the following labels: *csg* cool season grasses, *fear* *Festuca arundinacea*, *forb* forbs, *legume* legumes, *woody* woody plants, and *wsg* warm season grasses. Three vegetation structure variables that are correlated with the ordination appear as vectors to demonstrate their relationships with plant community composition: *bare* bare ground cover, *litter* litter cover, and *robel* vegetation height

with either of the two grazing treatments was characterized by habitat generalists (*C. philodice*, *C. eurytheme*, *Pieris rapae*, *P. themistocles*, *C. comyntas*, and *P. polyxenes*) (Fig 9). Burn-only pastures were characterized by two prairie specialists (*S. idalia* and *C. pegala*) and one habitat generalist (*D. plexippus*). Three of 12 vegetation variables from 2008/2009 were significantly correlated with the butterfly ordination: proportion native plant cover ($r^2 = 0.58$, $p = 0.02$), vegetation height ($r^2 = 0.52$, $p = 0.007$), and legume cover ($r^2 = 0.41$, $p = 0.03$). High values of proportion native cover and vegetation height were characteristic of the burn-only treatment, whereas high values of legume cover were characteristic of the two grazed treatments.

Discussion

Heterogeneous application of fire in grazed pastures: surprising results

We predicted that patch-burn grazing, when compared with homogeneity-based disturbance regimes (i.e. whole site burns), would enhance butterfly species richness and density of prairie specialist butterfly species by reducing fire-induced mortality and increasing

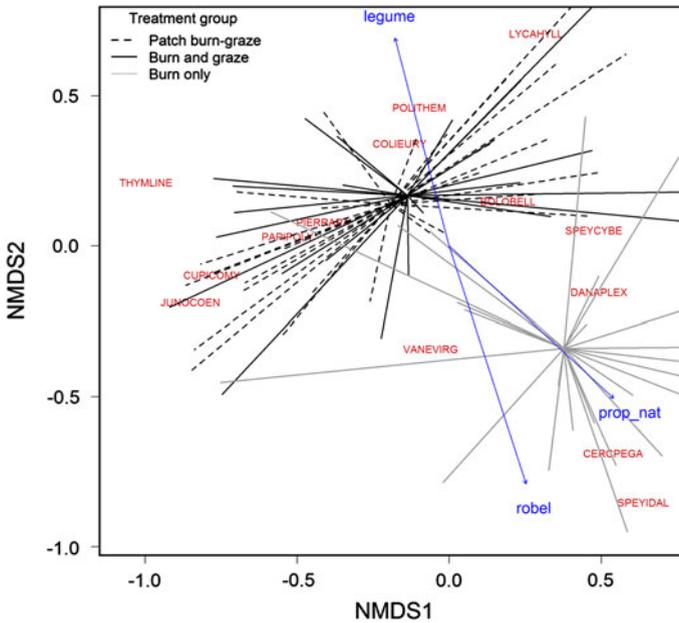


Fig. 9 Butterfly community ordination plot showing the results of NMDS analysis (NMDS) of butterfly density data from 2008 to 2009. Each treatment group is represented by its own spider plot, in which the terminus of each ray represents the position in ordination space of the butterfly community from a grassland patch, and the centroid represents the mean position of patches in that treatment group. The position of each butterfly species in ordination space is indicated by an *eight-letter abbreviation* of genus and species: BoloBell (*Boloria bellona*), CercPega (*Cercyonis pegala*), CupiComy (*Cupido comyntas*), DanaPlex (*Danaus plexippus*), JunoCoen (*Junonia coenia*), LycaHyll (*Lycaena hyllus*), PapiPoly (*Papilio polyxenes*), PierRapa (*Pieris rapae*), PoliThem (*Polites themistocles*), SpeyCybe (*Speyeria cybele*), SpeyIdal (*Speyeria idalia*), ThymLine (*Thymelicus lineola*), and VaneVirg (*Vanessa virginiensis*). Labels for three species (*Colias eurytheme*, *C. philodice* and *Phycodes tharos*) are omitted; all three are clustered near the centroids of the two grazing treatments. Three vegetation variables that are correlated with the ordination appear as vectors to demonstrate their relationships with butterfly community composition: legume (legume cover), prop_nat (proportion native plant cover) and robel (vegetation height)

habitat heterogeneity. Instead, we failed to find evidence of treatment effect on butterfly species richness, and found that two prairie specialists occurred at higher densities in burn-only pastures. We cannot rule out the possibility of direct, negative effects of grazing; while foraging, cattle may incidentally consume butterfly eggs, larvae and pupae. However, we hypothesize that the main causes of our surprising findings are: (1) cattle grazing reduced habitat quality for some species by reducing vegetation height, (2) historic variation in vegetation composition and structure was even more important than anticipated, (3) fire was less harmful than predicted, and (4) patch-burn grazing did not generate the anticipated levels of structural heterogeneity (Pillsbury et al. 2011; McGranahan et al. 2012).

To parse out the influences of treatments and historic pasture conditions, we review findings on the two most abundant prairie specialists, *C. pegala* and *S. idalia*. Both species had greater density in the burn-only pastures. A likely mechanism for this treatment effect is that burning without grazing allows burn-only pastures to develop denser, taller swards of vegetation. Both species showed a positive association with vegetation height. This latter association is corroborated by findings from a study in Minnesota grasslands

(Reeder et al. 2005). However, of the two species, we suspect that *C. pegala* density was influenced more by treatment implementation, as it appears to be more responsive to vegetation structure than to vegetation composition. *Cercyonis pegala* oviposits on a variety of grasses (Heitzman and Heitzman 2006); there is little evidence that host plant distribution is structuring the distribution of this species in our grasslands. Additionally, at our study sites, *C. pegala* appears to spend much of the day hiding in dense vegetation, and typically emerges from this vegetation for only a few seconds at a time. Finally, we point out that the effect of treatment on *C. pegala* density only became significant in 2009, after 3 years of treatment implementation, which counters the argument that pre-treatment conditions generated differences among treatment groups.

Although our finding that grazed pastures had lower densities of *S. idalia* than ungrazed pastures is corroborated by recent findings by Moranz (2010) in southern Missouri, we have reasons to believe that historic factors played a dominant role in determining the distribution and density of *S. idalia* at our study pastures. First, although butterfly density was not measured in 2007, relative abundance of *S. idalia* varied greatly among treatments even in that first year of treatment implementation. When compared with findings from southern Missouri (Moranz 2010), we doubt that such great variation in *S. idalia* relative abundance would be generated so quickly simply by implementation of grazing. Second, *S. idalia* density varied greatly among pastures in general, and variation was extreme among burn-only pastures. This reflected the pre-treatment and post-treatment variation in cover of *Viola* spp., the obligate host plants of *S. idalia*: the pasture with much greater *Viola* cover than the others had much higher densities of *S. idalia* (Moranz et al. unpublished data).

We suspect that excessive cattle stocking rate was to blame for the failure of patch-burn grazing to generate the anticipated levels of structural heterogeneity. Due to contractual obligations to cattle ranchers, grazed pastures were stocked at a higher rate than we would have preferred. Cattle chose to venture throughout the pasture to forage (instead of concentrating their time in the recently burned patch), and biomass removal differed little among patches.

Responses to fire

Our grassland management treatments provided us with the opportunity to examine responses of butterflies to fire, and the results surprised us. Two prairie specialists (*C. pegala* and *S. idalia*) we studied overwinter aboveground in prairie as larvae (Scott 1986; Kopper et al. 2001). We presumed that our March prescribed burns would cause greater mortality of these species in the larval stage, either directly by incineration, or indirectly from combustion of litter, which can protect larvae from desiccation (Vogel et al. 2007). Because of this, we expected these species to be less abundant the summer after fire. However, we found no evidence of a negative effect of fire. Instead, there were higher densities of *C. pegala* in pastures that had been burned that year in comparison to those that had not been burned, as was true for *D. plexippus*, a migratory habitat generalist. Perusal of data for *D. plexippus* show that its post-fire increase in density can be easily explained as a year effect, as density of this species increased in patch-burn grazed pastures, which did not see a change in fire coverage from 2008 to 2009. However, findings on *C. pegala* and *S. idalia* are not strongly confounded with a year effect, and contradict previous studies that demonstrated some prairie specialists take 3–5 years to recover after fire (Swengel 1996; Vogel et al. 2007, 2010). Landscape

context can mediate effects of fire on prairie insect species responses (Reed 1997; Panzer 2003; Moranz 2010), as can variation in fire spread and completeness (Reed 1997); both of these issues may have contributed to our unexpected findings. We suspect that population densities of these butterfly species remained high after fire because (1) the pastures reside within a larger grassland landscape, allowing for recolonization of recently-burned pastures from neighboring unburned pastures; and (2) some fires failed to consume all available fuel within their prescribed burn units, leaving substantial unburned refugia in 2009 (Ryan Harr, pers. comm.). Eight of the 13 experimental pastures were burned in their entirety during 2008 or 2009, but unburned grasslands occurred <0.5 km from the boundaries of all eight; this is well within the maximal lifetime dispersal distance for many butterfly species (Schneider 2003; Auckland et al. 2004). Landscape context clearly played a role in mitigating the effects of burning at Pawnee pasture in 2008. Although the burn there was quite complete, the burn unit made up just 11 % of the Pawnee Prairie Preserve's 190 ha, and was surrounded on all sides by grassland that was not burned that year. Given the completeness of the burn, and the high density of *C. pegala* and *S. idalia* only a few months after the burn, we conclude that the burn unit was recolonized by butterflies from the surrounding unburned prairie. In contrast, though the Lee Trail pasture was burned in March 2009, it was bordered primarily by habitat unsuitable for *S. idalia*. Contrary to our intentions, that fire was incomplete: 30–50 patches of vegetation (some as large as 3 m²) within the burn unit failed to burn. On June 12, 2009, our avian research team flushed 10 freshly-eclosed *S. idalia* butterflies at this pasture. These butterflies could not have flown in from nearby grasslands, as their wet, unhardened wings made them unable to fly more than 5 m, providing exciting evidence that patchy, incomplete burns can allow *S. idalia* to avoid extirpation.

Effects of nectar availability on butterfly populations

Although nectar availability can affect population densities of habitat specialist butterflies (Rudolph et al. 2006; Schultz and Dlugosch 1999), our study did not demonstrate this, as total nectar plant density was not correlated with the butterfly ordination. In retrospect, our expectation that total nectar plant density would be positively correlated with butterfly density was misguided, as this variable combined data on 88 nectar sources that vary in their usefulness to prairie butterflies. Unfortunately, in most transects, values of total nectar plant density were dominated by the abundance of *Lotus corniculatus* and *Trifolium repens*, both of which are small-flowered, exotic plants that were seldom utilized by large butterflies such as *S. idalia*. Some native nectar sources in the Grand River Grasslands (including *Asclepias tuberosa*, *Echinacea pallida* and *Liatris pycnostachya*) have been shown to be highly preferred by prairie specialist butterflies in southwestern Missouri grasslands (Moranz 2010), and all were utilized by butterflies in our study. However, average densities were less than 0.3 flowering ramets/100 m², and more than 80 % of our nectar sampling transects had no flowering ramets of these species. These data provide a stark contrast with data from grassland pastures in southwestern Missouri, where *E. pallida* density reached 13.2 flowering ramets/100 m², and *L. pycnostachya* densities averaged 2.0 flowering ramets/100 m² (Moranz 2010). Only one pasture had similarly high densities of preferred nectar sources, and we hypothesize that this fact (in addition to the high density of *S. idalia*'s host plants at that pasture) helps explain why densities of *S. idalia* were far greater there than at the other 12 pastures.

Conclusions

Two prairie specialist butterflies (*C. pegala* and *S. idalia*) thrived in pastures managed with the burn-only treatment. We suspect that the burn-only treatment is compatible with the conservation of these and perhaps other prairie specialist butterflies, but only in landscapes where application of fire is spatially and temporally heterogeneous, allowing butterflies from grasslands burned in past years to recolonize recently burned sites. On the other hand, implementation of patch-burn grazing does not appear to have enhanced grassland butterfly communities. In part, this was due to the failure of patch-burn grazing to generate structural heterogeneity, likely due to excessive stocking of cattle. Stocking rate is perhaps the most important variable to consider when planning grazing that is conducive to grassland butterfly conservation (WallisDeVries et al. 2007). In 2010, stocking rate was reduced from high to moderate in patch-burn graze pastures of the Grand River Grasslands. We predict this change will increase structural heterogeneity within 3 years, which in turn may increase pasture-level butterfly species richness. However, our optimism is tempered by the fact that more species responded to vegetation and landscape characteristics that were legacies of historic land uses such as intensive grazing and cultivation. Restoration of pre-Columbian disturbance regimes might prove insufficient to undo the legacies of past land use on altered plant community composition. In such cases, direct seeding of preferred host and nectar plants might also be necessary to restore habitat conditions required by butterfly species that respond more to plant community composition than to habitat structure.

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Appendix

See Appendix Tables 3, 4 and 5.

Table 3 Abundance of Lepidoptera species in 2008 at 12 pastures in Ringgold County, Iowa, and 1 pasture in Harrison County, Missouri

Scientific name	Common name	Habitat specificity	Patch-Burn Graze						Graze-And-Burn						Burn-Only			Total					
			JER	KLN	PYN	PYS	RIS	GIL	LTR	PYW	STE	KLT	PAW	RCH	RIN								
<i>Atalopedes campestris</i>	Sachem	G									1									1			
<i>Boloria bellona</i>	Meadow fritillary	G		1									3					2		1	7		
<i>Celastrina ladon</i>	Summer azure	G																6			6		
<i>Cercyonis pegala</i>	Common wood-nymph	P	12		2	4	1	5	17	4								7	26	8	7	93	
<i>Colias cesonia</i>	Southern degface	G	1																			1	
<i>Colias eurytheme</i>	Orange sulphur	G	13	10	3	4	5	4	13	3			14					2	1	3	3	78	
<i>Colias philodice</i>	Clouded sulphur	G	8	40	10	7	14	9	22	12			20					17	16	22	3	200	
<i>Cupido comyntas</i>	Eastern tailed-blue	G	58	76	35	64	79	70	34	38			75					73	21	8	8	639	
<i>Danaus plexippus</i>	Monarch	G	3	4	2	2		3	2				2					5	7	6	6	42	
<i>Epargyreus clarus</i>	Silver-spotted skipper	G							1										4			1	6
<i>Euphyes vestris</i>	Dun skipper	G	2						1														3
<i>Junonia coenia</i>	Common buckeye	G	3	1		3	1	8	1				4					1				22	
<i>Limenitis archippus</i>	Viceroy	G																					1
<i>Lycæna dione</i>	Gray copper	G			2																		3
<i>Lycæna hyllus</i>	Bronze copper	G											1										1
<i>Megisto cymela</i>	Little wood-satyr	W																					1
<i>Papilio cressphontes</i>	Giant swallowtail	W	1								2								1				4
<i>Papilio glaucus</i>	Eastern tiger swallowtail	W		1				1															4
<i>Papilio polyxenes</i>	Black swallowtail	G	3	6	16	8	1	3	6	11			3					9	4	1	4	75	
<i>Phyciodes tharos</i>	Pearl crescent	G	7	2	8	5	5	4	7	1			4					8	3	1	2	57	
<i>Pieris rapae</i>	Cabbage white	G	18	26		2	15	20	7	2			13					4	3	15	2	127	
<i>Polites origenes</i>	Crossline skipper	G	2										2					1				5	
<i>Polites themistocles</i>	Tawny-edged skipper	G	4	2	1		2	2		1			11					2			1	26	
<i>Pontia protodice</i>	Checkered white	G																	2				2

Table 3 continued

Scientific name	Common name	Habitat specificity	Patch-Burn Graze			Graze-And-Burn			Burn-Only			Total				
			JER	CLN	PYN	PYS	RIS	GIL	LTR	PYW	STE		KLT	PAW	RCH	RIN
<i>Pyrgus communis</i>	Common checkered-skipper	G								1					1	
<i>Satyrus titus</i>	Coral hairstreak	G												5	5	
<i>Speyeria cybele</i>	Great spangled fritillary	P	2			1	1	4	3		1	1	14		1	27
<i>Speyeria idalia</i>	Regal fritillary	P			1	1	1	6	2		6	70	2	22	111	
<i>Thymelicus lineola</i>	European skipper	G			1	1	8	1	1	30	1		1		43	
<i>Vanessa atalanta</i>	Red admiral	G	1											1	2	
<i>Vanessa cardui</i>	Painted lady	G			1		3								4	
<i>Vanessa virginiensis</i>	American lady	G			3			2					1		2	8
Total abundance			145	177	80	103	132	147	130	79	183	140	186	74	67	1643
Species richness			16	14	10	11	14	14	15	11	14	13	19	14	13	32

Species are categorized as prairie specialists (P), habitat generalists (G), and woodland specialists (W) (Vogel et al. 2007). Three-letter pasture codes correspond to pasture names: Gilleland (GIL), Jerome (JER), Kellerton North (KLN), Kellerton Tauke (KLT), Lee Trail Road (LTR), Pawnee (PAW), Pyland North (PYN), Pyland South (PYS), Pyland West (PYW), Richardson (RCH), Ringgold North (RIN), Ringgold South (RIS), and Sterner (STE). Pastures are grouped by treatment type. Abundances are summed across two rounds of surveys during June-August. Butterfly nomenclature follows that of Opler et al. (2012)

Table 4 Abundance of Lepidoptera species in 2009 at 12 pastures in Ringgold County, Iowa, and 1 pasture in Harrison County, Missouri

Scientific name	Common name	Habitat specificity	Patch-Burn Graze						Graze-And-Burn						Burn-Only						Total								
			JER		KLN		PYN		PYS		RIS		GIL		LTR		PYW		STE			KLT		PAW		RCH		RIN	
<i>Boloria bellona</i>	Meadow fritillary	G	1				7	2																					18
<i>Celastrina neglecta</i>	Summer azure	G			1																								3
<i>Cercyonis pegala</i>	Common wood nymph	P	7		1		4	2	5	4	4	2	4	2	4	2	4	2	4	2	4	2	4	2	4	2	4	2	194
<i>Chlosyne gorgone</i>	Gorgone checkerspot	G			3																								3
<i>Colias eurytheme</i>	Orange sulphur	G	16		14		4	5	6	8	8	9	7	4	5	1	87												
<i>Colias philodice</i>	Clouded sulphur	G	29		12		3	13	11	11	15	13	5	9	6	2	129												
<i>Cupido comyntas</i>	Eastern tailed blue	G	1		15		3	6	5	10	2	7	1	6	6	1	63												
<i>Danaus plexippus</i>	Monarch	G	2		7		2	6	3	3	4	6	7	14	10	12	16	89											
<i>Epargyreus clarus</i>	Silver-spotted skipper	G									1						1												
<i>Euptoieta claudia</i>	Variagated fritillary	G																										1	
<i>Junonia coenia</i>	Common buckeye	G									1																	2	
<i>Limenitis arthemis</i>	Red-spotted purple	G																										2	
<i>Lycæna dione</i>	Gray copper	G																										4	
<i>Lycæna hyllus</i>	Bronze copper	G	3		3		1	2																				12	
<i>Papilio glaucus</i>	Eastern tiger swallowtail	W																										2	
<i>Papilio polyxenes</i>	Black swallowtail	G	1		1																							9	
<i>Phycitodes tharos</i>	Pearl crescent	G	6		34		30	9	9	6	4	5	29	5	25	7	19	188											
<i>Pieris rapae</i>	Cabbage white	G	16		3		2	4	4	5	4	5	8	2	1	10	1	65											
<i>Polites peckius</i>	Peck's skipper	G																										5	
<i>Polites themistocles</i>	Tawny-edged skipper	G	1		20		9																					40	
<i>Sayrium titus</i>	Coral hairstreak	G																										1	
<i>Speyeria cybele</i>	Great spangled fritillary	P	4		1		2	4	6	3	4	5	5	3	2	6	45												
<i>Speyeria idalia</i>	Regal fritillary	P			5			4	3	3	2	3	15	137	3	13	185												
<i>Strymon melinus</i>	Gray hairstreak	G																										1	

Table 4 continued

Scientific name	Common name	Habitat specificity	Patch-Burn			Graze			Graze-And-Burn			Burn-Only			Total	
			JER	KLN	PYN	PYS	RIS	GIL	LTR	PYW	STE	KLT	PAW	RCH		RIN
<i>Thymelicus lineola</i>	European skipper	G					1								1	
<i>Vanessa atalanta</i>	Red admiral	G					1			1					3	
<i>Vanessa cardui</i>	Painted lady	G			1										1	
<i>Vanessa virginiensis</i>	American lady	G													2	
Total abundance			94	125	67	67	53	52	33	60	93	62	243	144	103	1196
Species richness			12	13	14	12	11	10	11	13	14	12	11	12	14	28

Species are categorized as prairie specialists (P), habitat generalists (G), and woodland specialists (W) (Vogel et al. 2007). Three-letter pasture codes correspond to pasture names: Gilleland (GIL), Jerome (JER), Kellerton North (KLN), Kellerton Tauke (KLT), Lee Trail Road (LTR), Pawnee (PAW), Pyland North (PYN), Pyland South (PYS), Pyland West (PYW), Richardson (RCH), Ringgold North (RIN), Ringgold South (RIS), and Sterner (STE). Pastures are grouped by treatment type. Abundances are summed across two rounds of surveys during June-August. Butterfly nomenclature follows that of Opler et al. (2012)

Table 5 Nectar sources ranked by the density of flowering ramets across 2008 and 2009 averaged across 13 pastures in the Grand River Grasslands

Rank	Nectar source	Density (flowering ramets/100 m ²)	Percent of total	Cumulative percent of total
1	<i>Trifolium repens</i>	120.7	31.1	31.1
2	<i>Lotus corniculatus</i>	100.8	26.0	57.1
3	<i>Erigeron strigosus</i>	38.2	9.9	67.0
4	<i>Pycnanthemum tenuifolium</i>	31.2	8.1	75.0
5	<i>Trifolium pratense</i>	27.1	7.0	82.0
6	<i>Leucanthemum vulgare</i>	17.0	4.4	86.4
7	<i>Monarda fistulosa</i>	14.7	3.8	90.2
8	<i>Rudbeckia hirta</i>	9.9	2.5	92.7
9	<i>Daucus carota</i>	5.9	1.5	94.2
10	<i>Achillea millefolium</i>	5.0	1.3	95.5
11	<i>Dianthus armeria</i>	2.0	0.5	96.0
12	<i>Teucrium canadense</i>	1.9	0.5	96.5
13	<i>Chamaecrista fasciculata</i>	1.5	0.4	96.9
14	<i>Ratibida pinnata</i>	1.3	0.3	97.2
15	<i>Melilotus officinalis</i>	1.0	0.3	97.5
16	<i>Potentilla arguta</i>	0.9	0.2	97.7
17	<i>Solanum carolinense</i>	0.7	0.2	97.9
18	<i>Ruellia humilis</i>	0.7	0.2	98.1
19	<i>Prunella vulgaris</i>	0.6	0.2	98.3
20	<i>Pycnanthemum verticillatum</i>	0.5	0.1	98.4
21	<i>Verbena stricta</i>	0.5	0.1	98.5
22	<i>Galium sp.</i>	0.5	0.1	98.6
23	<i>Pastinaca sativa</i>	0.4	0.1	98.7
24	<i>Dalea purpurea</i>	0.4	0.1	98.8
25	unknown Rubiaceae, white	0.4	0.1	98.8
26	<i>Lythrum alatum</i>	0.3	0.1	98.9
27	<i>Asclepias tuberosa</i>	0.3	0.1	99.0
28	<i>Lobelia spicata</i>	0.3	0.1	99.1
29	<i>Veronicastrum virginicum</i>	0.3	0.1	99.1
30	<i>Coreopsis tripteris</i>	0.3	0.1	99.2
31	<i>Hypoxis hirsuta</i>	0.2	0.1	99.3
32	<i>Coreopsis palmata</i>	0.2	0.1	99.3
33	<i>Helianthus pauciflorus</i>	0.2	0.1	99.4
34	<i>Medicago lupulina</i>	0.2	0.0	99.5
35	<i>Hypericum sp.</i>	0.2	0.0	99.5
36	<i>Vernonia baldwinii</i>	0.1	0.0	99.6
37	<i>Euphorbia corollata</i>	0.1	0.0	99.6
38	<i>Desmodium canadense</i>	0.1	0.0	99.6
39	<i>Echinacea pallida</i>	0.1	0.0	99.6
40	<i>Helianthus grosseratus</i>	0.1	0.0	99.7

Data are based on counts of flowering ramets within 100 × 1 m transects taken on the same date as the butterfly surveys. Plant nomenclature follows that of USDA, NRCS 2012

References

- Anderson RC (1990) The historic role of fire in the North American grassland. In: Collins SL, Wallace LL (eds) Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, pp 8–18
- Anderson RC (2006) Evolution and origin of the Central Grassland of North America: climate, fire, and mammalian grazers. *J Torrey Bot Soc* 133:626–647
- Archibald S, Bond WJ, Stock WD, Fairbanks DHK (2005) Shaping the landscape: fire-grazer interactions in an African savanna. *Ecol Appl* 15:96–109
- Auckland JN, Debinski DM, Clark WR (2004) Survival, movement, and resource use of the butterfly *Parnassius clodius*. *Ecol Entomol* 29:139–149
- Axelrod DI (1985) Rise of the grassland biome in central North America. *Bot Rev* 51:163–201
- Bergman KO, Askling J, Ekberg O, Ignell H, Wahlman H, Milberg P (2004) Landscape effects on butterfly assemblages in an agricultural region. *Ecography* 27:619–628
- Bond WJ (2008) What limits trees in C-4 grasslands and savannas? *Annu Rev Ecol Evol Syst* 39:641–659
- Branson DH, Joern A, Sword GA (2006) Sustainable management of insect herbivores in grassland ecosystems: new perspectives in grasshopper control. *Bioscience* 56:743–755
- Brower LP, Malcolm SB (1991) Animal migrations: endangered phenomena. *Am Zool* 31:265–276
- Brown JA, Boyce MS (1998) Line transect sampling of Karner blue butterflies (*Lycaeides melissa samuelis*). *Environ Ecol Stat* 5:81–91
- Brudvig LA, Mabry CM, Miller JR, Walker TA (2007) Evaluation of central North American prairie management based on species diversity, life form, and individual species metrics. *Conserv Biol* 21:864–874
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford
- Bushnell Performance Optics® (2004) Laser Rangefinder Yardage Pro® Sport 450®: user's manual. Bushnell® Performance Optics, Overland Park
- Christensen NL (1997) Managing for heterogeneity and complexity on dynamic landscapes. In: Pickett ST, Ostfeld RS, Shachak M, Likens GE (eds) The ecological basis of conservation. International Thomson Publishing, New York, pp 167–186
- Collins SL, Steinauer EM (1998) Disturbance, diversity, and species interactions in tallgrass prairie. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, pp 140–158
- Cook WM, Holt RD (2006) Fire frequency and mosaic burning effects on a tallgrass prairie ground beetle assemblage. *Biodivers Conserv* 15:2301–2323
- Coppedge BR, Engle DM, Fuhlendorf SD, Masters RE, Gregory MS (2001) Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. *Landsc Ecol* 16:677–690
- Crawley MJ (2007) The R book. Wiley, Chichester
- Curtin C, Western D (2008) Grasslands, people, and conservation: over-the-horizon learning exchanges between African and American pastoralists. *Conserv Biol* 22:870–877
- Daubenmire R (1959) A canopy-coverage method of vegetational analysis. *Northwest Sci* 33:43–64
- Davis JD, Debinski DM, Danielson BJ (2007) Local and landscape effects on the butterfly community in fragmented Midwest U.S.A. prairie habitats. *Landsc Ecol* 22:1341–1354
- Davis JD, Hendrix SD, Debinski DM, Hemsley CJ (2008) Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *J Insect Conserv* 12:69–79
- Engle DM, Fuhlendorf SD, Roper A, Leslie DM (2008) Invertebrate community response to a shifting mosaic of habitat. *Rangel Ecol Manag* 61:55–62
- Erhardt A, Mevi-Schutz J (2009) Adult food resources in butterflies. In: Settele J, Shreeve T, Konvicka M, Van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 9–16
- Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. *Bioscience* 53:77–88
- Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625–632
- Fuhlendorf SD, Engle DM (2004) Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *J Appl Ecol* 41:604–614
- Fuhlendorf SD, Harrell WC, Engle DM, Hamilton RG, Davis CA, Leslie DM (2006) Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol Appl* 16:1706–1716
- Fuhlendorf SD, Engle DM, Kerby J, Hamilton R (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv Biol* 23:588–598
- Heitzman JR, Heitzman JE (2006) Butterflies and moths of Missouri. Missouri Department of Conservation, Jefferson City

- Helzer CJ, Steuter AA (2005) Preliminary effects of patch-burn grazing on a high-diversity prairie restoration. *Ecol Restor* 23:167–171
- Kopper BJ, Margolies DC, Charlton RE (2001) Life history notes on the regal fritillary, *Speyeria idalia* (Drury) (Lepidoptera: Nymphalidae), in Kansas tallgrass prairie. *J Kans Entomol Soc* 74:172–177
- Kruess A, Tschamtk T (2002) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv Biol* 16:1570–1580
- Kubo M, Kobayashi T, Kitahara M, Hayashi A (2009) Seasonal fluctuations in butterflies and nectar resources in a semi-natural grassland near Mt. Fuji, central Japan. *Biodivers Conserv* 18:229–246
- McGranahan DA (2008) Degradation and restoration in remnant tallgrass prairie: grazing history, soil carbon, and invasive species affect community composition and response to the fire-grazing interaction. Thesis, Iowa State University
- McGranahan DA (2011) Species richness, fire spread, and structural heterogeneity in tallgrass prairie. Dissertation, Iowa State University, Ames
- McGranahan DA, Engle DM, Fuhlendorf SD, Winter SJ, Miller JR, Debinski DM (2012) Spatial heterogeneity across five rangelands managed with pyric-herbivory. *J Appl Ecol*. doi:10.1111/j.1365-2664.2012.02168.x
- Moranz RA (2010) The effects of ecological management on tallgrass prairie butterflies and their nectar sources. Dissertation, Oklahoma State University
- Motzkin G, Foster D, Allen A, Harrod J, Boone R (1996) Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecol Monogr* 66:345–365
- Munguira ML, Garcia-Barros E, Cano JM (2009) Butterfly herbivory and larval ecology. In: Settele J, Shreeve T, Konvicka M, Van Dyck H (eds) *Ecology of butterflies in Europe*. Cambridge University Press, Cambridge, pp 43–54
- Oates MR (1995) Butterfly conservation within the management of grassland habitats. In: Pullin AS (ed) *Ecology and conservation of butterflies*. Chapman & Hall, New York, pp 98–112
- Ockinger E, Smith HG (2006) Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia* 149:526–534
- Oksanen L (2009) Multivariate analysis of ecological communities in R: vegan tutorial. <http://cc.oulu.fi/~jarioksa/opetus/metodi/vegantutor.pdf>. Accessed 24 July 2010
- Opler PA, Kelly L, Thomas N, Coordinators (2012) Butterflies and moths of North America. <http://www.butterfliesandmoths.org/version18>. Accessed Nov 2011
- Panzer R (2003) Importance of in situ survival, recolonization, and habitat gaps in the postfire recovery of fire-sensitive prairie insect species. *Nat Areas J* 23:14–21
- Panzer R, Schwartz M (2000) Effects of management burning on prairie insect species richness within a system of small, highly fragmented reserves. *Biol Conserv* 96:363–369
- Pillsbury FC, Miller JR, Debinski DM, Engle DM (2011) Another tool in the toolbox? Using fire and grazing to promote bird diversity in highly fragmented landscapes. *Ecosphere* 2:1–14
- Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-PLUS*. Springer, New York
- Pocewicz A, Morgan P, Eigenbrode SD (2009) Local and landscape effects on butterfly density in northern Idaho grasslands and forests. *J Insect Conserv* 13:593–601
- Pollard E, Yates TJ (1993) *Monitoring butterflies for ecology and conservation*. Chapman & Hall, London
- Powell A, Busby WH, Kindscher K (2007) Status of the regal fritillary (*Speyeria idalia*) and effects of fire management on its abundance in northeastern Kansas, USA. *J Insect Conserv* 11:299–308
- Poyry J, Lindgren S, Salminen J, Kuussaari M (2005) Responses of butterfly and moth species to restored cattle grazing in semi-natural grasslands. *Biol Conserv* 122:465–478
- Poyry J, Luoto M, Paukkunen J, Pykala J, Raatikainen K, Kuussaari M (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos* 115:401–412
- R Development Core Team (2010) R: a language and environment for statistical computing. R foundation for statistical computing. <http://www.R-project.org>. Accessed 21 Aug 2010
- Reed CC (1997) Responses of prairie insects and other arthropods to prescription burns. *Nat Areas J* 17:380–385
- Reeder KF, Debinski DM, Danielson BJ (2005) Factors affecting butterfly use of filter strips in Midwestern USA. *Agric Ecosyst Environ* 109:40–47
- Robel RJ, Briggs JN, Dayton AD, Hulbert LC (1970) Relationship between visual obstruction measurements and weight of grassland vegetation. *J Range Manag* 23:295–298
- Rudolph DC, Ely CA, Schaefer RR, Williamson JH, Thill RE (2006) The Diana fritillary (*Speyeria diana*) and great spangled fritillary (*S. cybele*): dependence on fire in the Ouachita Mountains of Arkansas. *J Lepid Soc* 60:218–226
- Samson F, Knopf F (1994) Prairie conservation in North America. *Bioscience* 44:418–421

- SAS Institute Inc (2008) SAS 9.2 TS Level 2M3. SAS Institute Inc., Cary
- Schneider C (2003) The influence of spatial scale on quantifying insect dispersal: an analysis of butterfly data. *Ecol Entomol* 28:252–256
- Schultz CB, Dlugosch KM (1999) Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. *Oecologia* 119:231–238
- Scott JA (1986) *The butterflies of North America: a natural history and field guide*. Stanford University Press, Stanford
- Shepherd S, Debinski DM (2005) Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. *Biol Conserv* 126:51–61
- SPSS (2010) SPSS for Windows, Release 17.0.0. SPSS Inc., Chicago
- Stohlgren TJ, Falkner MB, Schell LD (1995) A modified-Whittaker nested vegetation sampling method. *Vegetatio* 117:113–121
- Swengel AB (1996) Effects of fire and hay management on abundance of prairie butterflies. *Biol Conserv* 76:73–85
- Swengel S, Schlicht D, Olsen F, Swengel A (2011) Declines of prairie butterflies in the Midwestern USA. *J Insect Conserv* 15:327–339
- Thomas L, Buckland ST, Rexstad RB, Laake JL, Strindberg S, Hedley SL, Bishop JRB, Marques TA, Burnham KP (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *J Appl Ecol* 47:5–14
- USDA, NRCS (2012) The PLANTS Database (<http://plants.usda.gov>. Accessed 20 May 2012). National Plant Data Team, Greensboro, NC 27401-4901 USA
- Vogel JA, Debinski DM, Koford RR, Miller JR (2007) Butterfly responses to prairie restoration through fire and grazing. *Biol Conserv* 140:78–90
- Vogel JA, Koford RR, Debinski DM (2010) Direct and indirect responses of tallgrass prairie butterflies to prescribed burning. *J Insect Conserv* 14:663–677
- WallisDeVries MF, Parkinson AE, Dulphy JP, Sayer M, Diana E (2007) Effects of livestock breed and grazing intensity on biodiversity and production in grazing systems. 4. Effects on animal diversity. *Grass Forage Sci* 62:185–197
- Wiens JA (1974) Habitat heterogeneity and avian community structure in North American grasslands. *Am Midl Nat* 91:195–213