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Fire frequency and mosaic burning effects on a tallgrass prairie ground beetle assemblage

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Abstract. Fire frequency has significant effects on the biota of tallgrass prairie, including mammals, vascular plants and birds. Recent concern has been expressed that widespread annual burning, sometimes in combination with heavy livestock grazing, negatively impacts the biota of remaining prairie remnants. A common management recommendation, intended to address this problem, is to create a landscape with a mosaic of different burn regimes. Pitfall trapping was used to investigate the impacts of fire pattern on the diversity and species composition of ground beetles (Coleoptera: Carabidae) at Konza Prairie Biological Station in eastern Kansas, USA. Trapping was conducted over three seasons in landscape units burned on average every 1, 4, or 20 years, and in a fourth season across the available range of vegetative structure to assess the variability of the community within the study system. In the fifth season communities were also followed immediately after two fire events to detect within-season effects of fire and to study short-term patterns of post-disturbance community assembly. Fire frequency had comparatively minimal effects on ground beetle diversity measures, and most numerically common species were observed widely across habitat and management types. Fire frequency effects were manifested primarily in changes in abundance of common species. Colonization of burned areas apparently did not occur from juxtaposed non-burned areas, but from underground or from long distances. While these results suggest that widespread annual burning of tallgrass prairie remnants may not have dramatic effects on prairie ground beetles, we urge caution regarding the application of these results to other taxa within tallgrass prairie.

Introduction

A principal goal of conservation biology is to explore the implications of different land management strategies for the maintenance of biodiversity and ecosystem function, and to use this understanding to make scientific recommendations to land managers. Such understanding is particularly important when the biological system is threatened or declining.

The tallgrass prairie of central North America, formally widespread, has largely been destroyed (Samson and Knopf 1994). At least 95% of presettlement tallgrass prairie has been transformed into cropland and urban areas (Samson and Knopf 1994), with the largest remaining unplowed area in the

Flint Hills of Oklahoma and Kansas (including our study site) (Reichman 1987; Knapp and Seastedt 1998). Beginning around 1980, most of the Flint Hills has been managed under a fire and grazing regime called early intensive stocking, which promotes annual burning of pasture land in March and April, followed by heavy grazing by cattle for the next 90–120 days (Smith and Owensby 1978; Launchbaugh et al. 1983). There has been concern that widespread annual burning of remaining prairie fragments, while desirable because it generates forage for livestock, is causing large-scale declines in prairie taxa (Walk and Warner 2000; Higgins et al. 2001; Robbins et al. 2002). Prescribed fire is important because it maintains prairie structure and function (Vogl 1974; Collins and Wallace 1990) but a uniform, intense application over a wide area could potentially be detrimental.

In response to this general concern that the uniform application of fire creates too a homogeneous a landscape, researchers working in several systems have recommended a spatial and/or temporal mosaic of management strategies (Chambers 1998; Law and Dickman 1998; Parr and Brockett 1999; Shriver and Vickery 2001; Swengel 2001; Pons et al. 2003). With such a general strategy, sites of the same habitat type are likely to vary in habitat structure and other characteristics, providing a wide array of potentially occupiable niches for species within the regional species pool. Thus, a mosaic of burn treatments may boost regional biodiversity and allow species to persist in heterogeneous communities, even if they have widely differing fire tolerances or habitat structure requirements. However, discussion of the application of fire mosaics to a comparable system (Australian arid grasslands) suggests that the details of management decisions may more reflect logistical concerns than ecological criteria relevant to target organisms (Keith et al. 2002). It is our goal to provide specific data that directly address the dynamics of grassland organisms within a burn mosaic, as called for by Keith et al. (2002).

In this paper we investigate the effects of fire and fire frequency in tallgrass prairie on ground beetles, a key group within the arthropod community. The broad question we address is whether mosaic burning facilitates beetle diversity at our study site. Previous work at our site, which is an experimental mosaic of fire treatments, indicates that differences in fire treatment have striking effects on vegetation structure (Briggs et al. 1992, 2002; Heisler et al. 2003). This impact of fire in turn seems likely to affect the availability of structured habitats and resources for beetles.

The effects of fire on ground beetles have been studied in grasslands (Larsen and Williams 1999) and in other habitats (Rickard 1970; Richardson and Holliday 1982; Holliday 1984; McCoy 1987; Villa-Castillo and Wagner 2002). While these studies do not come to a common conclusion about the effects of fire on carabids, together they provide evidence that fire intensity or its temporal pattern can alter ground beetle diversity and species composition. Ground beetles are often used as indicator organisms to assess environmental quality or condition (Refseth 1980; Rykken et al. 1997), most importantly because they are widely distributed, reasonably abundant and speciose in many terrestrial habitats (thus facilitating comparisons), and because their taxonomy is fairly well determined. These taxa are also convenient to study, and are usually generalist predators, tending to range widely at ground level (Thiele 1977; Allen 1979). Because of these behavioral traits, pitfall traps (see Morris 1960; Luff 1975; Baars 1979; Weeks and McIntyre 1997 for discussions of sampling procedures) permit one to capture a reasonable cross-section of local ground beetle communities. Ground beetles' mobility implies that they could potentially exhibit patch dynamics with recurrent colonization following local extinctions due to disturbance, and thus be able to effectively exploit a mosaic of habitats at different stages due to spatially varying fire intensity and frequency.

In this paper, we seek in general to determine how 'robust' a prairie beetle community is in response to fire and to landscape heterogeneity. We will test the following hypotheses: (1) Ground beetle community measures vary with fire frequency, and secondarily with variation in topography within the study site. (2) Fire frequency affects the occurrence or abundance of individual ground beetle species. (3) The proximity of landscape units with different fire regimes, or alternatively the proximity of distinct vegetation types (e.g. forest vs. grassland), affects community measures and population movements. If our results support the first two hypotheses, this may indicate that widespread annual burning leads to changes in this component of prairie biodiversity and regional species composition. If the third hypothesis is supported, and community composition varies significantly over treatment boundaries, mosaic burn treatments may be a useful conservation tool for these organisms.

Methods

This study was conducted at Konza Prairie Biological Station (Figure 1), an experimental reserve in eastern Kansas, USA, which is part of the United States National Science Foundation's Long Term Ecological Research network (Knapp et al. 1998b). The site consists of 3487 ha. of mostly never-plowed tallgrass prairie, occurring in a region of rolling topography with windswept, rocky hilltops and comparatively mesic lowlands. Konza features a mosaic of landscape treatments superimposed on natural watersheds, including factorial combinations of experimental fire frequency (at 1, 2, 4, 10 and 20 year intervals) and large-mammal grazing (bison, cattle, neither). These watersheds with associated treatments are hereafter referred to as landscape 'units'. Knapp et al. (1998b) provide a detailed description of the site history, vegetation patterns, and experimental design, which has remained broadly similar since the late 1970s. The current study (conducted entirely on ungrazed units, as we found trampling by large grazers leads to destruction of pitfall traps) takes advantage of this preexisting experimental design.

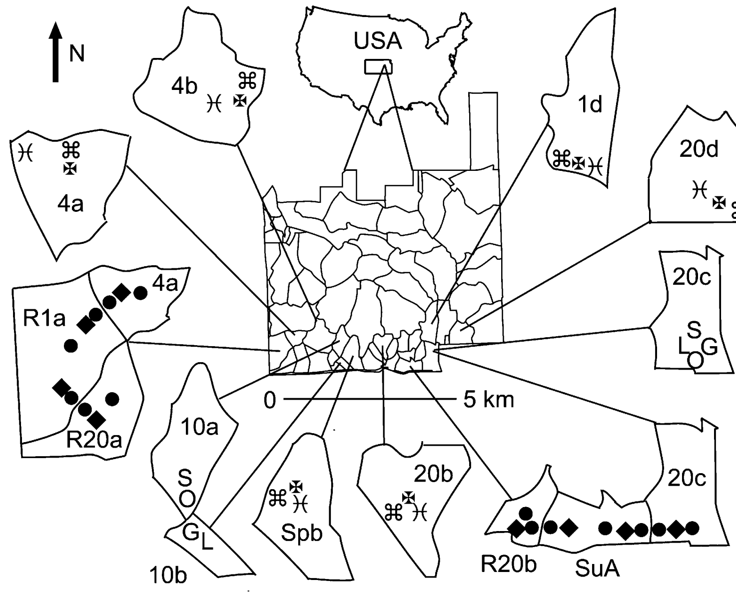

Figure 1. Map of Konza Prairie Biological Station, near Manhattan, Kansas, USA. The outline within the map of the USA (top center of figure) represents the State of Kansas. Scale refers to complete map of Konza Prairie in center of figure. Connecting lines indicate location of areas within the larger map. Expanded units are not to scale. The following symbols indicate locations of five-trap pitfall transects at 2 m intervals from 1997 to 1999: ⌘, upland transect; ✠, slope transect; ♓, lowland transect. The following indicate the location of five-trap pitfall transects at 2 m intervals in 2000: G = Gallery forest, L = Large shrubby islands, S = Small shrubby islands, O = Open prairie. The following indicate the location of five-trap transects in 2001: ●, 2 m intervals between traps; ◆, 5 m intervals between traps.

Field methods

Effects of fire frequency and topography

Two landscape units were selected for each of three preexisting treatments, for study from 1997 to 1999: annual burns (Units SpB and 1D, burned each year of study), burns on average every 4 years (4A, burned in 1994 prior to study and in 1999 during study; 4B, burned in 1994 prior to study and in 1998 during study), and burns every 20 years (20B and 20D, most recently burned in 1991; see (Figure 1). Within each unit, three sampling sites were chosen, one on the dry ridgetops, one in the comparatively moist lowlands, and one on the intervening rocky slope.

At each sampling location, a linear transect of five pitfall traps was established with traps at two meter intervals (hence, a total of 15 traps per unit). Specimens were collected in plastic cups 9 cm in diameter and 7 cm deep, which were implanted just below ground level, half-filled with dilute ethylene glycol and covered with plywood to exclude rain. Trapping occurred continuously from August 16 to November 15, 1997, again from May 12 to November 14, 1998, and then again from May 8 to November 1, 1999. Specimens were removed from traps approximately every 2 weeks, and stored in alcohol at the Kansas Natural History Museum and Biodiversity Research Center. Due to logistical constraints, traps in the three units (SpB, 4B, 20B) were established one week earlier and removed one week earlier than traps in the other three units (1D, 4A, 20D). This meant that collections were slightly out of temporal phase among units; insects captured in the former three units were taken to the laboratory one week, and specimens from the latter three units were collected the following week.

Two additional approaches were used to investigate how the Konza ground beetle community responds to landscape mosaics. In 2000 we investigated whether heterogeneity in gross vegetation structure (e.g., presence of woody vegetation), which is indirectly associated with land management strategies at Konza (Briggs et al. 2002; Heisler et al. 2003), affects beetle community composition over comparatively small scales. In order to assess the potential of transitory pulses in community composition drive by localized disturbance, in 2001 we examined variation in time and space in beetle communities across stark (but temporary) habitat boundaries, by sampling in adjacent burned and unburned landscape units from 2 weeks before to 8 weeks after the burn. Our detailed protocol to address the impact of landscape mosaics were as follows.

Effects of vegetation heterogeneity

We collected samples in 2000 from Unit 20C (last burned in 1992) and adjacent Units 10A (last burned in a wildfire in 1997) and 10B (last burned in 1996) (Figure 1). Within each of these two sites, ground beetles were collected from each of four habitats: gallery forest (G), large shrubby islands of wooded vegetation surrounded by prairie (L), small shrubby islands (S), and open prairie (O) (see Figure 1). Gallery forests consisted of mature trees (honey locust, *Gleditsia triacanthos* L.; elm, *Ulmus rubra* Muhl.; and cottonwood, *Populus deltoides* Bartr. ex Marsh.) found in stream valleys, with comparatively sparse understory vegetation. Large and small shrubby islands were composed of clumps of rough-leaved dogwood (*Cornus drummondii* C.A. Mey) and sumac (*Rhus glabra* L.), on gentle slopes, often at some distance from the gallery forest. (These two woody plant species have life-forms ranging from multi-stemmed shrubs to single-stemmed trees, sometimes exceeding 4 m in height.) We defined small shrubby islands as having a small spatial extent ($\leq$ 4 m in diameter), tree heights no larger than 2.5 m, and an understory that included prairie grasses and forbs. Large shrubby islands were larger (up to 20 m at greatest width) and better established, with tree heights $\sim$4 m and canopies sufficiently closed to exclude dense understory vegetation. Open prairie locations were characterized by dense grasses and prairie forbs with no overstory.

At each site (20C, 10A and 10B), transects of pitfall traps (similar to those described above) were established in each habitat. Due to the limited extent of small shrubby islands, there the five traps were split among several islands. Traps were located at ≥2 m from the habitat edge, except for the small shrubby islands, where they were placed in the center of the island. Traps were open continuously from May 20 until November 3, 2000, and emptied at two week intervals.

Short-term burn effects

Two sites were selected to study short-term fire effects on the beetle community: Unit R1a, burned in April 2001, and Unit SuA, burned in August 2001 (Figure 1). In each focal unit 25 pitfall traps (identical to those described above) were established. One transect of five traps at 2 m intervals was set near the center of the unit to sample species occurring in that unit. We also placed ten traps at the border between the focal unit and a neighboring unit with similar management, and another ten traps at the border of an adjacent unit with a different management protocol. Transects of five traps at 2 m intervals were also placed in the center of the bordering units. In each case, transects at the border of a unit consisted of five traps at 2 m intervals, beginning 2 m from the border running perpendicular to the edge, followed by five additional traps at 5 m intervals farther into the unit (see Figure 1). In the April–June study, the burned unit (R1A) was bordered by a unit burned the previous year (R20A) and one burned at 4-year intervals (4A, last burned in 1999); in the August–October study, the burned unit (SuA) was bordered by a unit burned earlier in 2001 (R20B) and a unit scheduled to be burned every 20 years (20C, last burned in 1992).

In both spring and summer, specimens were collected for 2 weeks before the burn in order to characterize the community at the time of the fire. Trapping was then conducted continuously for 8 weeks following the fire to document the recovery of the community and the magnitude of spillover among landscape units. In spring, before-fire trapping was conducted from April 11 to 25, 2001 and post-fire trapping was conducted until June 22. In summer, before-fire trapping was conducted from August 2 to 17, 2001 and post-fire trapping was completed on October 12. Specimens were removed from traps weekly.

Laboratory and statistical methods

Fire frequency and topography

In the laboratory, specimens were sorted and exemplars were later identified to species by carabid experts, Drs. D. Shpeley and G. Ball at the University of Alberta (this was the case for all specimens in this paper). Species occurrences and abundances were tabulated for each sampling period for each transect (i.e., the contents of all five traps on each transect were combined), and seasonal patterns of total beetle abundance were plotted. Because continuous pitfall trapping over a season is most likely to produce reliable indices of carabid population sizes (den Boer 1971; Baars 1979; Niemalä et al. 1990) and because individual ground beetle species are often either spring- or fall-active (Thiele 1977), we aggregated samples from transects for the Spring (May to mid-August), and for the Fall (mid-August to November) for full-season samples. These combined samples were the principal units of analysis for the 1997–1999 dataset, which thus included three Fall samples (1997–1999), two Spring samples (1998–1999) and two full year samples (1998–1999).

Species richness, total specimens collected, and Shannon–Weaver diversity (H') and evenness (J') were calculated for each transect cumulatively for each season (Spring, Fall). Because the species lists at a given transect were similar from year to year, and because species richness and H' are cumulative measures of biological diversity, the samples were combined from each transect for the three fall seasons, and also for the two spring seasons. General linear models (GLMs) with fire frequency (1, 4, 20 years) and topographic location (upland, slope, lowland) as predictor variables were used to test for statistical effects on carabid richness, H', J', and total individuals collected in both the spring and fall seasons. [We also calculated repeated measures ANOVAs including year as a predictor; we do not report these results below, as the emergent patterns are very similar.]

Because the GLM analyses described above are comparatively coarse (i.e., the predictor variables are all categorical), we also performed a detrended correspondence analyses (DCA; Hill and Gauch 1980) on the dataset to produce a graphical portrayal of multivariate patterns of variation in community structure. This ordination was conducted on a matrix with the five-trap transect on one axis, the species in the community on the other and their abundances as the matrix values (data from 3 years were pooled for each transect, with fall and spring seasons considered separately).

We also used repeated measures ANOVAs (rmANOVAs) to test for landscape and fire frequency effects on the abundance of individual species. For each of the 11 carabid species with >20 individuals observed from 1997 to 1999, abundance was assessed along each transect in each year, and a rmANOVA on abundance conducted with average fire frequency, topographic location and year as the predictor variables.

Effects of vegetation heterogeneity

Samples from transects in 2000 were aggregated according to Spring and Fall seasons as above, and species richness and community measures were tabulated. We also applied a detrended correspondence analysis to the (season) × (habitat) species-abundance data (data pooled for each habitat type, and season), and plotted scores on the first two components against each other.

Short-term burn effects

To explore the short-term effects of fire in 2001, we calculated species richness in focal and neighboring units before experimental burns, and calculated the weekly and cumulative richness for the succeeding 8 weeks. We inspected the data for population-level responses to fire, searching in particular for the following: (1) sudden disappearance of any species following fire, (2) sudden appearance following fire, (3) an abundant species in one unit before the fire which suddenly increases in an adjoining unit, or (4) a species decreasing exponentially in abundance within a transect with distance to the neighboring unit. All of these patterns, if observed, are potential indicators of landscape coupling between habitat units, driven by localized fire disturbance.

Results

A total of 29 carabid species were observed in this study, with a cumulative total of 22,477 specimens collected (1818 from Fall 1997, 11,632 from 1998, 6192 from 1999, 859 from 2000, and 2077 from 2001). Seasonal patterns in ground beetle abundance were strongly bimodal, and the temporal pattern was similar from year to year between 1997 and 1999 (Figure 2; data from 2000 and 2001 are not comparable and so not shown, because they were collected at different locations following a different protocol). Although abundance varied dramatically between 1997 and 1999, dominant species in each landscape unit were similar and in approximately similar proportions.

Effects of fire frequency and topography on community measures

From 1997 to 1999, aggregate species richness, H' and total carabids captured were somewhat higher in units burned at 4-year intervals, while aggregate

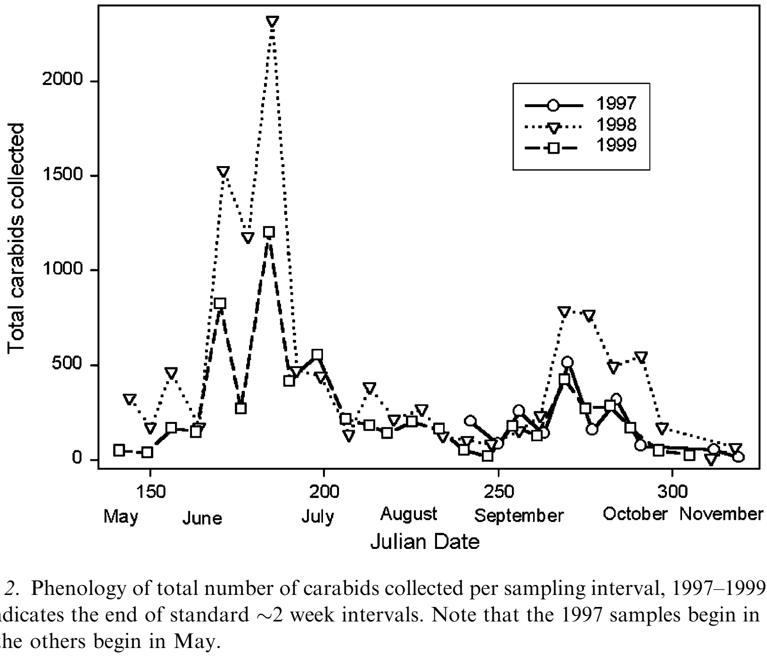

Figure 2. Phenology of total number of carabids collected per sampling interval, 1997–1999. Julian date indicates the end of standard ~2 week intervals. Note that the 1997 samples begin in August while the others begin in May.

Table 1. Aggregate specimens captured, species richness, Shannon diversity (*H*) and evenness (*J*) by fire treatment, 1997–1999.

Fire frequency	Carabids	Richness	*H*	*J*
1-year	5852	16	1.41	0.51
4-year	7535	20	1.50	0.50
20-year	6255	18	1.31	0.45

evenness was similar in all three fire treatments (Table 1). These effects can potentially be explained by variation in total carabid abundance. Moreover, aggregate measures for each transect varied substantially among treatments, and to some degree within treatments, suggesting that these standard measures of community structure are rather insensitive to fire frequency, as compared with background variation arising for other reasons (Tables 2–3). GLM analyses revealed a significant effect of topography on total carabids and a significant interaction between topography and carabid richness in fall samples, but none of the relationships were significant in spring samples Table 3). In fall samples richness per transect was overall highest on slope transects, and the significant interaction indicates that richness was highest within upland

Table 2. Aggregate specimens captured (Total), species richness (Rich), Shannon diversity (*H*) and evenness (*J*) for each transect collected in 1997–1999.

Freq	Unit	Top	Fall				Spring			
			Total	Rich	*H*	*J*	Total	Rich	*H*	*J*
1	SpB	L	150	7	1.09	0.56	696	10	0.77	0.33
1	SpB	S	345	11	1.27	0.53	1485	9	0.82	0.37
1	SpB	U	334	6	1.42	0.79	822	5	0.99	0.62
1	1D	L	96	5	1.09	0.68	531	8	0.49	0.23
1	1D	S	156	9	1.12	0.51	219	8	1.20	0.57
1	1D	U	359	6	1.13	0.63	659	7	0.84	0.43
4	4B	L	296	10	1.28	0.56	740	12	0.95	0.38
4	4B	S	485	6	1.32	0.74	1333	10	1.02	0.44
4	4B	U	705	7	1.32	0.68	1353	8	0.83	0.40
4	4A	L	334	8	1.39	0.67	761	10	1.34	0.58
4	4A	S	477	8	0.45	0.22	201	6	0.96	0.53
4	4A	U	375	5	0.31	0.19	475	8	1.30	0.63
20	20B	L	233	6	1.20	0.67	418	7	1.05	0.54
20	20B	S	398	8	1.10	0.53	1034	9	0.71	0.32
20	20B	U	1107	9	1.00	0.45	1054	10	0.87	0.38
20	20D	L	106	4	1.15	0.83	241	10	0.97	0.42
20	20D	S	505	9	0.84	0.38	400	11	1.24	0.52
20	20D	U	377	9	1.07	0.49	382	9	1.25	0.57

"Freq" = average fire frequency, "Top" = Topographic position (L = Lowland, S = Slope, U = Upland). "Unit" indicates the unit in which the transect was located; see Methods.

Table 3. General linear model results testing the significance of fire frequency and topography on aggregate community measures for each five-trap transect, 1997–1999.

	Fire frequency		Topography		Interaction	
	F	*p*	*F*	*p*	*F*	*p*
Fall total carabids	2.24	0.163	4.43	0.046	0.53	0.719
Fall species richness	0.04	0.961	4.12	0.054	6.88	0.008
Fall *H′*	0.44	0.659	0.53	0.604	0.65	0.644
Fall *J′*	0.52	0.613	1.43	0.290	0.62	0.657
Spring total carabids	0.30	0.747	0.38	0.694	0.09	0.982
Spring species richness	1.56	0.262	1.77	0.225	1.70	0.234
Spring *H′*	1.28	0.324	0.22	0.808	0.70	0.609
Spring *J′*	0.43	0.660	0.79	0.485	0.77	0.572

The summary data tested here are found in Table 2.
DF for each test: fire frequency, 2; topography, 2; interaction, 4. 2 replicate transects for each combination of fire frequency and topographic position.

samples on units burned at 20 year intervals, but did not vary discernibly within slope or lowland transects.

Species richness and *H′* do not incorporate information about species composition. The ordination technique of DCA does include compositional information. A DCA performed on this dataset reveals fairly clear effects of fire frequency and seasonality on the carabid community (Figure 3). Fall and spring samples separated readily along the first axis, and within each season communities sampled on yearly burned units tend to occur nearer one end of the axis, and communities from units burned every 20 years nearer the other. This pattern was clearer for spring samples. Transects did

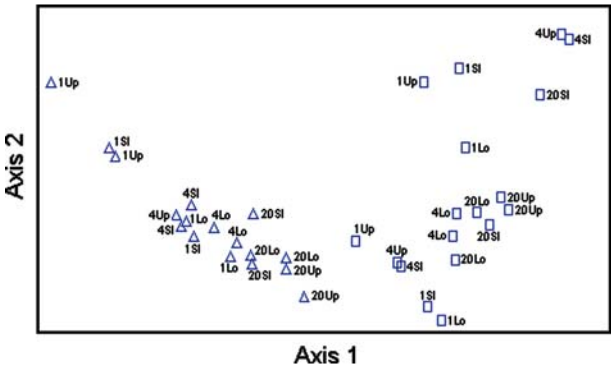

Figure 3. Five-trap transect locations (1997–1999) plotted on the first two ordination axes, as calculated by detrended correspondence analysis of aggregate species abundance for each transect. Numbers indicate average duration since fire, and Up = Upland, Sl = Slope, Lo = Lowland. Triangles = Spring samples, rectangles = Fall samples.

not show as clear a pattern according to topographic position, although in each season an upland transect on a yearly burned unit separated itself from the others. The lowland samples overall are somewhat lower on DCA2 (none have high scores on this axis). Taking into account information on individual species' abundances, there thus appear to be effects of phenology, fire frequency, and possibly of topography.

Ten of the 11 species with total abundance >20 in 1997–1999 were observed in all three fire treatments. Of these 11 species, repeated measures ANOVAs revealed three significant effects of fire frequency, four significant effects of topographic location, eight significant effects of sample year (mostly due to high numbers in 1998), and several significant interactions (Table 4). Several species were found only in a single treatment, but all of these were captured in very low total abundance, so it is difficult to separate true niche specialization from sampling artifacts.

Effects of vegetation heterogeneity

In 2000, species richness, species diversity (H') and evenness (J) were all highest in gallery forest, followed by open prairie in all measures except for richness. Gallery forests also contained the most species not detected in other habitats (Table 5); but these were all captured in very low abundance. In the DCA analysis, scores along Axis 1 are clearly separated according to whether the points represent spring or fall samples (Figure 4). Along Axis 1 the large islands were somewhat more similar to the gallery forest, and the small islands were more similar to the open prairie; this pattern was stronger in spring than in fall. Considering each pair of habitat types, in each season S and O were considerably more similar in their DC scores than were the other habitat pairs.

Short-term burn effects

At the times of both the 2001 April and August burn events, the focal and neighboring units all had similar ground beetle species richness (Table 6). After 8 weeks, the burned unit had slightly higher cumulative species richness than did its neighbors in both seasons (Table 6). We did not observe any population responses to fire that fit our search criteria (see Methods), except possibly in *Cyclotrachelus sodalis*, which exhibited a high and very brief peak in abundance in the third week after the April burn, and also in the first full week following the August burn. Instead, for the most part, during these experiments species abundances rose and fell in rough temporal accord with the phenological patterns observed in 1997–1999 (see Figure 2) and not in response to the burn schedule (e.g., *Pasimachus* spp. increased in abundance in June and

Table 4. Species abundances aggregated by fire treatment, 1998–1999.

	Spring			Fall			Total	Fire		Topography		Year		Significant interactions
	1-year	4-year	20-year	1-year	4-year	20-year		*F*	*p*	*F*	*p*	*F*	*p*	
Scaphinotus cavicollis Leconte	0	0	4	0	9	13	26	2.65	0.22	0.72	0.53	1.10	0.39	
Pasimachus californicus Chaudoir	390	718	47	32	113	10	1310	2.15	0.26	0.85	0.47	7.21	0.03	
Pasimachus elongatus LeConte	839	367	46	115	22	5	1394	9.09	0.05	28.6	0.01	11.5	0.01	F×T,F×Y,T×Y,F×T×Y
Scarites subterraneus Fabricius	25	5	52	4	1	23	110	9.69	0.05	20.2	0.01	7.78	0.02	F×T
Pterostichus permundus Say	150	188	707	484	747	944	3220	0.75	0.55	2.47	0.17	10.4	0.01	
Poecilus lucublandus Say	3	69	36	5	17	17	147	8.69	0.06	11.4	0.01	12.2	0.01	F×T,T×Y,F×T×Y
Cyclotrachelus torvus LeConte	1	1	0	1	0	0	3							
Cyclotrachelus sodalis LeConte	2925	3282	2437	224	407	246	9521	0.10	0.91	0.36	0.71	13.3	0.01	
Calathus opaculus LeConte	8	114	162	548	1319	1454	3605	2.18	0.26	2.66	0.15	5.40	0.05	T×Y
Harpalus caliginosus Fabricius	55	73	8	16	1	0	153	1.94	0.29	0.04	0.96	3.16	0.12	
Chlaenius tomentosus Say	13	0	1	1	8	0	23	1.84	0.30	0.07	0.93	0.95	0.44	
Chlaenius vafer LeConte	0	0	0	1	0	1	2							
Cymindis pilosa Say	0	0	0	1	3	0	4							
Galerita bicolor Drury	0	34	16	8	21	7	86	9.50	0.05	5.59	0.04	41.5	0.01	F×Y,T×Y,F×T×Y
Agonum nutans Say	0	0	0	0	0	1	1							
Agonum rufipes DeJean	1	0	0	0	0	0	1							
Amara pennsylvanica Hayward	0	1	0	0	2	0	3							
Anisodactylus rusticus Say	0	1	0	0	0	0	1							
Apenes sinuata (Say)	0	4	1	0	0	1	6							
Brachinus alternans Dejean	0	0	3	0	0	0	3							
Calosoma affine Chaudoir	0	1	0	0	1	0	2							
Calosoma externum Say	1	2	0	0	1	0	4							
Chlaenius nemoralis Say	0	2	0	0	0	0	2							
Dicaelus elongatus Bonelli	0	0	1	0	0	0	1							
Harpalus paratus Casey	1	0	7	0	0	4	12							
Harpalus pennsylvanicus DeGeer	0	1	1	0	0	0	2							

Statistics refer to repeated measures ANOVAs on fire frequency (1, 4, 20 years), topography (Lowland, Slope, Upland) and year sampled for each species, with abundance aggregated over each full year sampled (1998–1999). Tests not attempted for species with very low total abundance.

Df for each test: fire frequency, 2; topography, 2; two-way interactions, 4, 3-way interaction 8. 2 replicate transects for each combination of fire frequency and topographic position.

Table 5. Ground beetle species and abundances collected at Konza Prairie, May 20–November 3, 2000.

Species	G	L	S	O	Total
Scaphinotus cavicollis LeConte	1	4	13	14	32
Pasimachus californicus Chaudoir	0	0	0	6	6
Pasimachus elongatus LeConte	0	0	1	7	8
Scarites subterraneus Fabricius	3	15	8	15	41
Pterostichus permundus Say	11	19	1	2	33
Dicaelus elongatus Bonelli	17	2	1	3	23
Poecilus lucublandus Say	0	2	0	0	2
Cyclotrachelus sodalis LeConte	2	8	112	113	235
Calathus opaculus LeConte	47	232	107	59	445
Harpalus caliginosus Fabricius	0	0	0	1	1
Cymindis pilosa Say	0	0	1	0	1
Galerita bicolor Drury	10	1	4	4	19
Harpalus pennsylvanicus DeGeer	1	0	0	0	1
Harpalus paratus Casey	1	0	0	0	1
Brachinus alternans Dejean	5	0	0	0	5
Chlaenius laticollis Say	1	0	0	0	1
Synuchus impunctatus Say	2	0	0	0	2
Apenes sinuata (Say)	0	1	0	0	1
Chlaenius nemoralis Say	0	1	0	0	1
Chlaenius impunctifrons Say	1	0	0	0	1
Number of individuals	102	285	248	224	859
Number of species	13	10	9	10	20
Species found only in habitat	6	3	1	2	
H′	1.76	0.79	1.14	1.45	
J	0.68	0.34	0.52	0.63	

G = Gallery forest, L = Large shrubby islands, S = Small shrubby islands, O = Open prairie.

disappeared after August, and *Pterostichus permundus* and *Calathus opaculus* increased in abundance in mid-September, with the latter increasing solely in one unit).

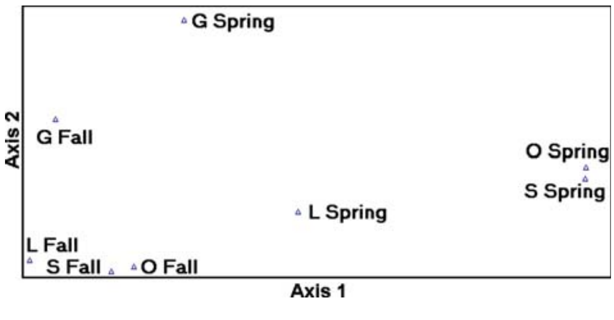

Figure 4. Plot of the two primary axes derived from a detrended correspondence analysis of 2000 samples collected in varied habitats. Each point represents samples aggregated from two replicate five-trap transects, and across a 6-week period (Spring = May 20–August 12, Fall = August 13–November 3). G = Gallery forest, L = Large shrubby islands, S = Small shrubby islands, O = Open prairie.

Table 6. Carabid species, and number of individuals, captured in studies of short-term burn effects in 2001.

Species	Before fire Spring			After fire Spring			Before fire Summer			After fire Summer		
	R1A	R20A	4A	**R1A**	R20A	4A	**SuA**	R20B	20C	**SuA**	R20B	20C
Pasimachus californicus	**3**	2	1	**42**	81	2	**44**	14	36	**4**	7	22
Pasimachus elongatus	**2**	2	14	**59**	126	64	**29**	37	1	**15**	13	2
Scarites subterraneus	**0**	0	0	**0**	0	0	**0**	0	0	**1**	0	3
Pterostichus permundus	**0**	0	0	**1**	0	6	**0**	0	0	**49**	17	12
Poecilus luclublandus	**1**	0	1	**6**	1	12	**0**	0	0	**1**	0	0
Cyclotrachelus torvus	**0**	0	0	**1**	0	0	**0**	0	0	**0**	0	0
Cyclotrachelus sodalis	**0**	0	1	**489**	43	200	**28**	5	9	**185**	33	38
Calathus opaculus	**0**	0	0	**4**	0	1	**0**	0	0	**0**	0	30
Harpalus caliginosus	**0**	0	0	**1**	0	0	**0**	0	0	**0**	0	0
Chlaenius tomentosus	**0**	0	0	**0**	1	0	**0**	0	0	**0**	0	0
Galerita bicolor	**0**	0	0	**1**	0	1	**0**	0	0	**1**	0	0
Richness	**3**	2	4	**9**	5	7	**3**	3	3	**7**	4	6

"Before fire" samples were collected over 2 weeks, and "After fire" samples were collected over 8 weeks. The landscape unit indicated in bold was burned in the indicated season, with the other two units immediately adjacent.

Discussion

Overall, we detected significant spatial and temporal variation in the ground beetle community at Konza Prairie. Some of this variation was related to fire and the mosaic landscape structure that fire creates (Figures 3–4 and Tables 1–6). However, the magnitude of these effects was rather minor compared to temporal variation (differences between the spring and fall faunas, including a strikingly consistent phenological pattern (Figures 2–3), and variation between years) and to variation from undetermined sources. Dominant species tended to occur widely across different burn regimes and gross vegetation types. Ordination analyses indicate that major components of community variation were associated with differences between the spring and fall faunas, and to some degree with management type. In general, the landscape mosaic of different fire frequencies and vegetation types at Konza Prairie does not appear to have had an overwhelming influence on the structure of the ground beetle community.

Temporal pattern

Although overall numbers were strongly variable among years, the timing of the two peaks in carabid activity was strikingly consistent (Figure 2). This differs from the single mid-season peak reported in South Dakota (Kirk 1971) and Iowa grasslands (Larsen and Williams 1999). Kansas is warmer in spring and hotter and dryer in summer than are northeast Iowa and South Dakota, so this phenological difference may reflect differences in temperature and rainfall. Eastern Washington, a more northerly but much more arid locality than Konza Prairie, also has a bimodal pattern (Rickard 1970), suggesting that precipitation may be an important factor in determining community-level phenology. Although life histories vary, temperate carabids in general are thought to primarily breed in either spring or fall (Thiele 1977), so our seasonal peaks may represent members of these two ecological groups, in effect distinct 'temporal guilds'.

Most carabids at Konza Prairie were much more active in one season than in the other (Table 4), a common pattern for the group as a whole (Thiele 1977; Epstein and Kulman 1990). Species appearing early in the season likely overwintered as adults, while species active at other times may have represented a cohort laid as eggs earlier in the season, or survived through the winter at the egg stage (Thiele 1977). Overall, phenology was strong and consistent, representing a major source of pattern in our datasets. These patterns suggest the importance of life history variables for determining patterns observed at the community level.

Effects of fire frequency

Considering the number of analyses and statistical tests we performed (Table 3), we found comparatively little evidence that fire frequency has strong effects on ground beetle diversity measures. Between 1997 and 1999, in aggregate samples species richness and H' were slightly higher on units burned at 4 year intervals (Table 1). However, these differences were small in magnitude, and the trend in richness may be related to the shape of accumulation (collection) curves, as overall abundance was also higher in 4-year burn treatments. Fire frequency was not a significant predictor of any measure in Spring samples in GLM analyses (Table 3), although it did appear in a significant interaction with topographic position in Fall samples. This suggests that fire frequency has some effect on richness in the Fall, particularly in upland locations. This is intriguing, as uplands generally face the harshest abiotic conditions, with greater exposure to summer heat and thinner soils than other areas. Overall, however, given that topographic position had only one main effect significant at the 0.05 level (Fall total carabids captured) and fire frequency had none, we must conclude that neither factor had a strong, consistent effect on the these gross beetle community measures.

Detrended correspondence analysis of the 1997–1999 data, in contrast, revealed comparatively clear effects of season and fire frequency on the Konza Prairie carabid community, especially in the Spring (Figure 3). Within each season, communities sampled on yearly burned units occurred towards one end of the axis, and communities from units burned every 20 years towards the other. Uplands and annually burned units at Konza tend to be dry and have little vegetation cover, and lowland and unburned sites tend to be wetter and have more plant biomass (Briggs et al. 1992; Knapp et al. 1998a), so interpretation of the primary DCA axis (Figure 3) is consistent with a field gradient in vegetation biomass, from low to high structure (from left to right in figure). Separation by season is also consistent with this, as units begin the spring with comparatively little aboveground vegetation structure (even in unburned units, due to stem breakage and snow packing over the winter), then accumulate it over the growing season.

Examination of species composition among management types indicates that any effects of fire are manifested not in changes in diversity or wholesale changes in species composition, but in variation in abundance of the most common species. Three of the eleven most common species have significant differences in abundance among fire treatments, and several others have clear trends (Table 4). All but one carabid species occurring in total abundance > 20 between 1997 and 1999 were detected in all three fire treatments, although numerous species were captured too infrequently to judge. Species also tended to occur in all topographic categories, unless very uncommon, and between-year variation was similar for most species. This pattern of habitat generalization is consistent with Larsen and Williams' (1999) study, where all species noted > 5 times were detected in all three treatments. Individual ground beetles at Konza likely travel widely around the prairie landscape either on foot or by flight (as is common for the taxon (den Boer 1970; Thiele 1977; Evans 1983)), which indicates that populations may quickly recognize and colonize new habitat, or at least can tolerate a variety of microhabitats.

Effects of vegetation heterogeneity

When sampling across different gross vegetation types at Konza in 2000, we found broadly similar patterns to those observed when sampling across burn regimes (see above). Higher diversity was observed in the gallery forests, which seems to be related to relatively high evenness (common species were less numerically dominant there), and to the occurrence of several species appearing in very small numbers. All species where >8 individuals were captured were detected in all four habitats, indicating that variation observed in the DCA analysis was influenced by contrasts in abundance of the most common species. Of the two reasonably abundant species found to be rarer in more open habitats, only *Dicaelus elongatus* is arguably dependent on the woody habitats (it is generally known to prefer shaded ground, and moderately moist soil; Larochelle and Larivière (2003)). *Pterostichus permundus*, although seemingly dependent on woody habitats in 2000, was found to be abundant in open habitats in the much more substantial 1997–1999 samples (Tables 4–5).

It is possible that these differences in abundance represent mass effects (Shmida and Wilson 1985; Holt 1997). These potentially occur when distinct habitats are juxtaposed, in each of which a subset of a regional species pool predominates. Given recurrent dispersal, there can be a spillover of individuals out of a species' preferred habitat, into habitats where their populations are not really self-sustaining. This seems most likely when considering small patches of woody vegetation, which using DCA to characterize variation proved to be very similar in composition and relative abundance to the open prairies which surround these habitats, in both the fall and spring (Figure 4). Previous studies in terrestrial systems (e.g., Cook et al. 2002) reveal that the communities of small habitat patches can be strongly influenced by the community of the surrounding habitat matrix. But we should caution that our methods do not directly document movements of individuals, and most species have been documented in a wider range of habitats than what is available at Konza (Larochelle and Larivière 2003). In the absence of any direct evidence of mass movements, the observed distributional patterns suggest that many of the common species in the Konza Prairie ground beetle community are sufficiently adaptable to survive in habitats with dramatically varied vegetation structure. If this is the case, then we must conclude that the juxtaposition of habitats with dramatically different vegetation structure does not necessarily have a detectable effect on cumulative species richness or community structure, at least in the Konza ground beetle community.

Short-term burn effects

In the experiments undertaken in 2001, we found no evidence that species accumulation in a landscape unit in the weeks following a fire results from colonization from an adjacent unburned unit (Table 6). The only apparent short-term population response to fire occurred in *Cyclotrachelus sodalis*, which spiked in burned units shortly after fire. Two potential explanations of this type of 'colonization' are consistent with the data: long-distance movements, and emergence from underground, with activity stimulated by the burn. These results provide no obvious support for the idea that patterns of local beetle diversity or species composition depend strongly on fire frequency, or on the structure of a landscape created by mosaic fire treatments.

Implications

The carabid beetle community at Konza Prairie exhibits complex responses to fire frequency, topographic position, landscape heterogeneity and season. Fire frequency, and the heterogeneous landscape formed by variation in the application of fire, both had discernable effects on the beetle community, but these were mostly manifested in shifts in the abundance of common species. These species generally were typically present in most treatments and habitat types. When 'new' habitat was made available by a fire, our observations were consistent with the hypothesis that species which soon populated these areas either arrived from significant distances away, or emerged from underground. There was no obvious spatial signal, in terms of clear and evident colonization from adjacent habitats, to fire disturbance. These general results suggest that ground beetles, a key group within the prairie arthropod community, form a resilient and ecologically generalized assemblage which may not be dramatically affected by regional changes in fire frequency or spatial arrangement of managed units. Few species in the Konza community are demonstrably and negatively influenced by annual burning, and the evidence that mosaic burning boosts site-wide species richness is equivocal at best. The most specific recommendation that we can take from our study is to avoid applying only one extreme fire regime (very high or low frequency) over very large areas for long periods of time (see 'Principle 7' from Burrows and Abbott 2003).

There remain some caveats to these conclusions, however. First, to our knowledge, none of the species in the Konza ground beetle community are mesic prairie specialists. Most of the species observed at Konza are actually documented widely across North America in a variety of habitats (Arnett 2000; Larochelle and Larivière 2003); indeed, the authors have regularly observed several taxa outside of the prairie, in suburban garages, and even in University offices (WMC, personal observation). Other authors have concluded that grassland burning may increase, or at least does not affect, carabid abundance (van Amburg et al. 1981; Larsen and Williams 1999). It may be that there are specialist tallgrass prairie taxa sensitive to fire, but missing at Konza. Given that the Konza represents a large reserve embedded in the largest remaining tract of tall grass prairies (Knapp and Seastedt 1998), and the generalist nature of the taxon, this seems to us an unlikely scenario. Nevertheless, we cannot rule out that undetected and unknown specialist species may have been driven to extinction by historic patterns of land management in the region; this possibility, however, will have to remain speculative and largely unprovable.

Second, we also observed a large number of species that were present in small numbers, sometimes only in one treatment or habitat. While the patterns at the community level may be intriguing, despite our large total sample size the sample sizes for many species are too small to forge any meaningful conclusions about individual species responses and habitat requirements. This general situation is a common one in insect community ecology. It is possible that some of these rarer species are much more sensitive to burn treatments and landscape structure than the dominant species for which we have adequate sample sizes to carry out statistical analyses.

Overall, Konza Prairie carabid communities appear to be relatively robust to change in fire frequency. While somewhat encouraging in the context of wider conservation issues, this conclusion likely cannot be generalized to other taxa in our tallgrass prairie system. Carabid beetles as a group can be expected to be more flexible in response to landscape change than are many other insect taxa. As Thiele (1977) notes (in Chapter 8), carabids are largely generalist predators, an ecological role that implies the capability to exploit a variety of invertebrate prey and an ability to travel significant distances. Species of carabids are not often closely associated with specific species of plants or prey (which may become locally extinct after a fire). Carabids have been documented to travel up to 80 m on the ground over short spans of time; it seems reasonable to assume that at least some of the Konza species are capable of traveling at least dozens of meters in a day, and possibly hundreds of meters over longer time scales. Additionally, many carabids can fly, which would allow individuals to colonize newly burned areas from neighboring or more distant landscape units within short periods of time. Carabids can also sometimes retreat underground for the short duration of a grassland burn. All of these features of basic carabid biology may make them relatively resistant as an assemblage to shifts in fire frequency or landscape structure.

Other arthropod taxa have a wide variety of life history characteristics, many of which make them much more susceptible to fires than carabids appear to be (Swengel 2001). Different insect taxa can be negatively affected by grassland fires (Fay and Samenus 1993; Panzer and Schwartz 1999; Panzer 2003). Several authors have recently concluded that vertebrate populations are negatively impacted by annual prairie burning (Kaufman and Kaufman 1997; Zimmerman 1997; Rohrbaugh et al. 1999; Sieg et al. 1999), and the greater prairie-chicken (*Tympanuchus cupido)* may be at risk of extinction because of annual burning combined with livestock grazing (Robbins et al. 2002). A mosaic of fire frequencies clearly would benefit the latter species, as it would provide both open areas for mating aggregations and more densely vegetated areas for food and cover. Fire has striking effects, both positive and negative, on many prairie ecological processes (Collins and Wallace 1990; Collins and Steinauer 1998), our study notwithstanding.

Overall, while changes in fire frequency and mosaic burning seem to have comparatively small effects on the ground beetle community of Konza Prairie, our study taxon may not be representative of larger patterns in the tallgrass prairie system. Communities are comprised of species with widely differing responses to disturbance (Setser and Cavitt (2003), working at the same site, recommend a landscape fire mosaic to sustain snake populations), and we urge caution in the application of our conclusions about the modest effects of fire on carabid assemblages to the effects of fire on other taxa. It would appear that carabid beetle assemblages are relatively robust to changes in fire frequency, and thus should be unlikely to be of immediate conservation or management concern, at least in the Konza tallgrass prairie landscape.

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