

Patch-burn grazing increases habitat heterogeneity and biodiversity of small mammals in managed rangelands

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Abstract. Habitat heterogeneity is a key driver of biodiversity in many ecosystems. Wildlife inhabiting the native prairies of North America evolved in a heterogeneous mosaic of habitat conditions created by fire and grazing by native ungulates. Current rangeland management practices in the tallgrass prairie ecosystem evenly distribute fire and grazing across management units and promote homogeneous habitat conditions. Patch-burn grazing is a rangeland management strategy that seeks to restore heterogeneity to rangelands via fire-grazing interactions. Our 3.5-year study tested the effects of patch-burn grazing on habitat heterogeneity and small mammal community dynamics in the Flint Hills ecoregion of eastern Kansas. To study the ecological effects of patch-burn grazing, we sampled habitat conditions and the small mammal community. We assessed habitat conditions once each growing season in a negative control that was annually burned and grazed, a positive control that was burned every four years and ungrazed, and within each of three units of a patch-burn grazing experiment (PBG) managed with rotational fire. Habitat conditions were significantly different among treatments, and a principal components analysis showed that the patch-burn grazing treatment had higher canopy cover of forbs and habitat heterogeneity than our two control units. To sample the small mammal community, we conducted monthly live trapping of small mammals on two randomly located trap grids in each of our two controls and three units of our PBG treatment. Small mammal diversity was significantly higher in the patch-burn grazing treatment and in the positive control, vs. the negative control. Moreover, a canonical correspondence analysis showed that a fire-grazing interaction was the major driver structuring small mammal communities. Patch-burn grazing is an effective strategy for restoring heterogeneity to vegetative structure and composition, and can increase biodiversity of small mammals in managed rangelands in the tallgrass prairie ecosystem.

Key words: fire; heterogeneity; pyric herbivory; rangeland management; rodent; tallgrass prairie.

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INTRODUCTION

Habitat heterogeneity is a key driver of biodiversity (MacArthur and MacArthur 1961, Lack 1969, Ostfeld et al. 1997, Fuhlendorf et al. 2010). In native ecosystems, habitat heterogeneity can arise from multiple drivers including nutrients, topographic conditions, and disturbance

(Fuhlendorf and Smeins 1999). The native prairies of North America evolved under pyric herbivory—a fire-grazing interaction where large ungulates preferentially graze areas that have recently burned (Fuhlendorf et al. 2009). Patches recovering from fire or grazing disturbance accumulate residual plant litter over multiple growing seasons, which reduces grazing intensity but

increases fuel load and the probability that a patch will burn again and restart the cycle (Fuhlendorf and Engle 2001, 2004). Patches in different states of recovery from fire and grazing across the landscape differ in vegetative composition and structure, and the resulting mosaic can provide habitat heterogeneity and promote biodiversity among native species of wildlife (Fuhlendorf and Engle 2004, Sandercock et al. 2015).

The tallgrass prairie ecosystem once covered ~67 million ha in the United States, but now has been reduced by more than 96% (Samson and Knopf 1994, DeLuca and Zabinski 2011). The Flint Hills ecoregion of Kansas and Oklahoma contains the largest remaining area of native tallgrass prairie in North America (Knapp and Seastedt 1998). The ecoregion supports an economically important grazing industry, and >95% of the area is privately owned (Hickman et al. 2004, With et al. 2008). Therefore, current rangeland management practices determine the quality of prairie habitat available to the native fauna (Fuhlendorf and Engle 2001, 2004, Churchwell et al. 2008). Common rangeland management practices in the Flint Hills include prescribed burning in the spring, followed by intensive early stocking with steers and heifers, or season-long stocking with cow-calf pairs (Wilds and Nellis 1988, With et al. 2008). Prescribed fire is widely used and up to 48% of the area of the Flint Hills may be burned in a given year, causing air quality issues for nearby urban centers (KDHE 2010, Mohler and Goodin 2012). Spring burns are typically applied to an entire pasture, which evenly distributes livestock and grazing intensity across the vegetation in a grazing unit (Fuhlendorf and Engle 2001). Annual burning coupled with intensive grazing prevents accumulation of residual plant material, so that vegetative cover is limited to the plant biomass that exceeds grazer utilization. Current rangeland management practices lead to homogeneity of structure in grassland ecosystems, with a limited number of functional niches for native species, leading to negative impacts on plant and animal biodiversity (Coppedge et al. 1998, 2008, Fuhlendorf et al. 2012).

Patch-burn grazing is an alternative rangeland management practice that has been proposed to employ pyric herbivory to mimic historical disturbance patterns that increase landscape

heterogeneity (Fuhlendorf and Engle 2001). Patch-burn grazing is managed with rotational fire and only a portion of a grazing unit is burned each year, instead of the entire grazing unit. Cattle are given access to the entire grazing unit without cross-fencing, and stocking densities are comparable to traditional grazing systems such as intensive early stocking or season-long stocking. Patch-burn grazing creates diverse microhabitats needed to fulfill the life cycles of grassland animals, such as the dense litter layer preferred by some small mammal species and vegetative cover needed for concealment by ground-nesting birds (Clark and Kaufman 1991, McNew et al. 2015, Sandercock et al. 2015). Patch-burn grazing is not widely used on private lands, but has the potential to improve biodiversity of grassland invertebrates (Engle et al. 2008), herpetofauna (Wilgers and Horne 2006), birds (Fuhlendorf et al. 2006, Coppedge et al. 2008, Holcomb et al. 2014, Hovick et al. 2014, Augustine and Derner 2015), and small mammals (Fuhlendorf et al. 2010).

Small mammals are an ecologically important group that impact ecosystems in various ways. Rodents and shrews are facilitators of ecosystem processes through their burrowing activity and nitrogen deposition (Laundre 1993, Ross et al. 2007), important prey items for mesocarnivores (Sperry 1941, Fichter et al. 1955, Brillhart and Kaufman 1994, 1995), raptors (Fitch et al. 1946, Huebschman et al. 2000), and snakes (Trauth and McAllister 1995, Colston et al. 2010), and can influence plant diversity through granivory or herbivory (Howe and Brown 2000, Reed et al. 2004, Ross et al. 2007, Bricker et al. 2010, Maron et al. 2012). Moreover, small mammals are short-lived species with high fecundity and short generation times that are likely to respond quickly to changes in environmental conditions (Reed et al. 2007). Therefore, small mammals are likely to be a useful indicator for the effects of rangeland management strategies on biodiversity.

Our goals for this field study were twofold. First, we tested the effects of patch-burn grazing on habitat conditions in the tallgrass prairie of the northern Flint Hills. Second, we tested the potential effects of patch burning on richness, diversity, and community structure of small mammals in the northern Flint Hills. We predicted that patch-burn grazing would increase heterogeneity in vegetative composition and

structure in tallgrass prairie and that greater habitat heterogeneity should increase species richness and diversity of the small mammal community.

METHODS

Study site

Our research project was conducted at the Konza Prairie Biological Station (hereafter, Konza Prairie), a 3487-ha prairie preserve in the Flint Hills ecoregion of northeast Kansas. Konza Prairie is a core Long-Term Ecological Research (LTER) site funded by the National Science Foundation. The biological station is a landscape-level fire and grazing experiment that is divided into >60 experimental units, with replicated units that receive different combinations of prescribed fire and grazing treatments (Fig. 1). Native warm season grasses such as big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), and switchgrass (*Panicum virgatum*)

dominate the plant community at Konza Prairie. Forbs are diverse, but dominant species include goldenrod (*Solidago* spp.), Baldwin's ironweed (*Vernonia baldwinii*), leadplant (*Amorpha canescens*), and round-head bush clover (*Lespedeza capitata*). Common woody shrubs include the following: rough-leaf dogwood (*Cornus drummondii*), wild plum (*Prunus americana*), smooth sumac (*Rhus glabra*), fragrant sumac (*R. aromatica*), inland ceanothus (*Ceanothus herbaceus*), and buckbrush (*Symphoricarpos orbiculatus*; Towne 2002).

A large-scale patch-burn grazing experiment (PBG) was initiated in 2010 and includes roughly the eastern third of the biological station (Fig. 1). The PBG replicates were subdivided into three patches, with one patch being burned each year on a rotational basis. Cattle had access to the entire management unit without cross-fencing. We included an annually burned and grazed treatment as a negative control (ABG), and an ungrazed treatment that was burned every

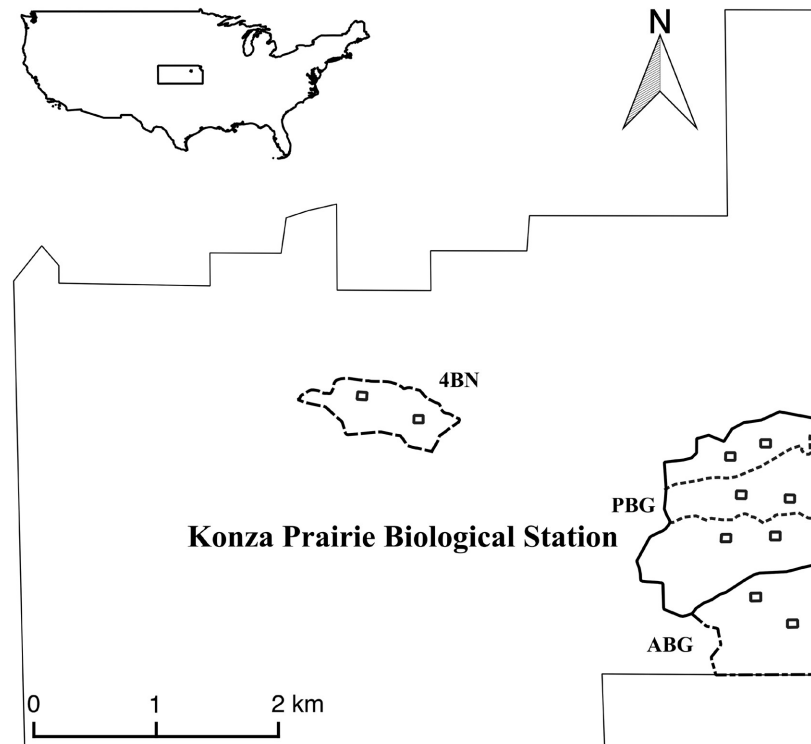


Fig. 1. Map of study site showing locations of treatments and trapping grids at Konza Prairie Biological Station, Kansas, United States. Treatments included a negative control that was annually burned and grazed (ABG), three units of the patch-burn grazed treatment (PBG), and a positive control that was ungrazed with a 4-year fire-return interval (4BN). Squares outline our 10 randomly located trap grids.

four years as a positive control (4BN). The ABG treatment was selected as a negative control, because it is a management strategy that seeks to uniformly distribute grazing disturbance across management units through the application of prescribed fire across the entire management unit. Moreover, we expected the ABG treatment to contain a reduced small mammal community dominated by disturbance positive species (Clark et al. 1989). We selected the 4BN treatment as a positive control, because previous research at Konza Prairie indicated that ungrazed sites not recently burned would likely contain more disturbance negative species (Clark et al. 1989, Rehmeier et al. 2005). Moreover, the 4BN treatment was ungrazed, but the 4-year fire-return interval was comparable to the 3-year fire-return interval in our PBG treatment. PBG and ABG sites were stocked with cow-calf pairs at a density of one pair per 3.24 ha for a 5-month grazing season from early May to early October each year. Patch size of units within the PBG treatment was 48.7–102.4 ha, and ABG and 4BN treatments were 93.8 and 54.5 ha, respectively.

Habitat composition and structure

We conducted habitat sampling in June and July of 2011–2014, including two drought years (2011–2012). We sampled habitat conditions during the mid-growing season, after cattle had reduced standing biomass in the grazed treatments. Habitat measurements were recorded at five points along eight 300-m transects in the grazed and ungrazed controls, as well as in each of patch of the PBG treatment. We quantified percent canopy cover of three major plant functional groups (grasses and sedges combined, broadleaf forbs, and woody shrubs), as well as percent cover of bare ground and dead plant litter with a 25 × 50 cm Daubenmire frame (Daubenmire 1959). We measured litter depth to the nearest 0.5 cm in the lower left corner of the Daubenmire frame. Visual obstruction readings (VORs) were measured using a standard Robel pole with 13 1-dm increments (Robel et al. 1970). At each sample point along each transect, we recorded visual obstruction at a distance of 4 m from the Robel pole and at a height of 1 m in each cardinal direction from the pole, for a total of four VORs per point. We measured percent canopy cover of habitat variables at three distances (0, 2, and 4 m) in

each cardinal direction from the Robel pole, for a total of 12 measurements of percent cover at each point along each transect. We averaged the 12 values to obtain a single overall measurement of each habitat variable per point. Our total sample size of points for each treatment and subtreatment was 160 points. A few points were censored due to observer errors, and our total sample sizes for habitat measurements over the four growing seasons ranged from 140 to 150 points per treatment.

Small mammal diversity

We established two trap grids for sampling small mammal communities in each of the three PBG patches and two controls, for a total of 10 grids (Fig. 1). Grid locations were selected at random, but subject to two constraints. To maintain independence among trap grids, grids were separated by at least 200 m, which corresponds to twice the length of the longest published home range axis for deer mice (*Peromyscus maniculatus*), the most abundant species of small mammal encountered in native prairie (Douglass et al. 2006, Yarnell et al. 2007). Trap grids were also located at least 100 m from unit boundaries to avoid potential boundary effects, and > 50 m from permanent or regularly flowing water to avoid flooding of traps during runoff from thunderstorms (Konza LTER data sets: GIS210 and GIS211).

Each trap grid was a five-by-five square design with 25 stations and 20-m spacing between adjacent trap stations for a total area of 0.64 ha. Two extra-large Sherman live traps were set at each trap station for a total of 50 traps per grid (Model LNG 12; H.B. Sherman Trap Company, Tallahassee, Florida, USA). Traps were baited with a mixture of peanut butter and rolled oats, and each trap was provisioned with polyester fiberfill to keep animals warm during October to May (Kaufman et al. 1988). To reduce heat stress to diurnal mammals, wooden A-frame structures (hereafter, trap shelters) were placed over traps for shading (Kaufman and Kaufman 1989). Trap shelters were left in place all year for weathering and to minimize potential neophobic responses of small mammals to trap stations. Our trap and bait combination effectively sampled a wide suite of the small mammal community at our site, and we captured animals ranging in mass from least shrews (*Cryptotis parva*; 3 g) up to subadult eastern cottontail rabbits (*Sylvilagus floridanus*; 400+ g).

During our 3.5-year study from June 2011 to December 2014, small mammals were trapped for three consecutive nights each month at 10 trapping grids in the PBG treatment, and ABG and 4BN controls. We marked small mammals with passive integrated transponders (PIT tags hereafter; Model AB10320, FDX-B 7 × 1.35 mm; Loligo Systems, Tjele, Denmark; or “Skinny” FDX-B 8 × 1.4 mm; Oregon RFID, Portland, Oregon, USA), and read tags with a handheld reader (Model APR 350 FDX/HDX Reader; Agrident, Manassas, Virginia, USA; or DataTracer FDX/HDX Reader; Oregon RFID). Passive integrated transponders were injected subcutaneously under loose skin at the nape, and massaged away from the insertion site to ensure tag retention. To obtain an estimate of PIT tag retention, 28% of the rodents were tagged with numbered monel ear tags (model 1005-1; National Band and Tag Company, Newport, Kentucky, USA). Passive integrated transponder losses were rare (<1%) and no corrections for tag loss were needed (A. M. Ricketts, unpublished data). All procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocols 3034 and 3443), and conducted under state wildlife permits from Kansas Department of Wildlife, Parks, and Tourism. Trap grids were sampled in 9 of 12 months per year with some trapping sessions missing due to inclement winter weather, or unpredictable winds during prescribed burns in March.

Statistical analyses

Habitat, species richness, and diversity.—All statistical analyses were conducted in R (version 3.2.2; R Core Team 2015). We used functions in the base package to test for differences among fire and grazing treatments using ANOVA or MANOVA. If a test statistic was significant, we made pairwise comparisons among treatments and years using post hoc Tukey’s tests. Additionally, we conducted a principal components analysis (PCA) on our scaled habitat data to examine relationships in habitat structure and composition among treatments. We opted to exclude percent cover of litter and shrubs from our PCA. Canopy cover of litter underestimates the amount of litter present, because standing vegetation obscures litter from above. We retained litter depth as a structural habitat

component needed by some small mammals. Shrub cover was removed from the habitat data set for the PCA, because we were primarily interested in the effects of PBG on grassland habitat, and shrubs were a minor habitat component in most treatments (<8%), except 4BN (~19%).

Species richness and diversity.—We tested for differences in the number of species of small mammals (hereafter, species richness) encountered in each treatment during each biological year. Biological years were defined as the first trapping session after a spring burn until the last trapping session prior to a burn the following spring. Treatment watersheds were usually burned during March, so the biological year of our study period ran from April to the following March. We used biological years instead of calendar years because spring fires drastically alter habitat conditions in tallgrass prairie, and effectively reset the community dynamics of small mammals at the start of the growing season (Clark and Kaufman 1990). We calculated the Shannon diversity index (hereafter, species diversity) for each grid per biological year. Here, we used the total number of captures of each species per 100 trap-nights and used the “diversityresult” function in the BiodiversityR package of R (Kindt and Coe 2005). We then used model selection based on Akaike information criterion corrected for small sample size (AIC_c) to identify the ANOVA models that best fit our data for species richness and diversity. Candidate model sets for species richness and diversity included the effects of state, treatment, biological year, a constant model, and models with additive (+) or interactive (×) effects. *State* models compared five treatments: ABG, PB0, PB1, PB2, and 4BN, where numbers following PB indicate time since fire for a given patch. *Treatment* models pooled the three PBG patches and compared three treatments: ABG, PBG, and 4BN. In preliminary analyses, we tested for but found no evidence for grid effects within treatments and we treated replicate grids as independent samples for further analyses (A. M. Ricketts, unpublished data).

To investigate the relationship between community dynamics of small mammals and our three treatments, we conducted a canonical correspondence analysis (CCA) on the number of captures per 100 trap-nights (CPUE) data for each

species using the vegan package of R (Oksanen et al. 2015). The small mammal data were constrained by four explanatory variables: treatment, year of study, time since fire (years), and grazing treatment (grazed or ungrazed). We did not test for the effects of state in the CCA, because state and time since fire were confounded in our PBG treatment. Prior to conducting the CCA, we standardized our CPUE data for trapping grids so that row totals in the community matrix were equal to 1 with the “total” standardization in the function “decostand” in R package vegan, and then further standardized the data by dividing values for each species by the highest value in the community matrix for that species with the “max” standardization of function “decostand” in R package vegan. Dominant species can drive ordination analyses, especially in small communities with few species (ter Braak 1994). Our scaling procedure was a reverse Wisconsin double standardization, and effectively reduced the influence of dominant species on the ordination (Holland and Patzkowsky 2004). Variance inflation factors for all explanatory variables were less than two, so there was no need to exclude any variables from our CCA during model selection. We identified the CCA model that best fit our data using stepwise AIC_c model selection. Last, we used variance partitioning to determine the amount of variation in the small mammal community explained by each explanatory variable retained in the top CCA model (function “varpart,” R package vegan).

RESULTS

Habitat responses

Across the four years of our study, habitat conditions differed significantly among the negative control (ABG), patch-burn grazing treatments (PBG), and positive control (4BN) in June and July (Wilk’s $\lambda = 0.27$, $F_{4,710} = 39.2$, $P < 0.001$). Canopy cover of grass was significantly lower in the year-of-fire patch than the other treatments and increased with time since fire within the PBG treatment. The 4BN treatment had significantly lower grass cover than the ABG treatment ($F_{4,710} = 25.1$, $P < 0.001$; Fig. 2A). Forb cover was highest in the 1-year-since-fire patch of the PBG treatment, and lowest in the 4BN treatment ($F_{4,710} = 38.5$, $P < 0.001$; Fig. 2B). Shrub cover was low overall and less than 20% of all treatment areas, but was highest in the 4BN treatment

($F_{4,710} = 36.2$, $P < 0.001$; Fig. 2C). Our 4BN treatment was established in 1980, and shrub cover in this unit was relatively high at the beginning of our study in 2011 (>16%). Bare ground decreased with time since fire, and was significantly different among each treatment and subtreatment ($F_{4,710} = 133.2$, $P < 0.001$; Fig. 2D). Both litter depth and VOR increased with time since fire within PBG, and were highest in the 4BN treatment ($F_{4,710} = 129.9$, $P < 0.001$, Fig. 2E; and $F_{4,710} = 36.6$, $P < 0.001$, Fig. 2F).

Our PCA revealed substantial heterogeneity in habitat structure and composition among patches within PBG, and each treatment had a distinct habitat structure and composition (Fig. 3). Principal components analysis axes 1 and 2 had eigenvalues of 1.95 and 1.25, and explained 39% and 25% of the variation in our habitat data, respectively. Loadings of variables on PCA axis 1 were ranked: percent cover of bare ground (+0.62), litter depth (−0.56), and VOR (−0.50). For PCA axis 2, the most important variables were percent cover of forbs (+0.74) and grass (−0.54). Principal components analysis axis 1 was associated with differences in habitat structure, whereas PCA axis 2 was associated with differences in habitat composition.

Small mammal community responses

From June 2011 to December 2014, we captured 1902 unique individuals of 11 species of small mammals, for a total of 6830 handling events during 52,500 trap-nights of sampling effort (Table 1). Our top ANOVA for species richness was a main-effects model with the effects of treatment ($F_{2,34} = 3.7$, $P = 0.04$) and year ($F_{3,34} = 9.7$, $P < 0.001$; Table 2). Treatment 4BN had significantly higher species richness at 7.5 species per grid per year than treatment ABG at ~5.5 species per grid per year (Fig. 4A), and 2013 and 2014 had significantly higher richness across all treatments than 2011 and 2012. Our top ANOVA for Shannon diversity index was a main-effects model with the effects of state ($F_{4,32} = 19.2$, $P < 0.001$) and year ($F_{3,32} = 9.6$, $P < 0.001$; Table 3). Averaged across four years and two grids per treatment, species diversity was lowest in the ABG treatment at 0.5, and increased from 0.8 in PB0 to 1.3 in PB2, and to 1.2 in treatment 4BN (Fig. 4D). Diversity was significantly lower in the drought year of 2012 (0.7) than the other three years of our study (0.9–1.2).

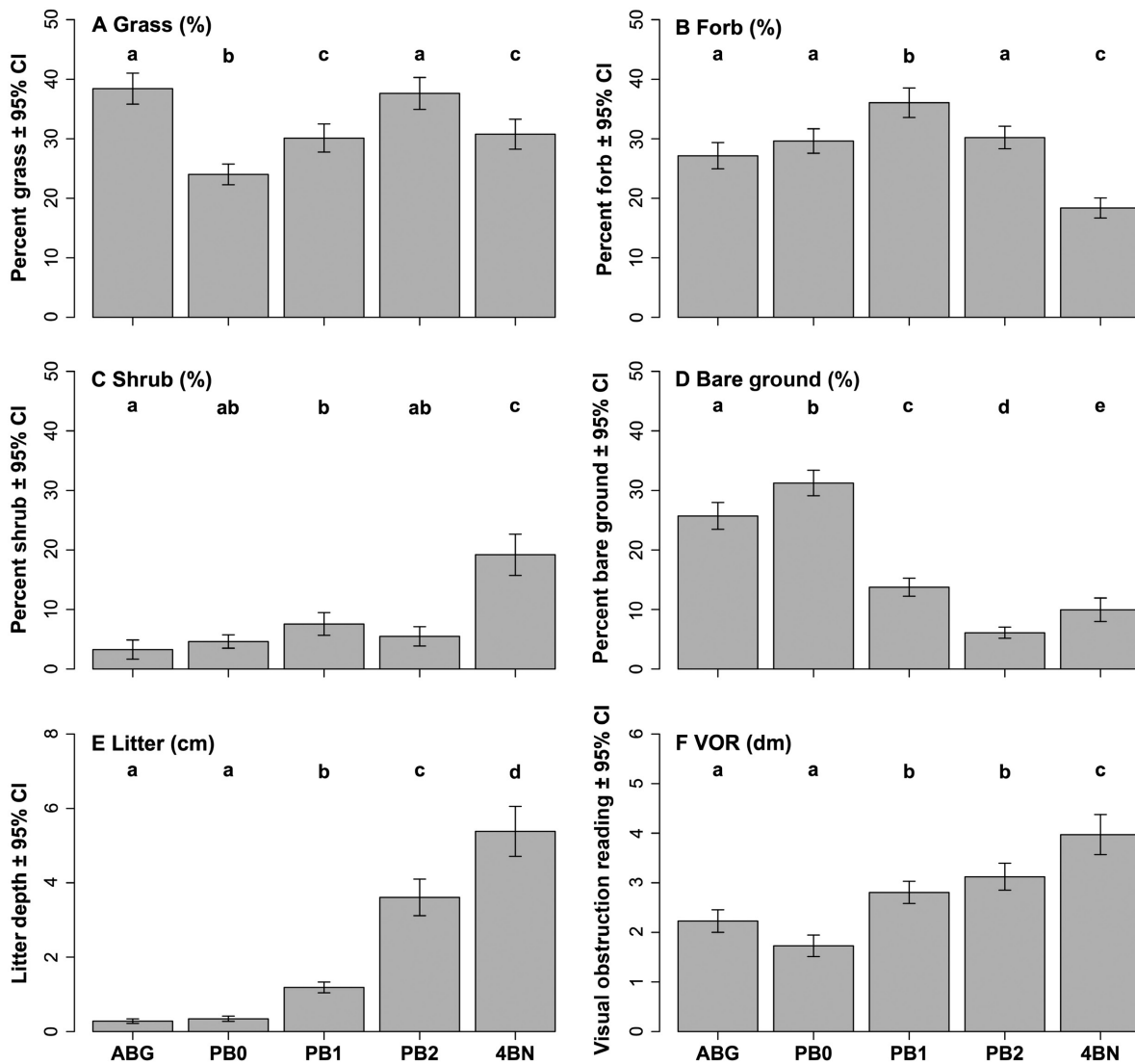


Fig. 2. Percent cover of grasses and sedges (A), forbs (B), shrubs (C), and bare ground (D), litter depth (E), and vegetation structure as visual obstruction reading (F) in an annually burned and grazed treatment (ABG), patch-burn grazed units (PB0–2), and an ungrazed treatment with a 4-year fire-return interval (4BN) at Konza Prairie Biological Station, Kansas, United States, from 2011 to 2014. Bars sharing letters above confidence intervals indicate nonsignificance. Sample sizes for each treatment were 140–150 points.

Stepwise AIC_c model selection indicated that our top CCA model for describing our small mammal communities included the effects of time since fire, grazing treatment, and year. Collectively, these three factors explained 47.6% of the variation in our small mammal community data. Our top CCA model produced five axes, and permutation tests indicated that the first four CCA axes explained significant variation

(Table 4). CCA axes 1 and 2 had eigenvalues of 0.31 and 0.21, and explained 18.4% and 12.8% of the variation in small mammal communities, respectively (Fig. 5). CCA axes 3 and 4 each explained less than 10% of the variation in the small mammal communities, and we did not consider these axes further (Table 4). Factor loadings indicated that CCA axis 1 was strongly associated with time since fire and grazing treatment,

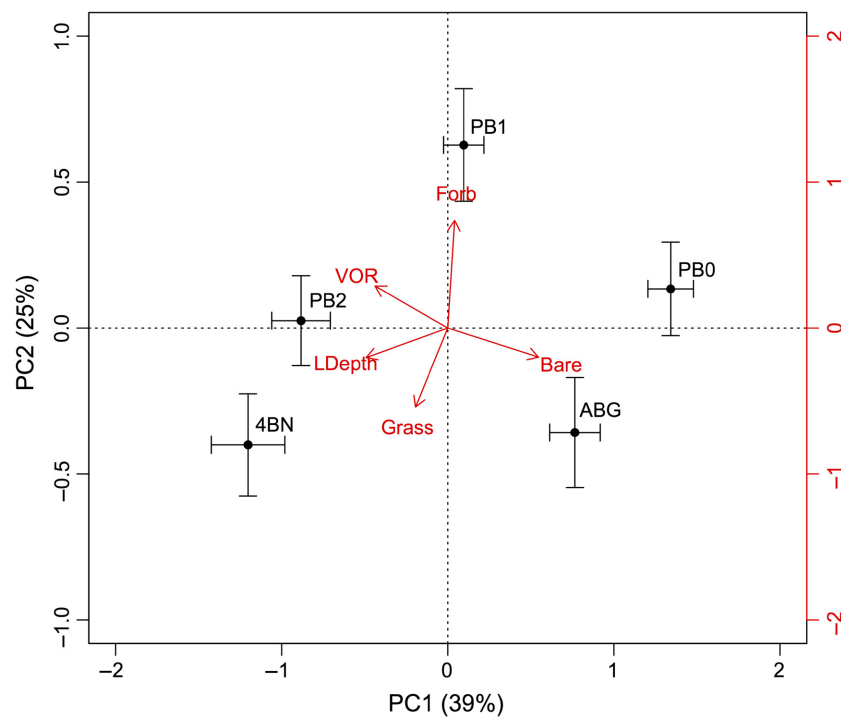


Fig. 3. Mean scores ($\pm 95\%$ CI) from the first two axes of a principal components analysis (PCA) of habitat measurements in a negative control that was annually burned and grazed (ABG), each patch of the patch-burn grazed treatment (PB0–2), and a positive control that was ungrazed with a 4-year fire-return interval (4BN) from June 2011 to December 2014 at Konza Prairie Biological Station, Kansas, United States. Red arrows illustrate loadings for percent canopy cover of grasses and sedges, forbs, and bare ground, as well as litter depth and visual obstruction reading (VOR). Numbers following PB indicate time since fire within the PBG treatment (0–2 yr).

but axis 2 was primarily associated with year effects (Fig. 5). Species with low scores for CCA axis 1 were associated with high disturbance (e.g., deer mice [pema] and 13-lined ground squirrels [ictr]), whereas species with high axis 1 scores were associated with longer time since fire and low grazing pressure (e.g., hispid cotton rats [sihi]), or woody vegetation (e.g., eastern wood rats [nefl] and white-footed mice [pele]). Variance partitioning indicated that year effects, grazing activity, and time since fire accounted for 17%, 15%, and 9% of the variation in the composition of our small mammal communities, respectively.

DISCUSSION

Our 3.5-year field project is one of the first field studies to examine the effects of patch-burn grazing on the community structure of small mammals, and our work resulted in three major

findings. First, patch-burn grazing created greater heterogeneity in vegetative structure and composition of plant functional groups, which was absent from the more homogeneous conditions in a negative control that was annually burned and grazed, and a positive control that was ungrazed with a 4-year fire-return interval. Second, habitat heterogeneity created by the interaction of fire and grazing had positive effects on both biodiversity and community structure of small mammals. Species richness and diversity were high in the patch-burn grazed treatment and comparable to our positive control. Last, our CCA showed that a large ecological niche was created by the patch-burn grazed treatment, and the niche encompassed the annually burned and grazed treatment, but was separate from an ungrazed treatment with a 4-year fire-return interval.

Our finding that patch-burn grazing increased habitat heterogeneity compared with the positive

Table 1. Total number of unique individuals for the 11 species of small mammals captured at Konza Prairie Biological Station, Kansas, United States, from June 2011 to December 2014.

Species	Negative control	Patch-burn grazing				Positive control	Total
	ABG	PB0	PB1	PB2	PBG	4BN	
Deer mouse (pema)							
<i>Peromyscus maniculatus</i>	217	216	160	100	476	58	751
White-footed mouse (pele)							
<i>Peromyscus leucopus</i>	14	85	67	86	238	168	420
Western harvest mouse (reme)							
<i>Reithrodontomys megalotis</i>	7	16	34	60	110	52	169
Prairie vole (mioc)							
<i>Microtus ochrogaster</i>	40	17	31	51	99	9	148
Hispid cotton rat (sihi)							
<i>Sigmodon hispidus</i>	1	6	12	41	59	47	107
Eastern wood rat (nefl)							
<i>Neotoma floridana</i>	3	10	12	4	26	51	80
Thirteen-lined ground squirrel (ictr)							
<i>Ictidomys tridecemlineatus</i>	16	23	23	14	60	2	78
Elliot's short-tailed shrew (blhy)							
<i>Blarina hylophaga</i>	8	8	11	27	46	11	65
Hispid pocket mouse (chhi)							
<i>Chaetodypus hispidus</i>	9	15	12	5	32	12	53
Plains harvest mouse (remo)							
<i>Reithrodontomys montanus</i>	3	6	8	6	20	2	25
Least Shrew (crpa)							
<i>Cryptotis parva</i>	0	1	0	4	5	1	6
Grand totals	318	403	370	398	1171	413	1902

Notes: Totals are given for the annually burned and grazed pasture (ABG), each patch of the patch-burn grazed pasture (PBG0–2), the patch-burn grazed pasture with all patches combined (PBG), the ungrazed treatment with a 4-year fire-return interval (4BN), and all treatments combined. Abbreviated scientific names used in Fig. 5 are given in parentheses following common names.

and negative controls was consistent with our predictions for tallgrass prairie and with previous work in Oklahoma (Fuhlendorf and Engle 2004). However, it is remarkable that patterns of heterogeneity created by patch-burn grazing were consistent among years, even when two of four growing seasons during our study experienced drought conditions (2011 and 2012). The consistency of habitat responses in a 2-year drought demonstrates that PBG can be an effective management strategy for creating habitat heterogeneity in the tallgrass prairie, even under adverse climatic conditions. Rangeland management strategies that restore heterogeneity to rangelands can also help to stabilize cattle performance during drought years (Allred et al. 2014).

The results of our gradient analysis showed that fire-grazing interactions were a key driver structuring small mammal communities in the tallgrass prairie of the northern Flint Hills. Annually burned and grazed prairie contained a small mammal community with fewer species that was dominated by generalist species such as the deer mouse.

Table 2. Candidate models and model statistics for species richness for the small mammal community at Konza Prairie Biological Station, Kansas, United States, from June 2011 to December 2014.

Model structure‡	Model statistics†				
	K	Dev	AIC _c	ΔAIC _c	w _i ≤
Treatment + year	7	134.1	151.6	0	0.672
Year	5	141.9	153.7	2.2	0.229
State + year	9	131.5	155.5	4.0	0.092
Treatment × year	13	120.8	160.8	9.3	0.007
Constant	2	163.2	167.5	15.9	0
Treatment	4	158.7	167.9	16.3	0
State	6	157.4	171.9	20.4	0
State × year	21	85.8	179.1	27.6	0

Notes: ABG, annually burned and grazed; PBG, patch-burn grazed; 4BN, 4-year fire-return interval.

† Model fit is described by the number of parameters (K), deviance or -2 log likelihood (Dev), Akaike's information criterion corrected for small sample size (AIC_c), differences in AIC_c from the minimum AIC_c model (ΔAIC_c), and AIC_c weights (w_i).

‡ State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Biological years of the study were 2011–2012, 2012–2013, 2013–2014, and 2014.

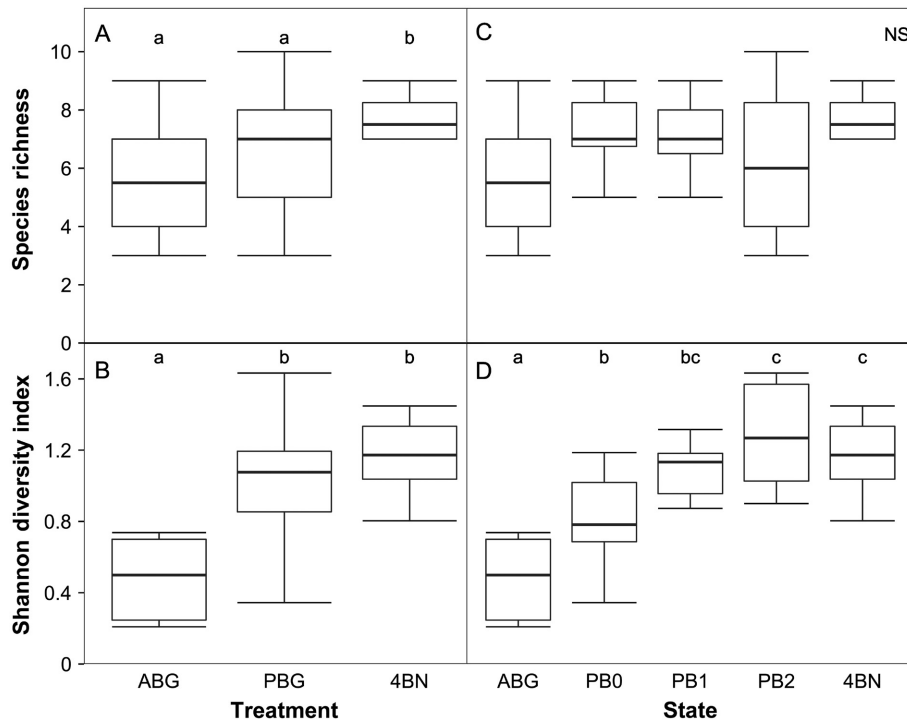


Fig. 4. Small mammal species richness (A, C) and Shannon diversity index (B, D) in annually burned and grazed (ABG), all patch-burn grazed treatments combined (PBG), each patch of the patch-burn grazed pasture (PB0–2), and the ungrazed treatment with a 4-year fire-return interval (4BN) at Konza Prairie Biological Station, Kansas, United States, from June 2011 to December 2014. Numbers following PB in the right panel correspond to time since fire for a patch (0–2 yr). Letters denote means that were significantly different in a Tukey test. NS, not significant.

In contrast, tallgrass prairie managed with pyric herbivory contained a small mammal community that encompassed the community in the ABG treatment and a larger niche based on CCA site scores in multivariate space. In the tallgrass prairie of Oklahoma, habitats in intermediate stages of recovery from disturbance were important for herbivores such as hispid cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*; Grant et al. 1982), and habitat heterogeneity increased small mammal diversity (Fuhlendorf et al. 2010).

Higher species diversity in our patch-burn grazing treatment and positive control was due to increased abundance of less common species rather than species additions. Deer mice respond positively to fire and grazing disturbance in tallgrass prairie (Grant et al. 1982, Kaufman et al. 1988, Matlack et al. 2001), and dominated the small mammal communities in our grazed treatments. However, as time since fire for a patch

increased within the PBG and 4BN treatments, relative abundance of deer mice decreased, whereas numbers of more specialist species, such as western harvest mice (*Reithrodontomys megalotis*) and hispid cotton rats, increased. Thus, the two years since fire patch contained the highest diversity of small mammals among patches (Fig. 4D). Similar patterns have been reported elsewhere for grassland bird communities. Generalist species of birds were common across all patch types within patch-burn grazed and traditional management treatments in tallgrass, shortgrass steppe, and sand sagebrush prairies, but specialist species selected different patch types and were absent from traditionally managed treatments (Fuhlendorf et al. 2006, Powell 2006, Holcomb et al. 2014, Hovick et al. 2014, Augustine and Derner 2015).

Separation of the small mammal community in our positive control without grazing and longer

Table 3. Candidate models and model statistics for Shannon diversity index for the small mammal community at Konza Prairie Biological Station, Kansas, United States, from June 2011 to December 2014.

Model structure‡	Model statistics†				
	K	Dev	AIC _c	ΔAIC _c	w _i ≤
State + year	9	-22.5	1.5	0	0.998
Treatment + year	7	-2.8	14.7	13.2	0.001
State	6	3.2	17.8	16.2	0
Treatment	4	14.8	23.9	22.4	0
Treatment × year	13	-5.0	35.1	33.6	0
Year	5	26.4	38.2	36.6	0
Constant	2	35.8	40.2	38.6	0
State × year	21	-34.7	58.7	57.1	0

Notes: ABG, annually burned and grazed; PBG, patch-burn grazed; 4BN, 4-year fire-return interval.

† Model fit is described by the number of parameters (K), deviance or -2 log likelihood (Dev), Akaike’s information criterion corrected for small sample size (AIC_c), differences in AIC_c from the minimum AIC_c model (ΔAIC_c), and AIC_c weights (w_i).

‡ State models compared five treatments: ABG, PB0, PB1, PB2, and 4BN where numbers following PB indicate time since fire within the PBG rotation. Treatment models compared three treatments: ABG, PBG, and 4BN. Biological years of the study were 2011–2012, 2012–2013, 2013–2014, and 2014.

fire-return intervals was largely due to reduced relative abundance of deer mice, and higher abundance of a suite of species known to select habitats with heavy cover or woody vegetation, including hispid cotton rats, white-footed mice (*Peromyscus leucopus*), and eastern wood rats (*Neotoma floridana*; Kaufman et al. 2000, Rehmeier et al. 2005, Matlack et al. 2008). Our positive control included encroachment by woody plants, and had more shrub cover than our other treatment areas (~20% cover). Moreover, our results show that the lack of grazing disturbance affected the process of vegetative cover and litter

accumulation, creating suitable habitat faster for disturbance negative species after a fire than grazed areas. However, our 4BN treatment is unlikely to be adopted as a management strategy by private landowners, because restricting grazing or prescribed fire is not compatible with cattle production, and promotes conversion of grassland to shrubland (Briggs et al. 2005, Ratajczak et al. 2014).

We captured the same set of species in the annually burned and grazed treatment that were captured in the patch-burn grazing and 4BN treatments, except least shrews (*Cryptotis parva*). However, several relatively common species in the PBG treatment were rarely encountered in the ABG treatment. For instance, we captured at least twice as many hispid cotton rats, western harvest mice, and plains harvest mice in each unit of the PBG treatment than in the ABG treatment. The pattern of higher abundance for some species in the heavily disturbed state (PB0) of the PBG treatment than in ABG suggests that the temporal heterogeneity within patches created by PBG may allow persistence of these species in less suitable habitat.

An expanded ecological niche and greater diversity of small mammals in rangelands managed with patch-burn grazing is promising for other trophic levels. Deer mice are a highly nocturnal species, and are available as prey items for owls (Rehmeier et al. 2006). On the other hand, hispid cotton rats, prairie voles, and western harvest mice are often active during the daytime, and are likely more accessible prey for diurnal raptors (Swihart and Slade 1985, Danielson and Swihart 1987; A. M. Ricketts, *personal observation*). Deer mice can influence species composition of

Table 4. Results of a canonical correspondence analysis (CCA) for the small mammal community at Konza Prairie Biological Station, Kansas, United States, from June 2011 to December 2014.

Model Characteristic	Eigenvalue (λ)	% Variance	F	df	P ≤
Total inertia	1.71	—	—	—	—
Constrained (CCA)	0.814	47.6	6.2	5	0.001
Unconstrained	0.897	52.4	—	—	—
CCA axis 1	0.314	18.4	11.9	1	0.001
CCA axis 2	0.218	12.8	8.3	1	0.001
CCA axis 3	0.164	9.6	6.2	1	0.001
CCA axis 4	0.103	6.0	3.9	1	0.003
CCA axis 5	0.015	0.9	0.6	1	0.878

Note: F statistics and P values are from permutation tests of the full CCA model or axes.

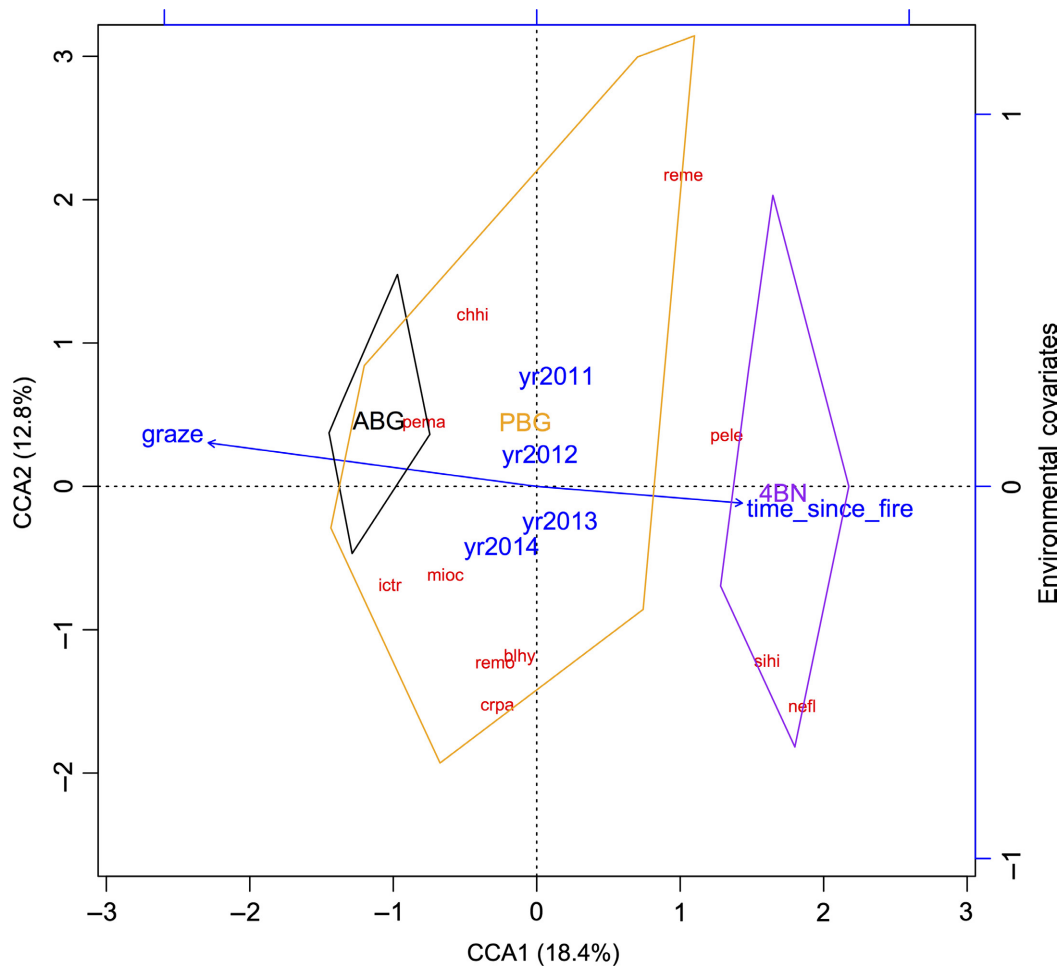


Fig. 5. Ordination of the first two axes from a canonical correspondence analysis (CCA) showing the relationships among the small mammal community, three treatments, four biological years, and the interaction of fire and grazing from June 2011 to December 2014 at Konza Prairie Biological Station, Kansas, United States. Treatments include annually burned and grazed (ABG), patch-burn grazed (PBG), and ungrazed with a 4-year fire-return interval (4BN). Eleven species of small mammals were encountered, and species codes are given in Table 1.

plant communities by selectively depredated large seeds, so reduced abundance of deer mice in PB1 and PB2 could have positive feedbacks on the plant community (Bricker et al. 2010, Maron et al. 2012). Last, patch-burn grazing could affect disease dynamics. Prevalence and transmission of zoonoses such as hantaviruses and Lyme disease are often reduced in mammalian communities with higher species diversity (Keesing et al. 2010, Dearing et al. 2015).

Our field results provide strong evidence that patch-burn grazing promotes diversity of small mammals in the tallgrass prairie in Kansas. Our study joins emerging results from a suite of field

studies that show that restoring pyric herbivory to create spatial and temporal heterogeneity in rangelands is a useful conservation practice for maintaining biodiversity in grassland ecosystems. In the future, focal population studies are needed to quantify the effects of habitat conditions on demographic rates of key species of small mammals. Moreover, the effects of habitat heterogeneity created by patch-burn grazing on predator behavior, including movements, foraging efficiency, and energetic costs associated with moving through different habitats have not yet been studied. Nevertheless, our results show that patch-burn grazing is an effective management strategy

to restore heterogeneity and increase biodiversity on rangelands managed for cattle production.

Management decisions of stakeholders in working landscapes are complex, and can be influenced by diverse factors including culture and economics. One important consideration for introducing management practices to private lands are the financial and time costs that can be barriers for livestock producers willing to implement new practices. Landowners in the Flint Hills of Kansas regularly burn tallgrass prairie to control woody vegetation and increase cattle gains, but prescribed fires are often applied using county roads or other natural firebreaks to minimize the effort required for safe application of a controlled burn. Introducing patch-burn grazing on private lands may require establishment and maintenance of firebreaks, and could increase the amount of time and effort required to complete a burn safely. Cost sharing programs, such as Partners for Fish and Wildlife of the US Fish and Wildlife Service and the Environmental Quality Incentives Program of the Natural Resources Conservation Service, provide financial and technical assistance to landowners and are promising for implementation of conservation strategies such as patch-burn grazing on private lands (USFWS 2012, NRCS Kansas 2015).

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