Community Responses of Arthropods to a Range of Traditional and Manipulated Grazing in Shortgrass Steppe

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ABSTRACT Responses of plants to grazing are better understood, and more predictable, than those of consumers in North American grasslands. In 2003, we began a large-scale, replicated experiment that examined the effects of grazing on three important arthropod groups—beetles, spiders, and grasshoppers—in shortgrass steppe of north-central Colorado. We investigated whether modifications of the intensity and seasonality of livestock grazing alter the structure and diversity of macroarthropod communities compared with traditional grazing practices. Treatments represented a gradient of grazing intensity by cattle and native herbivores: long-term grazing exclosures; moderate summer grazing (the traditional regime); intensive spring grazing; intensive summer grazing; and moderately summer-grazed pastures also inhabited by black-tailed prairie dogs (*Cynomys ludovicianus* Ord). Beetles and spiders were the most common groups captured, comprising 60% and 21%, respectively, of 4,378 total pitfall captures. Grasshopper counts were generally low, with 3,799 individuals observed and densities $<4 \text{ m}^{-2}$. Two years after treatments were applied, vegetation structure differed among grazing treatments, responding not only to long-term grazing conditions, but also to the short-term, more-intensive grazing manipulations. In response, arthropods were, in general, relatively insensitive to these grazing-induced structural changes. However, species-level analyses of one group (Tenebrionidae) revealed both positive and negative effects of grazing treatments on beetle richness and activity-density. Importantly, these responses to grazing were more pronounced in a year when spring–summer rainfall was low, suggesting that both grazing and precipitation—which together may create the greatest heterogeneity in vegetation structure—are drivers of consumer responses in this system.

KEY WORDS grasshopper, habitat structure, livestock grazing, spider, tenebrionid beetle

Livestock grazing on grasslands and shrublands is a global phenomenon, with grazing impacts strongly context dependent (Milchunas and Lauenroth 1993). For example, in systems where grazing is considered an exogenous disturbance (Milchunas et al. 1998)—that is, where large herbivores are not an integral part of the system's evolutionary history—grazers and their activities can exact a heavy ecological toll (Jones 2000). In contrast, in systems where plant communities coevolved with large herbivores, grazing is considered an endogenous disturbance, and responses can be quite different (Mack and Thompson 1982). Grazing in these latter systems is needed to maintain "healthy" conditions, whereas exclusion of grazers leads to more degraded conditions, such as increased susceptibility to invasion by exotic or weedy species (Milchunas et al. 1992). The shortgrass steppe of North America is one system where plant communities are well adapted and resilient to grazing (Milchunas et al. 1988, Milchunas and Lauenroth 1993). The resilience of the plant community raises the question of whether consumer communities are similarly resilient (Milchunas et al. 1998). Comparative studies of the effects of varying intensities of livestock grazing on shortgrass steppe animals suggest that some groups, namely birds and macroarthropods, are more sensitive to grazing than others (reviewed in Milchunas et al. 1998). It is increasingly recognized, however, that modifications of traditional grazing practices, i.e., of the intensity, patchiness, and seasonality of grazing, can be used to increase spatial and temporal heterogeneity in vegetation at the landscape scale, and improve habitat quality for species of conservation concern in some grasslands (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, Derner et al. 2009, Toombs et al. 2010). To assess their utility for meeting conservation goals, studies are needed that demonstrate the

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effects of these nontraditional grazing practices on native consumer communities.

In shortgrass steppe, arthropods represent a critical component of the consumer community (Lauenroth and Milchunas 1991). They comprise an important resource base for small vertebrates (Flake 1973, Lauenroth and Milchunas 1991, Stapp 1996), and play important roles in community-level dynamics and ecosystem functioning (reviewed in Crist 2008). Although effects of livestock grazing on arthropods tend to be taxon-specific (e.g., Di Giulio et al. 2001, Swengel 2001, Cagnolo et al. 2002, DeBano 2006, Batary et al. 2007, Joern and Laws 2013), in shortgrass steppe many groups decline with increased grazing intensity (Lavigne et al. 1972, Capinera and Sechrist 1982, Lauenroth and Milchunas 1991, and references therein, Welch et al. 1991). While we might expect these consumer groups to show similar sensitivity to novel, nontraditional practices such as heavier grazing intensity than previously experienced, the response of arthropods to such conditions has not yet been evaluated.

Here, we used grazing treatments that expanded on the natural range of grazing conditions on shortgrass steppe to ask how vegetation structure and arthropods respond to grazing. Specifically, we assessed how major macroarthropod groups—carnivores (ground spiders), omnivores (beetles), and herbivores (grasshoppers)—respond to changes in the seasonality (spring vs. summer) and intensity (i.e., twice the stocking rate) of grazing relative to moderate summer grazing by cattle that represents the traditional grazing regime in shortgrass steppe (Bement 1969, Hart and Ashby 1998). Because arthropod abundance and distribution are strongly influenced by changes in vegetation structure (e.g., spiders, Hatley and MacMahon 1980; ground-dwelling beetles, Mazia et al. 2006; insect herbivores, Stinson and Brown 1983), we focused on evaluating how grazing-induced simplification of vegetation architecture affects abundance and richness of these arthropod groups. The relatively simple structural complexity and short stature of vegetation in shortgrass steppe (Lauenroth and Milchunas 1991) suggests that grazing effects may be less dramatic than in other more productive systems (e.g., tallgrass prairie, Sims and Singh 1978). Nevertheless, even small changes in important characteristics, such as vegetation height (e.g., Noordijk et al. 2010), may affect the arthropod communities.

We expected the following changes with increased grazing intensity: 1) a reduction in vegetation height and an increase in the amount of bare ground, 2) a decrease in spiders, grasshoppers, and most beetles, and 3) an increase in abundance of scarab beetles in association with increased availability of cattle dung. One of the more predictable effects of livestock grazing on the structural complexity of grassland vegetation is reduced vegetation height (Scimone et al. 2007, Augustine and Derner 2012). With this modification, the literature suggests spider communities in grasslands (Gibson et al. 1992, Churchill and Ludwig 2004, Horvath et al. 2009, Mysterud et al. 2010), and specifically in shortgrass steppe (Lavigne et al. 1972),

respond negatively, though responses to grazing can be variable and species-specific (Gibson et al. 1992). Similarly, grasshoppers (Capinera and Sechrist 1982, Welch et al. 1991) and beetles (Lavigne et al. 1972) also appear to be sensitive to grazing-induced changes in habitat structure, and are predicted to decline with simplified vegetation and increased bare ground (e.g., for tenebrionids, McIntyre 1997, Stapp 1997). In contrast, we assumed that an increase in the availability of cattle dung, an important food resource for dung beetles (Scarabaeidae), would promote increased abundance of scarab beetles on the most heavily grazed treatments (e.g., Verdu et al. 2007). Those most heavily grazed plots may also have positive effects on arthropods, in general, owing to associations with the unique microhabitats generated by prairie dog burrows (Davidson and Lightfoot 2007); overall, however, we anticipated arthropod declines with increased grazing intensity. Our study incorporates two levels of taxonomic resolution, family and species level, and includes an assessment of how plant community composition may differ among grazing treatments in the final year of the study (2006), both of which may help further explain any observed responses among these arthropod groups to grazing.

Materials and Methods

Study Area and Sampling Design. The study was conducted at the United States Department of Agriculture (USDA)-Agricultural Research Service Central Plains Experimental Range (CPER) in north-central Colorado, located ≈60 km northeast of Fort Collins, CO. Vegetation is classified as shortgrass steppe, and is dominated by two perennial C_4 grasses, *Bouteloua gracilis* ([Willd. ex Kunth] Lag. ex Griffiths) and *Bouteloua dactyloides* (Nutt.) J. T. Columbus. Climate is semiarid, with long-term mean annual precipitation of 341 mm, with 70% received as rainfall between April and September (Lauenroth and Milchunas 1991). Annual precipitation during both sampling years of the study was below the long-term mean (2004: 293 mm; 2006: 301 mm). A drier spring and early summer (April–June) occurred in 2006 (54 mm) versus 2004 (114 mm). Sampling during the first year of the study (2004) coincided with the end of a multiyear drought (2000–2004).

In 2003 and 2004, 25 study plots (0.81 ha each) were established on replicated pastures representing a grazing gradient from no grazing to very heavy grazing: 1) long-term (since 1939) large-herbivore grazing exclosures ("EXCLO"; *n* = 5 replicate 1-ha exclosure plots within moderately grazed pastures), 2) moderate summer grazing ("MODSUM"; *n* = 5 plots within three replicate 65–130-ha pastures), representing the typical grazing practice (Bement 1969, Hart and Ashby 1998, Milchunas et al. 1998), with a stocking rate of 1.44 ha per yearling steer per month for the mid-May to October grazing season; 3) heavy summer grazing ("HVYSUM"; *n* = 4 plots within two replicate 65-ha pastures), with a stocking rate of 0.72 ha per yearling steer per month, double the moderate stock-

ing rate for the mid-May to October grazing season; 4) very heavy spring grazing ("HVYSPR"; $n = 6$ plots within two replicate 65-ha pastures), with a stocking rate of 0.52 ha per yearling steer per month for the early March to mid-May grazing season in which livestock consume stockpiled forage from the prior year until new growth begins in mid-April, and 5) moderate summer grazing by cattle with black-tailed prairie dog (*Cynomys ludovicianus* Ord) colonies ("PDOG"; $n = 5$ plots within five prairie dog colonies), with the combination of livestock and history of prairie dog grazing (since 1997) leading to the most intensive grazing treatment. Study plots were randomly located within treatment pastures. In the HVYSPR pastures, plots were located in areas near supplemental feed sites for livestock, rather than randomly, to ensure sampling of heavy-use sites. In addition, EXCLO plots were centered within the 1-ha exclosures to minimize edge effects. For additional detail regarding grazing management regimes on the CPER, see Augustine and Derner (2012).

These five treatment types encompassed a wide range of grazing regimes for the region (Lauenroth and Milchunas 1991, Milchunas et al. 1998), and the HVYSPR and HVYSUM treatments are more intensive grazing practices than have been previously investigated in shortgrass steppe (Bement 1969, Hart and Ashby 1998). In 2003, before the establishment of grazing treatments in 2004, all grazed sites were grazed at moderate (=MODSUM) intensities. We distinguished between treatments that have either been installed for long periods of time (EXCLO plots) or dominated by native grazers (PDOG plots) from short-term, experimentally manipulated plots (HVYSPR and HVYSUM) using the terms "long-term" treatments and "short-term" treatments, respectively.

Habitat Characteristics and Plant Community Composition. We measured the following structural characteristics of vegetation within 1 m of 30 points per plot: height of grasses, forbs, and shrubs, and number of dwarf shrubs (primarily *Artemisia frigida* Willd.). Sampling points were located at 10-m intervals along three randomly placed, 100-m transects with 10 points per transect. Mean values were calculated using these 30 measurements per plot. Sampling occurred in July–August 2004 and in June–July 2006. In 2004, a subset of plots were sampled for structural characteristics ($n = 16$ of 25; EXCLO, $n = 5$, MODSUM, $n = 3$, HVYSPR, $n = 3$, PDOG, $n = 5$). This more limited sampling allowed us to make comparisons among treatments and years for all treatment combinations except those including HVYSUM, which was not sampled in 2004.

In 2006, in addition to measuring structural characteristics of vegetation, we estimated percent canopy cover of plants by species, and cover of lichens, litter, and bare ground to the nearest 5% using a 20- by 50-cm Daubenmire frame (Daubenmire 1959) at each of the 30 sampling points per plot. Plant taxonomy followed the USDA PLANTS Database (USDA 2012). Canopy cover sampling coincided with structural vegetation sampling in June–July 2006.

Density of cattle fecal pats was estimated by counting the number of pats observed while walking within four, randomly placed belt transects (5 by 50 m) per plot between July and August 2006. Mean fecal pat density was calculated using the four subsamples per plot and provided a measure of grazing intensity and the amount of habitat available for insects attracted to dung.

Arthropod Communities. Arthropods were captured on each plot using live pitfall traps established in a three by four array, with 10-m spacing between traps. Traps consisted of plastic cups (90 mm in diameter, 120 mm in depth), including a plastic funnel (90 mm in diameter), buried flush with the ground surface. Traps were shaded with wooden covers held in place with nails; traps could be closed when not operational by nailing the cover flush to the ground. Traps were open for four consecutive days on a staggered schedule, with all plots trapped within a 2-wk period during a single trapping session. Plots were trapped during three sessions, once each in June, July, and August. Arthropods were sorted, identified to either the family or species level, counted, and released. Though a wide range of arthropods were captured in our pitfalls, we restricted our analyses to beetles and spiders, which together comprised 81% of total captures. Tenebrionid beetles were the one group identified to the species level using an identification key developed specifically for this group on the CPER, which we carried with us in the field. When identification of a particular beetle was uncertain, the individual was collected and compared with known individuals in a comprehensive reference collection housed at the Shortgrass Steppe Long Term Ecological Research field station on the CPER. We focused on tenebrionids because of their numerical dominance, high species richness, and important role as detritivores in shortgrass steppe (Whicker and Tracy 1987, Stapp 1997, Crist 2008). Counts of each arthropod group were pooled at the plot level, averaged across the three sampling sessions for each year, and the number of individuals per 48 trap-days (i.e., 12 traps × 4 days) was used as a measure of activity-density (Hatten et al. 2010). While sacrificing statistical power, we pooled data to consolidate sparse observations for certain arthropod groups owing to low trapping rates. For tenebrionids, analyses were restricted to the nine most common species (activity-density >0.005 [number/trap-day] on any plot in either year).

Grasshoppers, which are not effectively sampled by pitfalls (Stapp 1996), were quantified using the ring count method (Onsager and Henry 1977, Joern 2005) by flushing grasshoppers from 0.78-m^2 circular plots (hoops) constructed of plastic sprinkler pipe. Twenty hoops were distributed in a four-by-five array adjacent to the pitfall-trapping grid, with 10-m spacing between hoops. Hoops were installed and left in place for three consecutive days to allow grasshoppers to naturally redistribute; on the fourth day, we counted the number of grasshoppers flushed from each hoop as an observer slowly approached the hoop (Welch et al.

1991). Orthopterans flushed from hoops were identified to the ordinal taxonomic level. Grasshopper sampling coincided with the three pitfall trapping sessions. Densities (individuals per square meter) were pooled at the plot level, and averaged across the three sampling sessions for each year.

Statistical Analyses. We used Repeated Measures Analysis of Variance (RMANOVA), with Tukey–Kramer multiple-comparisons tests, to determine significant differences among treatments (**EXCLO, MODSUM, HVYSUM, HVYSPR,** and **PDOG**) in response variables between years (2004, 2006). Response variables include grass, forb, and shrub height, number of dwarf shrubs, family-level richness of spiders and beetles, activity-density of spiders and beetles, activity-density of total scarab beetles separately, activity-density of tenebrionid beetles by species, and density of grasshoppers. Family-level richness is defined as the number of families represented by individuals of a particular taxonomic group (e.g., within Coleoptera) captured on a given plot (Fahrig and Jonsen 1998). Because we were also particularly interested in assessing differences in these same response variables among MODSUM plots (reference plots) with HVYSPR and HVYSUM plots (manipulated plots), we conducted separate repeated-measures ANOVAs including only MODSUM and HVYSPR or MODSUM and HVYSUM. For these analyses, because our initial sampling coincided with short-term treatment implementation in 2004, and differences among some short-term treatments were already evident in 2004 (see Table 1), we interpreted a significant interaction between the main effects of grazing treatment and year as a continuation of those changes in the response variable over time that were dependent on the grazing treatment (Read 2002). Analysis of Variance (ANOVA) was used to determine differences among treatments in 2006 in mean percent canopy cover of vascular plant species, mean percent cover of lichens, litter, bare ground, and density of cattle fecal pats. When necessary, data were transformed to meet assumptions of parametric tests. All analyses were performed in SAS 9.1 (SAS Institute 2005). We note that the method generally recommended for determining the denominator degrees of freedom (i.e., ddfm = kenwardroger) using the Proc MIXED procedure for RMANOVA (Schaalje et al. 2001) may report different degrees of freedom for analyses with the same number of observations owing to differences in variance estimates among response variables, which was the case in our analyses here (see Results).

We generated individual-based rarefaction curves (Gotelli and Colwell 2001, Colwell 2009) to compare richness of tenebrionid species among the five grazing treatments while adjusting for variation in number of individuals sampled among treatments and between years. Coleman rarefaction curves, and associated measures of variance ($\pm$ SD), were created using EstimateS version 8.2 software (Colwell 2009) using average activity-densities of beetles combined across the three sampling sessions per year and standardized

Table 1. Vegetation structure and arthropod characteristics among grazing treatments and across years on the Central Plains Experimental Range, Colorado

Response variables	2004 Grazing treatment[a]					2006 Grazing treatment				
	EXCLO (5)	MODSUM (5)	HVYSUM (4)	HVYSPR (6)	PDOG (5)	EXCLO (5)	MODSUM (5)	HVYSUM (4)	HVYSPR (6)	PDOG (5)
Vegetation structure[b]										
Grass ht (cm)	12.93 ± 2.86	5.36 ± 1.41	ND	6.52 ± 2.38	6.09 ± 3.36	12.09 ± 4.04	5.65 ± 2.73	4.72 ± 1.96	4.11 ± 0.95	5.14 ± 1.76
Forb ht (cm)	9.07 ± 3.37	4.26 ± 0.90	ND	5.39 ± 2.37	4.51 ± 1.33	5.21 ± 1.25	3.87 ± 0.81	3.77 ± 0.70	3.83 ± 0.54	4.09 ± 0.95
Shrub ht (cm)	23.42 ± 6.16	12.36 ± 2.89	ND	13.74 ± 2.91	7.77 ± 2.40	19.80 ± 6.76	13.66 ± 3.33	11.61 ± 3.58	8.68 ± 2.14	6.34 ± 3.25
No. of dwarf shrubs (no.)	1.92 ± 2.21	1.87 ± 2.65	ND	1.60 ± 2.24	1.00 ± 2.14	2.11 ± 1.01	2.29 ± 1.34	3.38 ± 1.52	3.55 ± 2.27	1.52 ± 1.46
Arthropod characteristics										
Spider richness (no. families)	4.0 ± 0.7	3.4 ± 1.0	4.5 ± 0.3	4.5 ± 0.4	3.6 ± 0.4	4.6 ± 0.4	5.0 ± 0.8	4.5 ± 0.9	5.7 ± 0.2	4.8 ± 0.4
Spider activity-density (no./trap-day)	0.07 ± 0.02	0.10 ± 0.04	0.12 ± 0.01	0.15 ± 0.03	0.06 ± 0.01	0.14 ± 0.03	0.15 ± 0.01	0.14 ± 0.02	0.13 ± 0.02	0.13 ± 0.02
Beetle richness (no. families)	4.4 ± 0.8	3.6 ± 0.9	4.8 ± 0.5	4.0 ± 0.4	3.6 ± 0.8	5.2 ± 0.6	4.0 ± 0.4	5.3 ± 0.3	4.8 ± 0.4	4.6 ± 0.5
Beetle activity-density (no./trap-day)	0.26 ± 0.06	0.19 ± 0.09	0.38 ± 0.07	0.35 ± 0.07	0.20 ± 0.06	0.32 ± 0.06	0.31 ± 0.08	0.34 ± 0.07	0.53 ± 0.12	0.37 ± 0.08
Scarab activity-density (no./trap-day)	0.01 ± 0.008	0.003 ± 0.003	0.01 ± 0.006	0.002 ± 0.002	0.008 ± 0.007	0.01 ± 0.005	0.004 ± 0.003	0.02 ± 0.003	0.03 ± 0.015	0.01 ± 0.006
Grasshopper density (no./m²)	2.43 ± 0.40	2.48 ± 0.37	1.98 ± 0.42	2.62 ± 0.28	2.56 ± 0.41	1.05 ± 0.32	1.19 ± 0.14	0.88 ± 0.27	0.94 ± 0.23	0.31 ± 0.10

Values are means ± SE pooled from replicate treatment plots (no. plots/treatment shown in parentheses). Significant treatment, year, and treatment-by-year differences were evaluated with Repeated Measures ANOVA (see Results for details).

[a] Abbreviations for grazing treatments, in order of increasing grazing intensity, are: EXCLO, exclosures; MODSUM, moderate summer grazing; HVYSUM, intensive summer grazing; HVYSPR, intensive spring grazing; PDOG, moderate summer grazing in areas with prairie dogs.

[b] In 2004, a subset of plots were sampled for vegetation structure characteristics (see Materials and Methods; EXCLO, n = 5, MODSUM, n = 5, HVYSUM, n = 0, HVYSPR, n = 3, PDOG, n = 5; ND, no data).

by number of trap-days (same as activity-density above). These activity-density values were then rounded to the nearest whole number to meet requirements of EstimateS. Differences among treatments were assessed by visually comparing the 2004 and 2006 curves for each treatment to the MODSUM curves, which served as our reference condition.

Multivariate analyses of vegetation characteristics, plant community composition, and arthropod communities were conducted by nonmetric multidimensional scaling (MDS) in PRIMER version 5.0 software (Clarke and Gorley 2001). MDS is a nonparametric ordination procedure that produces visual graphs of samples, in our case study plots, in 2-dimensional space, in which samples that are more similar are clustered together more closely than samples that are dissimilar. A stress coefficient provides an estimate of goodness-of-fit for the MDS graph; STRESS values (>0.20) indicate difficulty in expressing the relationships among samples in two dimensions. Data were transformed (square root, arcsine square root, or log [y + 1]) before MDS analysis. Significant differences in vegetation and arthropod community patterns among grazing treatments were analyzed using an analysis of similarity procedure (ANOSIM), which includes a global test of treatment differences, as well as a multiple comparisons test. The SIMPER procedure was used to determine which variables contributed most to observed differences among grazing treatments (Clarke and Gorley 2001). Metrics used to produce each set of ordinations include: 1) for vegetation structure—grass, forb, and shrub height, and number of dwarf shrubs; 2) for plant community composition—percent cover of vascular plant species, and cover of lichens, litter, and bare ground; and 3) for arthropod communities—activity-density of spiders by family, activity-density of beetles by family, and activity-density of tenebrionid beetles by species. Test statistics from MDS analyses were included in the text for all comparisons regardless of their statistical significance; however, only MDS graphs depicting significant results were shown in Fig. 1.

Results

Habitat Characteristics and Plant Community Composition. Habitat structure differed among grazing treatments. Comparisons of vegetation height revealed that EXCLO plots consistently supported taller grasses ($F = 20.17$; df = 4, 20; $P < 0.0001$), forbs ($F = 9.47$; df = 4, 22; $P = 0.0001$), and shrubs ($F = 6.68$; df = 4, 22; $P = 0.0011$) than other treatments (Table 1). In addition, structure varied significantly between the 2 yr of the study; height of forbs ($F = 19.09$; df = 1, 18; $P = 0.0004$) and shrubs ($F = 5.77$; df = 1, 14; $P = 0.030$) was significantly shorter in 2006 compared with 2004 across treatments (Table 1).

In 2004, multivariate analyses revealed that treatment plots were significantly clumped and distinct based on dissimilarities in structural attributes ($R = 0.268$, $n = 16$, $P = 0.012$), with EXCLO plots significantly different from PDOG plots ($P = 0.008$) and

MODSUM plots ($P = 0.036$; Fig. 1A). Structural differences among treatments were largely attributed to differences in the height of shrubs (85–88%; SIMPER analysis), which were taller on EXCLO plots compared with other treatments (Table 1). While differences were detected across the five grazing treatments in 2004, no differences were evident for "short-term" treatments HVYSPR and HVYSUM relative to MODSUM during that same year.

In 2006, EXCLO and PDOG continued to differ from each other ($R = 0.277$, $n = 25$, $P = 0.001$; posthoc pairwise comparison, $P = 0.016$), while HVYSPR differed from both EXCLO ($P = 0.002$) and PDOG ($P = 0.048$; Fig. 1B). In addition, and in contrast to patterns on "short-term" experimental treatment plots in 2004, HVYSPR plots differed from MODSUM plots ($P = 0.006$; Fig. 1B). Most of the dissimilarity between the experimental treatment plots (73%) was again explained by differences in shrub height (SIMPER analysis). Additional, planned comparisons of MODSUM and HVYSPR plots confirmed that shrub structure continued to diverge on these plots; shrub height showed a significant reduction on the manipulated HVYSPR plots in 2006 compared with 2004, while MODSUM reference plots showed no reduction (Table 1), with the treatment-by-year interaction term significant ($F = 9.43$; df = 1, 8; $P = 0.015$). Although not significant, grass height also tended to be reduced on HVYSPR plots relative to MODSUM plots (treatment-by-year interaction, $F = 3.65$; df = 1, 8; $P = 0.089$; Table 1).

Thirty plant species were recorded on plots in 2006 (Table 2 lists the predominant species). Percent cover of *Aristida purpurea* (Nutt.), *B. gracilis*, *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Pascopyrum smithii* (Rydb.) A. Love, *Opuntia polyacantha* (Haw.), and bare ground differed among grazing treatments, with EXCLO plots supporting higher cover of *H. comata* and *P. smithii*, and PDOG plots having higher cover of bare ground and lower cover of *O. polyacantha* (Table 2). These differences were mirrored in multivariate analyses; plots differed based on dissimilarities in plant species composition ($R = 0.341$, $n = 25$, $P = 0.001$), but only in response to the "long-term" treatments; EXCLO plots significantly differed from all other treatments ($P < 0.05$), and PDOG plots differed from HVYSPR plots ($P = 0.015$), MODSUM plots ($P = 0.024$), and EXCLO plots ($P = 0.008$) in 2006 (Fig. 1C). Percent cover of *H. comata*, *P. smithii*, and *B. gracilis* contributed the most (11–15, 8–11, and 10–11%, respectively) to pairwise dissimilarities between EXCLO plots and the other treatments, while the cover of *B. gracilis* and bare ground contributed the most (12 and 11%, respectively) to dissimilarities between PDOG plots and HVYSPR and MODSUM plots (SIMPER analyses; Table 2).

Not unexpectedly, the density of fecal pats differed significantly among treatments, with twice the density of fecal pats on HVYSPR plots compared with MODSUM plots (Table 2).

Arthropods. Spiders were the second most common arthropod group captured in our pitfall arrays after
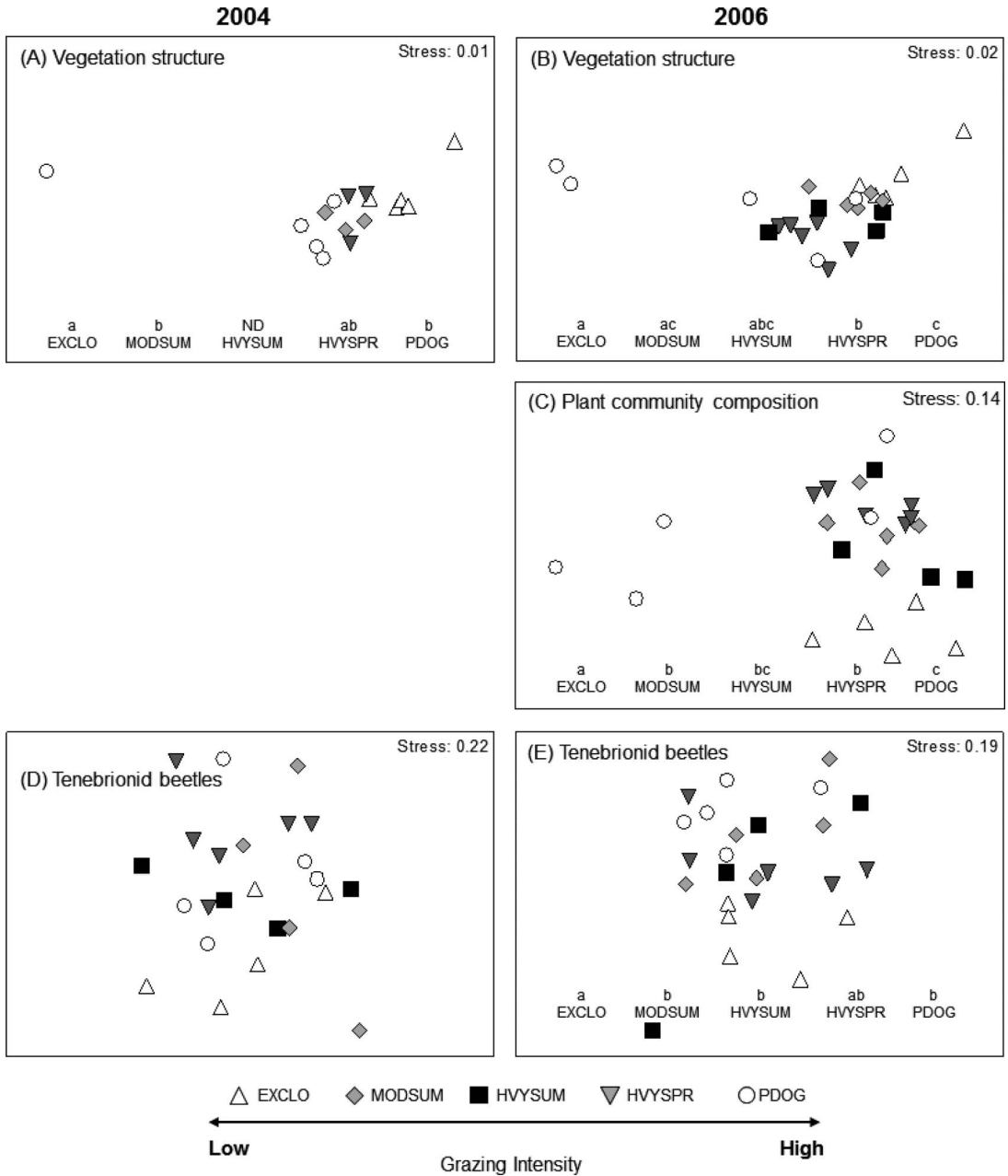
Fig. 1. Nonmetric MDS plots showing relationships among response variables with respect to grazing treatments in 2004 and 2006 for structural attributes of vegetation (A and B), plant community composition (C), and tenebrionid beetle communities (D and E). Plant community data were not collected consistently on all plots in 2004 and therefore are not included here. MDS plots for spiders and beetles were not shown owing to nonsignificant results (see Materials and Methods). Abbreviations for grazing treatments are: EXCLO, exclosures; MODSUM, moderate summer grazing; HVYSUM, intensive summer grazing; HVYSPR, intensive spring grazing; PDOG, moderate summer grazing in areas with prairie dogs. For those response variables where differences among treatments were detected, treatments with different letters are significantly different based on analysis of similarity (ANOSIM; $P < 0.05$). No data (ND) for structural attributes of vegetation were collected on HVYSUM plots in 2004.

beetles (60%), comprising 21% of 4,378 total individuals captured during the study. The most common spiders trapped were members of the Lycosidae and Theridiidae, which comprised 31 and 25%, respectively, of 928 total spiders and solpugids captured. Five spider families were represented in our captures; these included Gnaphosidae, Lycosidae, Salticidae, Theridiidae, and Thomisidae. Spiders showed no significant response to grazing treatments in total activity-density ($F = 1.18$; df $= 4, 20$; $P = 0.35$) or family-

Table 2. Percent canopy cover of predominant vascular plants, and cover of lichens, litter, and bare ground among grazing treatments on the Central Plains Experimental Range, Colorado in 2006

Species[a]	Grazing treament[b]				
	EXCLO	MODSUM	HVYSUM	HVYSPR	PDOG
Grasses and sedges					
Aristida purpurea Nutt.	0.1 ± 0.1a	1.1 ± 0.6b	0.04 ± 0.04a	0.8 ± 0.4b	0.6 ± 0.2ab
Bouteloua dactyloides (Nutt.) J. T. Columbus	4.3 ± 1.6	4.9 ± 1.1	8.2 ± 1.6	1.3 ± 0.2	6.8 ± 3.1
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	9.4 ± 3.0a	23.4 ± 1.2b	14.7 ± 4.3ab	23.6 ± 2.0b	9.3 ± 5.0a
Carex duriuscula C. A. Mey	3.1 ± 1.0	3.2 ± 1.1	2.6 ± 0.7	3.3 ± 0.7	1.7 ± 0.4
Hesperostipa comata (Trin. & Rupr.) Barkworth	10.7 ± 3.8a	1.0 ± 0.7bc	2.1 ± 1.0b	0.006 ± 0.006c	0.05 ± 0.04bc
Pascopyrum smithii (Rydb.) A. Love	9.5 ± 3.9a	2.0 ± 0.8b	0.9 ± 0.5b	0.7 ± 0.3b	3.5 ± 1.6ab
Vulpia octoflora (Walter) Rydb.	0.3 ± 0.3	4.5 ± 1.7	5.1 ± 2.9	3.6 ± 1.5	1.1 ± 1.0
Other species[c]	0.6	0.3	0.1	0.0	0.0
Shrubs and succulents					
Artemisia frigida Willd.	1.1 ± 0.6	0.6 ± 0.4	0.3 ± 0.2	1.5 ± 0.6	0.2 ± 0.2
Atriplex canescens (Pursh) Nutt.	0.0 ± 0.0	0.6 ± 0.4	1.0 ± 0.6	0.03 ± 0.03	0.0 ± 0.0
Eriogonum effusum Nutt.	1.4 ± 0.9	0.5 ± 0.3	0.8 ± 0.5	0.2 ± 0.1	0.8 ± 0.7
Opuntia polyacantha Haw.	3.7 ± 0.8a	3.1 ± 0.6a	4.5 ± 1.2a	3.3 ± 0.5a	0.4 ± 0.4b
Other species	0.1	0.7	0.8	0.7	0.2
Forbs					
Sphaeralcea coccinea (Nutt.) Rydb.	1.6 ± 0.4	1.8 ± 0.3	1.6 ± 0.3	2.5 ± 0.3	3.8 ± 1.6
Other species	0.7	0.1	0.4	0.5	3.7
Lichens	0.1 ± 0.1	2.6 ± 1.3	2.8 ± 1.5	2.4 ± 1.1	2.0 ± 1.3
Litter	38.3 ± 2.1	31.5 ± 2.8	38.9 ± 5.0	34.7 ± 3.6	27.9 ± 4.4
Bare ground	14.8 ± 2.6a	18.4 ± 1.2a	15.1 ± 2.6a	21.1 ± 2.1a	38.1 ± 8.7b
Cattle fecal pat density (no./m²)	0.0002 ± 0.0001a[d]	0.04 ± 0.002bc	0.06 ± 0.006c	0.09 ± 0.008d	0.02 ± 0.0009ab

Also included are density estimates of cattle fecal pats observed on plots in 2006.

Values are means ± SE pooled from replicate treatment plots (no. plots/treatment shown in parentheses). Values within rows with different letters are significantly different ($P < 0.05$) based on ANOVA with Tukey–Kramer multiple-comparisons tests.

[a] Of the 30 total species recorded on treatment plots, only those species with mean cover >1% within any treatment are included here.

[b] Abbreviations for grazing treatments, in order of increasing intensity, are EXCLO, exclosures; MODSUM, moderate summer grazing; HVYSUM, intensive summer grazing; HVYSPR, intensive spring grazing; PDOG, moderate summer grazing in areas with prairie dogs.

[c] "Other species" includes the sum of cover values for the remaining species within a life form, each with cover <1% within any treatment.

[d] A single cattle fecal pat was found in one of five exclosure plots, suggesting a breach of the exclosure fence in one instance.

level richness ($F = 0.94$; df = 4, 20; $P = 0.46$; Table 1); however, activity-density and richness increased significantly from 2004 to 2006 (activity-density, $F = 6.49$; df = 1, 20; $P = 0.019$; family-level richness, $F = 6.03$; df = 1, 20; $P = 0.023$). Consistent with our findings based on activity-density and richness, MDS analyses revealed no significant clustering of spider assemblages among grazing treatments in either 2004 ($R = -0.028$, $n = 16$, $P = 0.62$) or 2006 ($R = 0.053$, $n = 25$, $P = 0.23$).

Among beetles, individuals from the families Carabidae and Tenebrionidae were the most common of the eight families (Carabidae, Cerambycidae, Chrysomelidae, Curculionidae, Meloidae, Scarabaeidae, Silphidae, and Tenebrionidae) represented in pitfall captures; carabids comprised 44%, and tenebrionids 31%, of 2,629 total beetles captured. Scarabs, which comprised only 3% of total beetles captured, tended to increase in activity-density on HVYSPR plots in 2006 compared with 2004, as expected, while MODSUM reference plots showed no change during this same period (Table 1), but the effect was not significant (RMANOVA, treatment × year interaction, $F = 2.14$; df = 1, 9; $P = 0.16$). This nonsignificant trend in increased scarab activity-density coincided with an increase in fecal pat density on HVYSPR plots in 2006 (Table 2).

As with spiders, there were no strong patterns in total activity-density or family-level richness of beetles among grazing treatments (Table 1), and activity-density and richness tended to increase from 2004 to 2006 across treatments (activity-density, $F = 4.10$; df = 1, 20; $P = 0.056$; family-level richness, $F = 2.86$; df = 1, 20; $P = 0.11$). Further, we detected no differences in beetle community structure among grazing treatments in either 2004 ($R = 0.053$, $n = 16$, $P = 0.25$) or 2006 ($R = 0.026$, $n = 25$, $P = 0.37$). Therefore, beetles, again evaluated at the family level, appeared to be unresponsive to grazing intensity, both in response to the full spectrum of grazing treatments and to the "short-term" experimental treatments (HVYSPR and HVYSUM).

In contrast, at finer taxonomic resolution, we detected grazing effects on the tenebrionid beetle community. *Eleodes obsoleta* (Say) and *Eleodes obscura* (Say) were the most common of 12 species of tenebrionid beetles captured, comprising 39 and 16%, respectively, of 702 total individuals captured. Of these, two groups showed significant responses to grazing; *Eleodes fusiformis* (LeConte) and *Embaphion* spp. (three species combined) were consistently more common on EXCLO plots compared with the other treatments (*E. fusimornis*, RMANOVA, $F = 5.47$; df = 4, 20; $P = 0.0038$; *Embaphion* spp., RMANOVA, $F = 3.45$; df = 4, 20; $P = 0.027$; Fig. 2D and F). In opposite fashion, although not significant, certain species tended to be more abundant on the heavily grazed plots (HVYSPR and PDOG) compared with other treatments (*E. obsoleta*, RMANOVA, $F = 2.31$; df = 4,
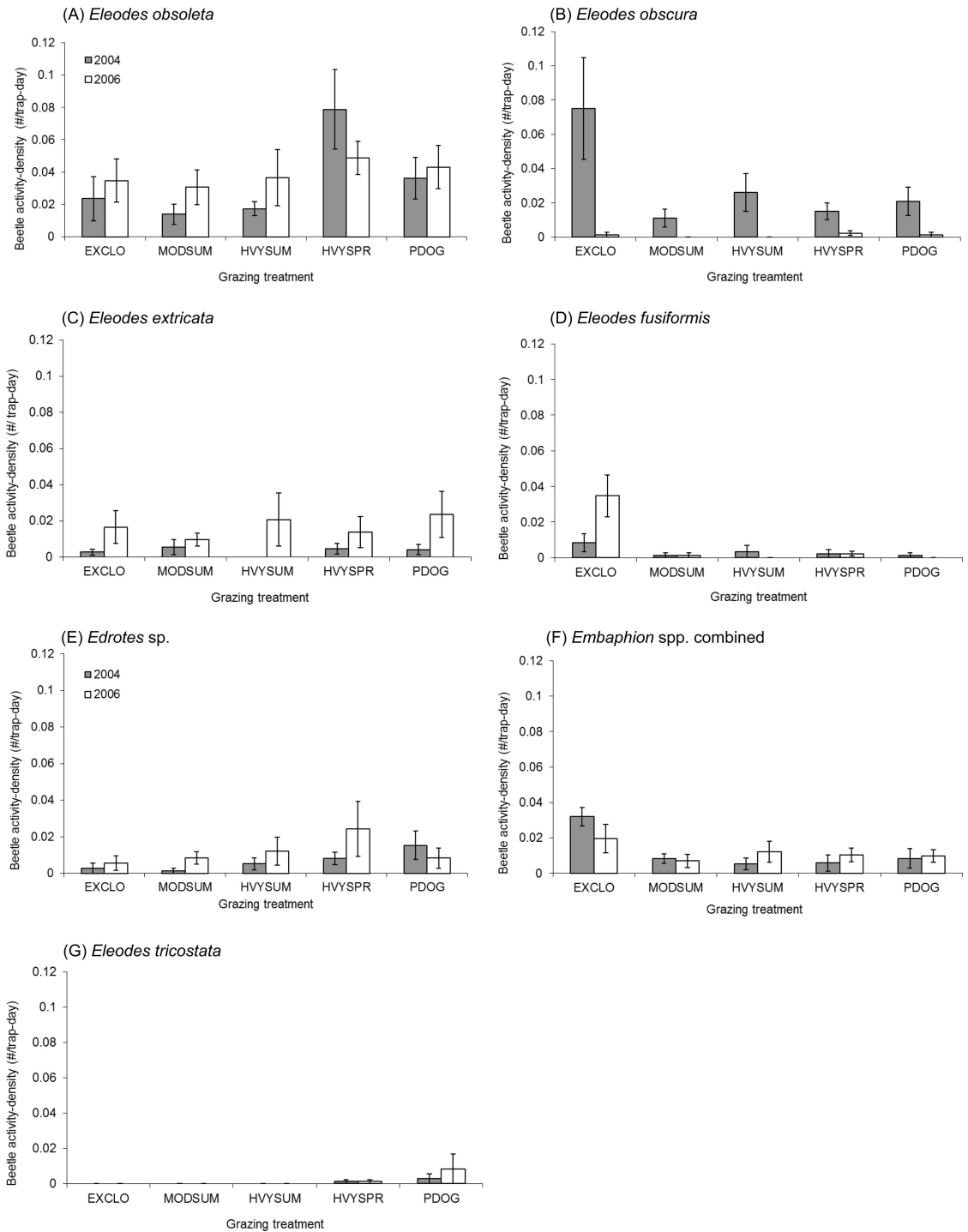
Fig. 2. Activity-density (mean ± SE) of tenebrionid beetles in response to grazing treatments in 2004 and 2006 for (A) *E. obsoleta*, (B) *E. obscura*, (C) *E. extricata*, (D) *E. fusiformis*, (E) *Edrotes* sp., (F) *Embaphion* spp., and (G) *E. tricostata*. Study plots were established and first sampled in 2004, coincident with treatment implementation. Measurements in 2006 correspond to responses 2 yr after treatments were implemented. Data presented are untransformed values. Abbreviations for grazing treatments are: EXCLO, exclosures; MODSUM, moderate summer grazing; HVYSUM, intensive summer grazing; HVYSPR, intensive spring grazing; PDOG, moderate summer grazing in areas with prairie dogs.
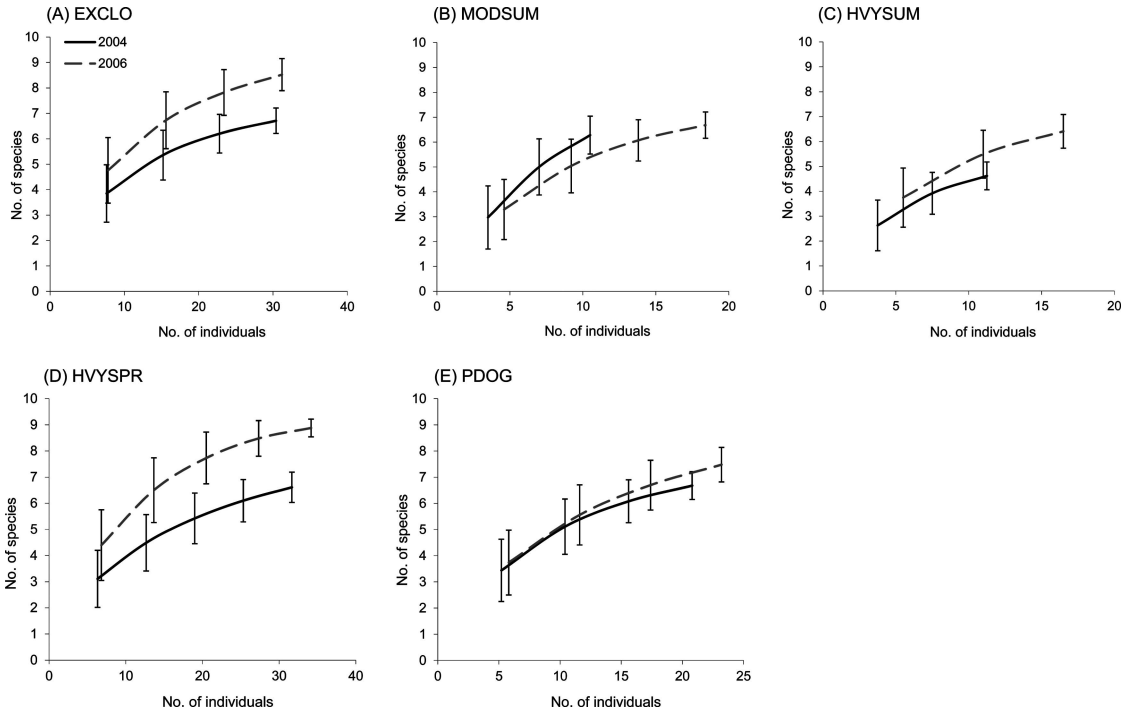
Fig. 3. Individual-based rarefaction curves (±SD) for tenebrionid beetles among grazing treatments in 2004 and 2006: (A) EXCLO, exclosures; (B) MODSUM, moderate summer grazing; (C) HVYSUM, intensive summer grazing; (D) HVYSPR, intensive spring grazing; (E) PDOG, moderate summer grazing in areas with prairie dogs.

20; $P = 0.09$; *Eleodes tricostata* (Say) and *Edrotes* sp., $P > 0.10$; Fig. 2A, E, and G).

In contrast to spiders and beetles in general, which tended to increase in mean activity-density from 2004 to 2006, tenebrionid species demonstrated varied responses through time. *E. obscura* declined dramatically in 2006 (RMANOVA, $F = 51.48$; df = 1, 20; $P < 0.0001$), while *Eleodes extricata* (Say) increased during the same period (RMANOVA, $F = 10.92$; df = 1, 20; $P = 0.0035$; Fig. 2B and C). Finally, although some patterns suggested that there might be significant treatment-by-year interactions between MODSUM and HVYSPR and HVYSUM for some species (e.g., *E. obsoleta*, Fig. 2A), none of these potential interactions were significant.

Rarefaction curves revealed that the number of tenebrionid species increased with sampling intensity more rapidly in 2006 compared with 2004 on EXCLO (8.5 vs. 6.7, respectively) and HVYSPR (8.9 vs. 6.6) plots compared with MODSUM plots (i.e., reference plots), which showed little change during the same period (6.7 vs. 6.3; Fig. 3). For both EXCLO and HVYSPR, observed richness was greater (no overlap in SD at the greatest common sample size) between years, while no difference in richness was observed for MODSUM, HVYSUM, or PDOG treatments during that same period.

In 2004, as the experimental grazing treatments were first being initiated, tenebrionid beetle communities showed no significant clustering among grazing treatments in multivariate analyses ($R = 0.019$, $n = 16$,

$P = 0.37$; Fig. 1D). Moreover, the stress value associated with the MDS plot was 0.22, suggesting difficulty expressing the data in two dimensions. In contrast, 2 yr after the initiation of the treatments (2006), beetle communities tended to cluster together ($R = 0.099$, $n = 25$, $P = 0.078$; Fig. 1E); tenebrionid beetles on EXCLO plots were significantly different from other grazing treatments ($P < 0.05$) except HVYSPR ($P = 0.17$). Not surprisingly, the activity-density of *E. fusiformis*, which was common only on EXCLO plots, and increased in 2006 (Fig. 2D), contributed the most (24–27%) to pairwise dissimilarities between treatments (SIMPER analysis).

Finally, grasshopper densities ranged from 0.06 to nearly 4 individuals m^{-2} among study plots. Patterns across treatments mirrored those for beetle and spider families in general, with grasshopper density showing no response to grazing treatments ($F_{4,\ 20} = 0.56$; $P = 0.69$; Table 1). Notably, in contrast to responses of other arthropods, grasshoppers declined rather sharply between 2004 and 2006 ($F_{1,\ 20} = 105.34$; $P < 0.0001$; Table 1).

Discussion

Grazing had a significant effect on vegetation structure, plant species composition, and bare ground cover, as evidenced by results from the extremes of our grazing gradient (i.e., long-term exclosures and prairie dog colonies). Not unexpectedly, and in accordance with previous studies (e.g., Milchunas et al.

1992), sites where livestock had been excluded for ≈70 yr exhibited unique vegetation structural characteristics in both years of the study; vegetation height, an important attribute of habitat structure, was significantly higher within long-term exclosure plots (EXCLO). Similarly, these same plots (EXCLO) differed from other treatments based on plant community composition, supporting higher percent cover of mid-height, cool-season grasses (e.g., *H. comata*). Plots established on prairie dog colonies (PDOG) also differed from other treatments, with significantly lower percent cover of cactus (*O. polyacantha*) and higher cover of bare ground. In general, bare ground cover increased with increasing grazing intensity, and was highest on the most heavily grazed PDOG plots. Finally, there was evidence that our short-term experimental manipulations of grazing intensity also affected vegetation; comparisons between the moderately grazed, reference plots (MODSUM) and the newly initiated heavily grazed plots revealed that very heavy spring grazing (HVYSPR) reduced grass and shrub height. Therefore, we detected vegetation responses to both short- and long-term grazing treatments.

Despite our expectations that ground-dwelling spiders and beetles would be sensitive to reduced vegetation height (e.g., spiders, Weeks and Holtzer 2000; beetles, Southwood et al. 1979) and increased bare ground cover (e.g., spiders, Costello and Daane 1998, Silva et al. 2010; beetles, McIntyre 1997, 2000; Stapp 1997), these arthropod groups, including measures of their community structure (i.e., family-level composition), activity-density, and richness, showed no significant responses to grazing. We speculate that lack of response at the family level may indicate a certain level of redundancy among functional groups such that there may be enough species that show positive and negative responses to each set of grazing conditions that the net overall effect is one of no change in richness or abundance. Other potential explanations for these findings include an inherently resilient arthropod community to grazing effects as has been suggested for shortgrass steppe plant communities (Milchunas et al. 1988, Milchunas and Lauenroth 1993), lack of sufficiently dramatic vegetation changes given the short stature of grasses in the shortgrass steppe, or interactions with the timing and intensity of precipitation (see below). Alternatively, by pooling across broad taxonomic groups and assessing family-level responses to grazing, we may have obscured effects on particular species (see Simelane 2010), which, for example, was the case here when we examined tenebrionids at the species level. Thus, concluding that these arthropods are insensitive to grazing may be somewhat misleading.

In contrast, the tenebrionid community was sensitive to grazing. Tenebrionids are a conspicuous group of ground-foraging, detritivorous beetles that are relatively common in shortgrass steppe (Allsopp 1980, Hoffman and Wiens 2004, Crist 2008), and species richness in our study ($n = 12$ species) was comparable with reports from others in this system (e.g., Stapp

1997, $n = 14$; McIntyre 2000, $n = 9$; Hoffman and Wiens 2004, $n = 17$). Our hypothesis that tenebrionids would be reduced with increasing grazing intensity received only partial support. We found higher species richness and greater abundances of certain species (e.g., *E. fusiformis*) within the long-term grazing exclosures (consistent with our hypothesis); however, some species tended to increase with grazing (e.g., *E. tricostata* and *Edrotes* sp.), similar to observed responses following wildfire (Parmenter et al. 2011), which may be attributed, in part, to trap bias (Stapp 1997, Parmenter et al. 2011), and richness was elevated on HVYSPR and EXCLO plots in 2006 (inconsistent with our hypothesis). Importantly, many of these patterns were stronger in 2006, a drier year compared with 2004 (e.g., Fig. 2D), suggesting that *both* exclusion from grazing and precipitation are presumably necessary to create pronounced differences in vegetation structure to which arthropod consumers then respond.

Grasshoppers also seemed to respond to the drier conditions in 2006 when vegetation height was generally reduced (Table 1). The marked difference in response between beetles and spiders, which both increased in 2006, versus grasshoppers, which declined in 2006, underscores the fact that grasshoppers, as aboveground herbivores, are likely to be especially sensitive to aboveground vegetation change (e.g., Spalinger et al. 2012). However, somewhat surprisingly, that apparent sensitivity did not translate into a measurable response to grazing treatments, which also produced variability in aboveground plant availability. Low grasshopper densities (<4 individuals m^{-2}), although similar to what others have reported in this system (Capinera and Sechrist 1982, Welch et al. 1991), may have contributed to our inability to detect grazing effects (Branson and Sword 2010). Further, as noted above, pooling across such a broad taxonomic group (Orthoptera) likely masked species-specific responses (e.g., O'Neill et al. 2010). While grasshopper response may be more closely tied to aboveground plant biomass as their primary food resource, the increase for beetles and spiders observed in 2006 may suggest a positive response to a more pronounced mosaic of microhabitat structure, with patches of bare ground interspersed with vegetation of varying heights.

Finally, as expected, with increased quantities of cattle dung deposited on plots with increased stocking rates (HVYSUM and HVYSPR), scarab beetles, some of which were dung beetle species, tended to be more common on these plots relative to the moderately grazed (MODSUM) plots. Although it has been shown that moderate-intensity, traditional grazing in systems with a long history of grazing can promote dung beetle diversity (Verdu et al. 2000, 2007; Lobo et al. 2006; Jay-Robert et al. 2008), excessive grazing pressure can lead to more depauperate communities, as intolerant species are extirpated (discussed in Verdu et al. 2007).

Our selection of grazing treatments—both "long-term" conditions and "short-term" manipulations—was a deliberate attempt to evaluate the effects of a broader range of grazing conditions on shortgrass

steppe consumers than have been previously considered. These two sets of treatments differed in both subtle and substantial ways, and therefore our expectations concerning responses to these treatments differed as well. Exclosures and prairie dog colonies are conditions that have been in place for decades, or are a natural component of the study system (e.g., prairie dogs are widespread in the shortgrass steppe and at the CPER since 1997). Pastures where MODSUM plots were established have been grazed at moderate intensities since 1939. Conversely, the manipulations designed to stress the system using increased grazing intensity (HVYSPR and HVYSUM plots) were initiated recently. Given the inherently low productivity and high resiliency of the shortgrass steppe to grazing (Milchunas et al. 1988, Milchunas and Lauenroth 1993), even extreme manipulations of seasonality and intensity of grazing may not have been translated into consistent differences in arthropod consumer communities over the short term (2 yr), even when significant impacts were observed on vegetation structure (e.g., on HVYSPR plots). Further, although responsive to the long-term grazing treatments, species-specific responses by tenebrionids to our manipulations may also require more time to manifest owing to the relatively slow development time and longer life span of these beetles, characteristics which may delay responses to environmental change (Crist 2008, and references therein).

Grazing is, and historically has been, a prominent driver of ecosystem structure in the shortgrass steppe (Mack and Thompson 1982, Milchunas et al. 1988, Lauenroth and Milchunas 1991). Adaptations by plants to grazers have resulted in a plant community that is, for the most part, resilient to grazing pressure by large herbivores (Milchunas and Lauenroth 1993). We found that both "short-" and "long-term" grazing treatments affected vegetation structure, but generally not arthropods, and that only longer-term treatments, those with greater differences in vegetation height and plant species composition, seemed to affect arthropod populations at the species level (i.e., tenebrionids). Thus, our results suggest, at least in the short term, that shortgrass steppe arthropods also appear to be resilient to grazing. These findings may be particularly relevant in the context of balancing sustainable production of livestock with preservation of rangeland biodiversity and associated ecosystem services (Watkinson and Ormerod 2001, Kemp and Michalk 2007). Moreover, there is growing interest in conservation grazing—the use of carefully managed grazing, including increasing grazing intensity (e.g., Vavra 2005), as a conservation tool (Severson and Urness 1994, Vavra 2005, Fuhlendorf et al. 2006, Derner et al. 2009, Augustine and Derner 2012). Management that supports a range of grazing treatments that are variable in time and space and that create a mosaic of habitat types (Fuhlendorf and Engle 2001, Derner et al. 2009, Davidson et al. 2010) may be the best option for land managers confronted with issues at the production-conservation interface (Toombs et al. 2010).

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