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Livestock exclusion increases the spatial heterogeneity of vegetation in Colorado shortgrass steppe

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Abstract. Spatial heterogeneity, an important characteristic in semi-arid grassland vegetation, may be altered through grazing by large herbivores. We used Moran's *I*, a measure of autocorrelation, to test the effect of livestock grazing on the fine scale spatial heterogeneity of dominant plant species in the shortgrass steppe of northeastern Colorado. Autocorrelation in ungrazed plots was significantly higher than in grazed plots for the cover of the dominant species *Bouteloua gracilis*, litter cover and density of other bunchgrasses. No species had higher autocorrelation in grazed compared to ungrazed sites. *B. gracilis* cover was significantly autocorrelated in seven of eight 60-yr ungrazed exclosures, four of six 8-yr exclosures, and only three of eight grazed sites. Autocorrelograms showed that *B. gracilis* cover in ungrazed sites was frequently and positively spatially correlated at lag distances less than 5 m. *B. gracilis* cover was rarely autocorrelated at any sampled lag distance in grazed sites. The greater spatial heterogeneity in ungrazed sites appeared linked to patches characterized by uniformly low cover of *B. gracilis* and high cover of C_3 grasses. This interpretation was supported by simple simulations that modified data from grazed sites by reducing the cover of *B. gracilis* in patches of ca. 8 m diameter and produced patterns quite similar to those observed in ungrazed sites. In the one exclosure where we intensively sampled soil texture, autocorrelation coefficients for sand content and *B. gracilis* cover were similar at lag distances up to 12 m. We suggest that the negative effect of sand content on *B. gracilis* generates spatial heterogeneity, but only in the absence of grazing. An additional source of heterogeneity in ungrazed sites may be the negative interaction between livestock exclusion and *B. gracilis* recovery following patchy disturbance.

Keywords: Disturbance; Grazing; Moran's *I*; Plant competition; Spatial dependence.

Introduction

Most ecological studies focus on how a treatment affects the mean value of a variable, and rarely consider changes in the spatial distribution of the variable. However, description of spatial pattern, and how it is altered by perturbation, is important for at least two reasons. First, patterns must be observed before underlying mechanisms can be identified (Levin 1992). Pioneering work by Greig-Smith (1979) was designed primarily to infer mechanism from pattern. Second, as recognized over 50 yr ago (Watt 1947), pattern may influence processes such as the spread of disturbance, the movement and persistence of organisms, and the redistribution of matter and nutrients (reviewed by Turner 1989; Pickett & Cadenasso 1995).

While a great deal of research has examined the response of large herbivores to landscape and resource heterogeneity (Coughenour 1991; Bailey et al. 1996; Hobbs 1999) a smaller body of work documents the effect of large herbivores on spatial heterogeneity of vegetation. Herbivores may dramatically alter vegetation structure, influencing habitat diversity and in turn the abundance of small mammals, birds and insects (Smith 1940; Bock et al. 1984; Milchunas et al. 1998). Grazing has been shown to increase spatial heterogeneity in some grasslands (Bakker et al. 1983; McNaughton 1984) and decrease heterogeneity in others (Sala et al. 1986; Gibson 1988b; Fuhlendorf & Smeins 1998; Tracy et al. 1998).

The shortgrass steppe, which occupies the western, driest portion of the Great Plains, is exceptionally grazing-tolerant (Milchunas et al. 1989). As a result of the complementary selection pressures of semi-aridity and a long evolutionary history of grazing, changes in species composition and above-ground net primary production with grazing are small compared to other grasslands. The short C_4 bunchgrasses *Bouteloua gracilis* and *Buchloë dactyloides* are relatively more abundant under moderate and heavy grazing, while the taller C_3 grasses, as well as forbs, are more abundant in ungrazed and lightly grazed areas (Milchunas et al. 1989; Hart & Ashby 1998). But much less is known about how grazing influences the distribution of these dominant plant species. At the landscape scale, grazing reduced the difference in species composition between level uplands and swales (Milchunas et al. 1989). At very small scales, within 0.25 m^2 quadrats, grazing produced a more uniform distribution of both above- and below-ground biomass compared to ungrazed controls (Milchunas & Lauenroth 1989). Both results suggest that grazing reduces the spatial heterogeneity of shortgrass steppe vegetation, though neither study used spatial statistics to test the effect of grazing on spatial patterns. Earlier work using a blocked-quadrat approach reached the opposite conclusion, finding more intense spatial pattern, or greater heterogeneity, in grazed than in long-term ungrazed sites (Mitchell 1971). These contrasting results may be due to differences in statistical analysis, the spatial scale of measurement, or the particular sites studied. In fact, descriptions of vegetation spatial pattern in long-term, replicated grazing trials are rare in all ecosystems.

Our primary objective was to describe how long-term (60 yr) protection from moderate, summer cattle grazing has affected the abundance and fine scale spatial heterogeneity of the dominant plant species at a shortgrass steppe site in northeastern Colorado. In addition, we developed hypotheses for processes that could generate the observed patterns.

Defining and measuring spatial heterogeneity

Different definitions of spatial heterogeneity may be one reason for the conflicting results among studies of grazing effects on vegetation pattern. The simplest definition of spatial heterogeneity is a 'departure from randomness of distribution' (Greig-Smith 1979). However, with respect to point patterns, spatial heterogeneity refers to density variation among locations, whereas in the context of surface patterns, spatial heterogeneity 'refers to variation over space of the observed values of a qualitative or quantitative descriptor' (Dutilleul & Legendre 1993). Since plant community composition and structure are measured with continuous variables such as percent cover, we will use spatial heterogeneity in the sense of surface patterns.

The spatial heterogeneity of surface patterns can be measured by spatial dependence, the relationship between values of a variable as a function of distance between observations. More intense spatial dependence implies stronger heterogeneity (greater departure from randomness). Previous authors have quantified spatial heterogeneity using measures of spatial dependence such as semivariance, which is based on a covariance function (Sarnelle et al. 1993; Pastor et al. 1998), autocorrelation, which is based on a correlation function (Riera et al. 1998), and fractal dimension (Milne 1991; Palmer 1988). We chose autocorrelation as our measure of spatial heterogeneity because it allows tests of statistical significance (Oden 1984).

Methods

Study area

The research was conducted at the Central Plains Experimental Range (40° 49' N; 107° 47' W) located in northeastern Colorado. Mean annual precipitation is 310 mm, of which 85 % falls during May, June and July. Air temperature averages 15.6 °C in summer and 0.6 °C in winter. The mean annual temperature is 8.6°C. Soils are coarse, with sand content ranging from 54 to 72 % (Yonker et al. 1988). The vegetation is dominated by the short C_4 perennial bunchgrasses *Bouteloua gracilis* and *Buchloë dactyloides*. The subdominant C_3 grasses include *Agropyron smithii, Stipa comata, Aristida longiseta,* and *Sitanion hystrix*. The cactus *Opuntia polyacantha* is also important. On deep sandy soils, normally sparse shrubs such as *Atriplex canescens* increase in density. Precipitation was above average during the period of fieldwork, the summers of 1998 and 1999 (annual totals of 331 and 513 mm, respectively).

Sampling

Since 1939, livestock exclosures of ca. 0.5 ha have been maintained within pastures grazed moderately (40 % of above-ground net primary production consumed) during summer (typically June 1 - October 1) (Kipple & Costello 1960). In eight pastures we sampled paired plots inside and outside the exclosures. In six of these pastures the exclosures were enlarged in 1991, allowing a comparison of the effects of short versus long-term protection from grazing. We sampled these sites as well.

In each plot we established two perpendicular 40 m transects crossing at the center point (forming an 'X') to minimize the influence of gradients. We randomly located quadrats (25 cm × 25 cm) within each meter of each transect (80 quadrats total). We recorded the canopy cover of all perennial species, exposed litter and bare soil, as well as the density of forbs and C_3 grasses. In one exclosure, we extracted soil cores (to 20 cm depth) within each quadrat to analyse fine scale variability in soil texture.

To evaluate the level of small mammal activity inside and outside the exclosures, we counted both gopher mounds and all other burrow holes along 200 m of 1-m wide belt transects in the long-term grazed and ungrazed treatments at six sites during July 1999. We estimated the surface area of gopher mounds and other burrows by measuring the longest axis of each mound or burrow and a second axis perpendicular to the first.

Statistical analysis

We analysed the autocorrelation of individual species abundances measured as percent cover or density, depending on the growth form of each species. In addition, we analysed the spatial dependence of a multivariate index of plant community composition as follows: After performing a Detrended Correspondence Analysis (DCA) on the quadrat level data within each site, we used the quadrat scores from the first DCA axis in an autocorrelation analysis (Dale 1999). We ran the DCA with Canoco 4.0 (ter Braak & Šmilauer 1998).

We used Moran's *I* to compare the strength of spatial dependence in different treatments (Sokal & Oden 1978). A value of Moran's *I* approaching 1 indicates high positive spatial correlation, a value near 0 indicates no spatial relationship or a random spatial distribution, and values approaching –1 indicate high negative spatial correlation. We calculated Moran's *I* in two forms. The first, which we call a 'global' coefficient, includes all distance comparisons, but weights the paired-observations as an inverse of their lag distance (Reich et al. 1994). Thus, points close together contribute more to the statistic than points far apart. The global coefficient summarizes a great deal of information in one number, allowing convenient comparison across treatments, but it provides no information about the scale of pattern, and in fact the intensity of pattern will appear to increase with the scale of pattern. We calculated a second form of Moran's *I* to construct autocorrelograms, solving the scale problem by showing the strength of autocorrelation as a function of lag distance (Legendre & Fortin 1989). For autocorrelograms, we calculated separate coefficients of Moran's *I* for observations separated by discrete lag distance classes. The observations within each distance class were weighted equally. We then plotted these autocorrelation coefficients over increasing lag distance. To test for spatial cross-correlation between *B. gracilis* abundance and soil texture we used a form of Moran's *I* extended to two variables (Reich et al. 1994). To evaluate the significance of each correlogram we used a Bonferroni correction for multiple comparisons, setting the significance level at $p < 0.0033 = 0.05/15$ (15 distance classes tested). A correlogram is significant only if it contains at least one *p*-value below the Bonferroni corrected level. We calculated Moran's *I* using S-Plus 4.5 and a library of spatial functions developed by Venables & Ripley (1994) and modified by Reich & Davis (1998). We used SPSS 9.0 for paired *t*-tests of vegetation cover values and global Moran's *I* coefficients.

Data exploration

To test our interpretation of the field observations, we explored ways of altering the *B. gracilis* data from the grazed plots to produce the spatial structure observed in *B. gracilis* in the ungrazed plots. Long-term protection from grazing lowered *B. gracilis* cover but increased its spatial dependence. To simulate this process, we altered the observed data from the grazed treatments by lowering *B. gracilis* cover in selected quadrats. After first determining that autocorrelation was not increased by reducing *B. gracilis* cover in randomly selected quadrats, we selected randomly located groups, or 'patches', of quadrats. We designed a three-way factorial experiment using three levels of reduction in cover (original cover in quadrat minus 20 %, 40 % or 80 %, all negative values fixed at 0), three numbers of patches (1, 2 and 4), and three levels of quadrats per patch (4, 8 and 12). Each treatment combination was replicated three times. These treatments were applied to data from the grazed plots of four sites that had strong autocorrelation in the ungrazed treatment, but no autocorrelation in the grazed treatment. The mean *B. gracilis* cover and the global Moran's *I* of *B. gracilis* cover in the simulated data sets were then compared with the observed values of each site using mean squares.

Results

Abundance

Percent cover of *B. gracilis* and bare ground were significantly higher in grazed compared to ungrazed plots (Table 1). In contrast, cover of litter and density of *A. smithii* individuals were higher in the ungrazed treatments. Grazing treatment had no significant effect on the abundance of bunchgrasses, a category in which we include all perennial bunchgrasses at the site with the

Table 1. Differences in mean abundance of dominant vegetation components between grazed and ungrazed treatments (n= 8) based on paired *t*-tests. Abundance measured as percent canopy cover (%) or density per quadrat (#). 'Bunchgrass' includes all perennial bunchgrasses other than *B. gracilis*.

Variable	Mean grazed	S.E.	Mean ungrazed	S.E.	*t*	*p*
Litter (%)	17.4	4.0	27.8	3.3	–5.1	<0.01
A. smithii (#)	1.9	0.7	5.9	1.5	–4.6	<0.01
B. gracilis (%)	37.0	4.1	25.7	5.1	3.7	0.01
Bare ground (%)	20.6	2.0	15.7	1.6	3.28	0.01
Bunchgrass (%)	7.2	2.9	9.2	4.6	–0.9	0.41

Table 2. Frequency of positive and negative Pearson correlation coefficients for cover of *B. gracilis* and other vegetation components. Abundance measured as cover (%) or density (#).

Correlation of *B. gracilis* and:	Grazed (n = 8) positive	Grazed (n = 8) negative	Ungrazed (n = 8) positive	Ungrazed (n = 8) negative
Litter (%)	1	2	0	3
A. smithii (#)	0	2	0	4
Bunchgrass (%)	1	5	0	3
Carex spp.	0	3	2	2

Table 3. Difference in mean global Moran's *I* among treatments, and number of sites with significant global Moran's *I*. Superscript letters refer to significant treatment differences based on LSD in a one-way ANOVA.

Treatment	Mean Moran's *I*	Sites with significant Moran's *I*	Total sites
Grazed	0.05^a	3	8
8-yr ungrazed	0.07^a	4	6
60-yr ungrazed	0.12^b	7	8

exception of *B. gracilis*. These results are consistent with previous work (Milchunas et al. 1989) both in the direction and small magnitude of the responses: cover of *B. gracilis* and litter inside and outside exclosures differed by less than 12 and 11% respectively.

B. gracilis abundance was seldom positively correlated with abundance of other vegetation components, but frequently negatively correlated (Table 2). Correlations between *B. gracilis* and other vegetation components were not clearly affected by grazing treatment.

Autocorrelation

The mean 'global' Moran's *I* coefficient was significantly higher in the ungrazed compared to grazed treatments for *B. gracilis* cover, litter cover, and density of other bunchgrasses (Fig. 1). Scores from the first DCA axis (p = 0.07) and the density of *A. smithii* (p = 0.11) both showed a trend of higher autocorrelation on ungrazed sites (Fig. 1). Cover of bare ground had very low autocorrelation in both grazed and ungrazed plots. Although the density of *Carex* spp. was significantly autocorrelated in many of the sites, the mean coefficient was not significantly higher in the ungrazed treatments.

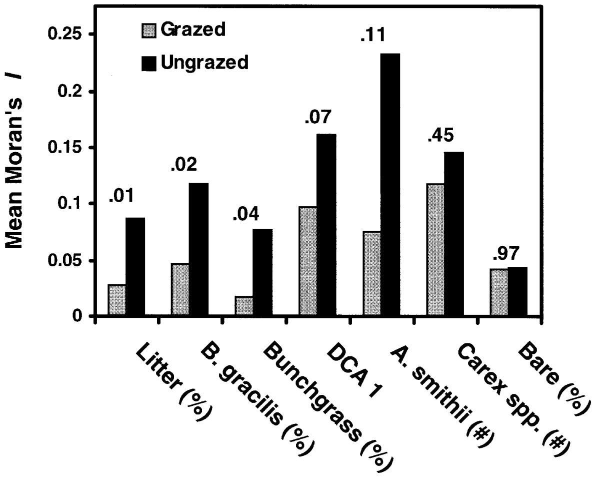

Fig.1. Difference in mean 'global' Moran's *I* for grazed and ungrazed treatments (n = 8). Calculations based on canopy cover (%) or density per quadrat (#). 'DCA 1' refers to quadrat values from the first axis of a detrended correspondence analysis performed within each site. *P*-values from a paired *t*-test listed above bars.

Cover of the dominant species, *B. gracilis*, was significantly autocorrelated in three of the eight grazed sites and seven of eight long-term ungrazed sites. In the short term (8-yr) exclosures, Moran's *I* for *B. gracilis* cover was significant in four of six sites and averaged 0.07, not significantly different from the grazed mean of 0.05, but significantly lower than the long-term ungrazed mean of 0.12 (Table 3). Paired differences in mean *B. gracilis* cover were not related to differences in autocorrelation of *B. gracilis* cover.

Autocorrelograms for *B. gracilis* in grazed and ungrazed treatments (Fig. 2), show positive autocorrelation at lag distances less than 5 m, especially in the ungrazed sites. At these distances, Moran's *I* values were frequently significant at the conservative level of $p < 0.00335$ in the ungrazed treatments, but, in all grazed plots combined, only two individual values of Moran's *I* were significant. Neither treatment displayed autocorrelation at distances between 5 and 15 m. Averaging the autocorrelograms by treatment further demonstrated that at lag distances less than 5 m, *B. gracilis* cover was more positively autocorrelated in the ungrazed plots than in the grazed (Fig. 3). At distances greater than 15 m, the ungrazed sites demonstrated a tendency towards more negative autocorrelation. The scale of pattern of the other vegetation components (not shown) was consistent with patterns in *B. gracilis*.

Soil texture

At the one exclosure in which we intensively sampled soil texture, the spatial dependence of sand content (%) closely matched the spatial dependence of *B. gracilis* cover at lag distances from 1 to 12 m (Fig. 4a). A negative Pearson's correlation coefficient between

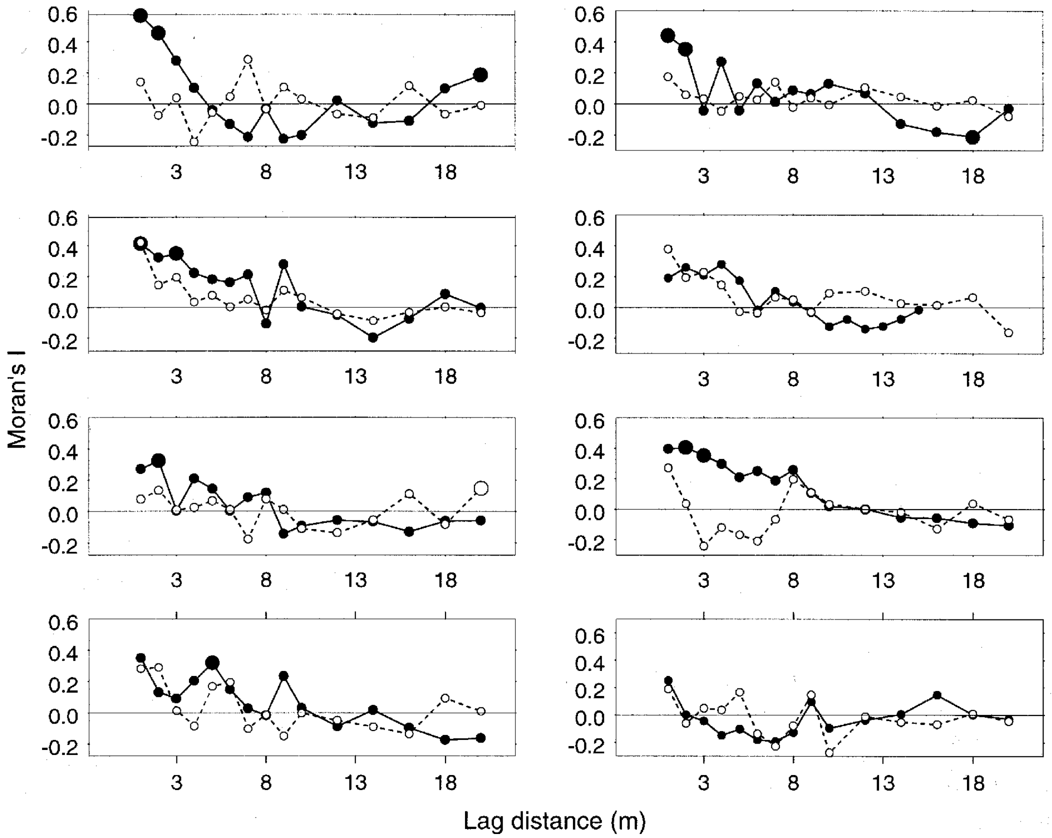

Fig. 2. Autocorrelograms based on cover of *B. gracilis* for long-term grazed and ungrazed treatments at all eight sites. Solid circles show ungrazed data, open circles show grazed data. Large symbols indicate values of Moran's *I* significant at the Bonferroni corrected level $p < 0.00335$.

sand content and *B. gracilis* cover ($r = -0.22, p = 0.048$) suggests that these patterns reflect a negative interaction. The cross-correlation analysis (Fig. 4b) also shows a negative spatial correlation between *B. gracilis* and sand content measured in locations separated by less than 3 m, and a positive spatial correlation between *B. gracilis* and sand content measured 5 to 15 m apart.

Rodent activity

We found no difference in gopher activity with grazing. The percent of surface area disturbed by gopher activity ranged from 0 to almost 1.5 % (142 cm^2/m^2). The density of burrows of other rodents was significantly higher in ungrazed than grazed treatments in a paired *t*-test (0.05 burrows/m^2 ungrazed, 0.03 burrows/m^2 grazed; $p = 0.024$). However, the surface area of burrows, which ranged from less than 1 to 9 cm^2/m^2, did not differ between grazed and ungrazed plots.

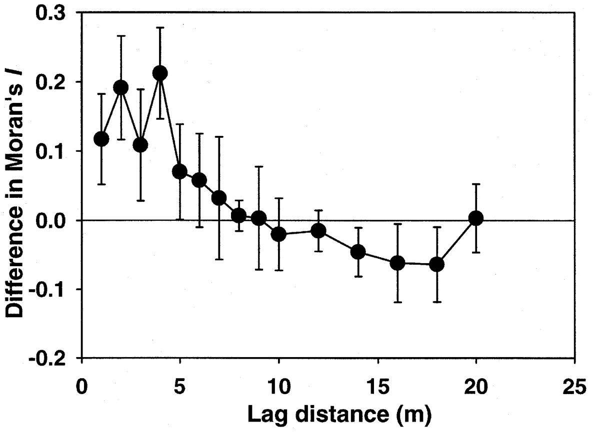

Fig. 3. The mean difference in Moran's *I* (ungrazed – grazed, $n = 8$) at each lag distance. Bars indicate standard error of the mean difference.

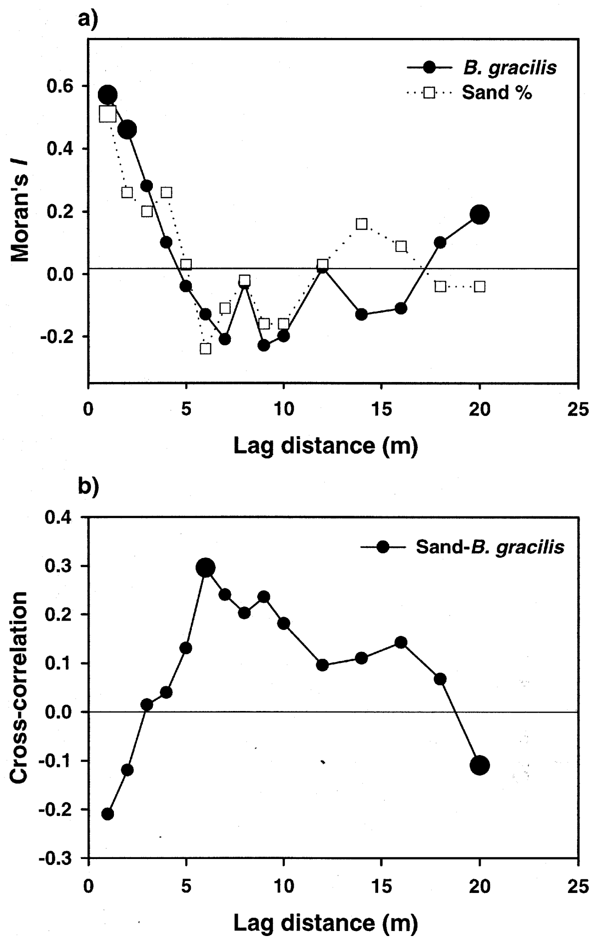

Fig. 4. Spatial patterns in soil texture and *B. gracilis* cover. **a.** Autocorrelograms for sand content (%) and B. gracilis cover. **b.** Cross-correlation between sand content and *B. gracilis* cover. Large symbols indicate values of Moran's *I* significant at the Bonferroni corrected level $p < 0.00335$.

Data exploration

Increases in autocorrelation were directly related to the number of patches created, with the greatest autocorrelation in simulations using four patches (Fig. 5). Simulations that reduced cover by up to 40% per quadrat caused greater increases in autocorrelation than simulations that reduced cover by 20% or 80%. Likewise, simulations using eight quadrats per patch caused greater autocorrelation increases than simulations that used four or 12 quadrats per patch. The best fit to the observed values of Moran's *I*, based on mean squares, were the simulations using 4 patches, with eight quadrats per patch, and 40% reduction in cover. The mean Moran's *I* for these simulations was 0.132, compared to an observed mean Moran's *I* of 0.138. The best fit for mean cover of *B. gracilis* (not shown) occurred in the simulations using four patches, 40% reduction, and 12 quadrats per patch, but the mean square for the simulations using eight quadrats per patch was only marginally higher.

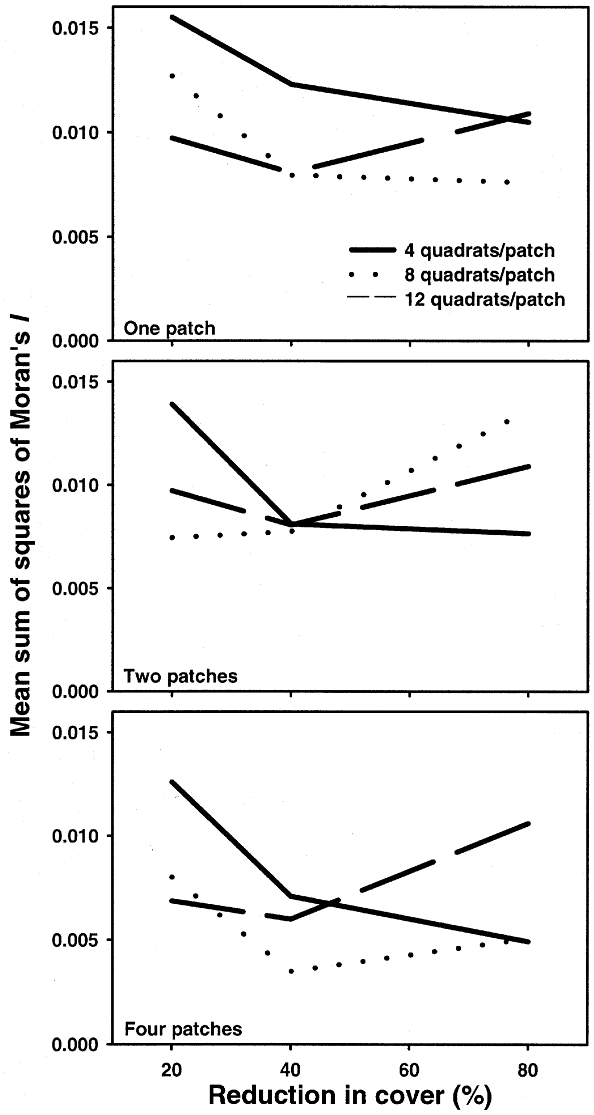

Fig. 5. Profile plots for the mean square difference between simulated and observed values of Moran's *I*. Each panel shows simulations using a different number of patches (1,2 or 4). Each graph shows, for a given number of quadrats per patch, the relationship between percent reduction in *B. gracilis* cover on the X-axis (20, 40 or 80 %) and mean square on the Y-axis.

Discussion

Pattern description

Both the paired *t*-tests of the global Moran's *I* results and the autocorrelograms showed that the dominant components of the vegetation tended to be randomly distributed in the grazed treatments, but were significantly autocorrelated at distances less than 5 m in the long-term ungrazed treatments. Based on our definition of spatial heterogeneity, the greater spatial dependence in the ungrazed exclosures represents an increase in spatial heterogeneity relative to grazed treatments. While *B. gracilis* is extremely dominant in grazed treatments, patches of C_3 grasses in which *B. gracilis* cover is very low occur in the ungrazed treatments. These patches of uniformly low *B. gracilis* cover may be the source of the observed autocorrelation; where *B. gracilis* dominates, its cover is continuous and lacks spatial structure.

The results of our data exploration support our interpretation that the key difference in pattern between treatments is the occurrence of patches of very low *B. gracilis* cover in the ungrazed sites. These simulations also provide information about the scale of pattern, showing that reducing *B. gracilis* cover in multiple patches of 8 m in diameter can reasonably mimic the observed spatial structure of ungrazed vegetation.

The increases in spatial heterogeneity with livestock exclusion demonstrated in our study are consistent with observations from previous work in the shortgrass steppe at landscape and individual plant scales (Milchunas et al. 1989; Milchunas & Lauenroth 1989). Research in the tallgrass prairie of Kansas also showed that within-site spatial heterogeneity decreased with grazing (Glenn et al. 1992), even though species richness increased with grazing (Collins et al. 1998). If the effect of grazing on spatial heterogeneity is similar in these two Great Plains ecosystems, then the processes controlling plant distributions and their interactions with grazing may be consistent as well.

Grazing appears to increase randomness in the spatial structure of ungrazed vegetation. But what underlying process introduced this spatial structure in the first place? Here we consider how grazing might interact with four pattern-generating processes.

Interaction 1. Fine scale pattern in soil characteristics influences vegetation in ungrazed sites, but not grazed sites (Fuhlendorf & Smeins 1998). Spatial heterogeneity in environmental variables may influence plant species composition and introduce pattern in vegetation. If grazing has a greater influence on plant species composition, however, the effect of environmental heterogeneity would be overwhelmed. In the shortgrass steppe, soil texture is an important influence of species composition (Hyder et al. 1966), but the selective pressure of grazing allows *B. gracilis* to dominate even on soil types that, in the absence of grazing, might favor other species. In the one site at which we intensively sampled soil texture, the close match between spatial patterns in sand content and *B. gracilis* cover suggest that soil heterogeneity does indeed generate heterogeneity in vegetation. Given the lack of differences in soil texture inside and outside the exclosures (Milchunas unpubl. data) but the significant difference in the spatial heterogeneity of vegetation, we speculate that grazing dampens the patterns created by sand content.

Interaction 2. Patchy-disturbances, primarily created by rodent activity, are more common in ungrazed exclosures. Small mammal activity can generate spatial heterogeneity in vegetation (Morton 1974). Greater spatial heterogeneity could be found in ungrazed treatments if small mammal activity is higher in the exclosures than in grazed areas. However, our results and previous research showed no effect of grazing on gopher activity (Grant et al. 1980). The significantly higher density of other rodent burrow holes in the ungrazed exclosures is unlikely to affect spatial patterns of vegetation due to the very small areas disturbed. Furthermore, the thirteen lined ground squirrel (*Spermophilus tridecemlineatus*), responsible for many of the burrows we observed, is omnivorous and would be unlikely to have a significant direct effect on vegetation through herbivory. The high density of burrows in ungrazed treatments may be a response to lower soil bulk density in the exclosures relative to the long-term grazed areas. Although we cannot reject the hypothesis that rodent disturbance is more frequent in ungrazed treatments, we think it is unlikely to explain the differences we observed in vegetation pattern. Alternatively, even if no difference in the frequency of rodent disturbance exists, a difference in the spatial pattern of small mammal activity inside and outside the exclosures could have produced the observed treatment effects. To test this possibility, we would need far more intense sampling.

Interaction 3. Spatial patterns generated by individual plant interactions are apparent only in ungrazed sites. A number of biological processes operating at the individual plant scale can generate spatial patterns, such as trade-offs between competitive ability and colonization rates (Whittaker 1975; Tilman 1994), clonal growth (Klimeš 1999), local seed rain (Coffin & Lauenroth 1989; Pastor et al. 1999), priority effects (Pacala & Levin 1997), and alteration of environmental conditions or resource availability by established species (Whittaker 1975; Tilman 1982). These spatial processes, which operate unhindered in the absence of grazing, could be overwhelmed by the selection pressures and mortality caused by grazing. No direct evidence exists for the presence or absence of these processes in the shortgrass steppe.

Interaction 4. Succession after patch disturbance follows different trajectories in grazed and ungrazed sites (Thompson 1985). Pocket gophers, ant mounds, livestock fecal pats, and outbreaks of below-ground herbivory create fine scale disturbance in the shortgrass steppe (Coffin & Lauenroth 1988). Recovery of *B. gracilis* proceeds more quickly in grazed sites than ungrazed sites, probably because of its increased competitive advantage under grazing (Coffin et al. 1998). On disturbed patches in ungrazed sites, C_3 grass and forb abundance remains high for a longer period than in grazed sites. The persistence of patches of C_3-dominated vegetation in ungrazed sites, over time, could create a mosaic with greater spatial heterogeneity than in grazed sites dominated by *B. gracilis*.

Of these four interactions, we have direct evidence for the importance of soil texture in generating spatial heterogeneity in vegetation, direct evidence against small mammal activity, indirect evidence for grazing mediation of succession following patchy disturbance, and no evidence for or against the role of individual plant dynamics. However, we are not suggesting that soil texture is the only source of heterogeneity. More likely, multiple processes operate simultaneously. For example, individual plant interactions such as clonal growth might maintain or strengthen patchiness introduced by soil heterogeneity or patchy disturbance.

Effect of pattern on process

Because the spatial dependence we observed in the ungrazed treatments is fine scale and subtle, implying an equally fine scale and subtle effect on ecosystem process, we focused our discussion on the mechanisms underlying the observed pattern. However, we wish to outline three possible influences of the observed patterns on ecosystem processes. First, differences in pattern at the scale of single square metres may affect habitat use by small animals such as insects (Wiens & Milne 1989). Second, plant composition may interact with spatial pattern to influence nutrient availability (Gibson 1988a). In boreal forests, moose browsing can have a dramatic effect on species composition and the spatial structure of nitrogen availability (Pastor et al. 1998). Strong feedbacks between composition and nutrient availability appear possible in grasslands as well (Wedin & Tilman 1990). Therefore, the subtle patchiness we observed in ungrazed shortgrass steppe may produce spatial structure in nutrient dynamics not present in grazed vegetation. Third, spatial pattern may influence the invasibility of plant communities. Bergelson (1990) showed that a *Senecio* population grew faster when planted among aggregated grasses compared to randomly distributed grasses. In the shortgrass steppe, high uniform cover of *B. gracilis* in grazed areas can limit fine scale (< 3 m^2) species richness (Singh et al. 1996), and may explain why invasive non-native species were more successful in ungrazed compared to grazed areas (Milchunas et al. 1992). Greater patchiness may favor invasion, especially if patches of fast growing plants with high quality litter cause local increases in nutrient availability.

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References

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M. & Sims, P.L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manage.* 49: 386-400.

Bakker, J.P., de Leeuw, J. & van Wieren, S.E. 1983. Micropatterns in grassland vegetation created and sustained by sheep-grazing. *Vegetatio* 55: 153-161.

Bergelson, J. 1990. Spatial patterning in plants: opposing effects of herbivory and competition. *J. Ecol.* 78: 937-948.

Bock, C.E., Bock, J.H., Kenney, W.R. & Hawthorne, V.M. 1984. Responses of birds, rodents, and vegetation to livestock exclosure in a semidesert grassland site. *J. Range Manage.* 37: 239-242.

Coffin, D.P. & Lauenroth, W.K. 1988. The effects of disturbance size and frequency on a shortgrass plant community. *Ecology* 69: 1609-1617.

Coffin, D.P. & Lauenroth, W.K. 1989. Disturbances and gap dynamics in a semiarid grassland: A landscape level approach. *Landscape Ecol.* 3: 19-27.

Coffin, D.P., Laycock, W.A. & Lauenroth, W.K. 1998. Disturbance intensity and above- and belowground herbivory effects on long-term (14 y) recovery of a semiarid grassland. *Plant Ecol.* 139: 221-233.

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J M. & Steinauer, E.M. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280: 745-747.

Coughenour, M.B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. *J. Range Manage.* 44: 530-542.

Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge.

Dutilleul, P. & Legendre, P. 1993. Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. *Oikos* 66: 152-171.

Fuhlendorf, S.D. & Smeins, F.E. 1998. The influence of soil depth on plant species response to grazing within a semi-arid savanna. *Plant Ecol.* 138: 89-96.

Gibson, D.J. 1988a. The maintenance of plant and soil heterogeneity in dune grassland. *J. Ecol*. 76: 497-508.

Gibson, D.J. 1988b. The relationship of sheep grazing and soil heterogeneity to plant spatial patterns in dune grassland. *J. Ecol.* 76: 233-252.

Glenn, S.M., Collins, S.L. & Gibson, D.J. 1992. Disturbances in tallgrass prairie: Local and regional effects on community heterogeneity. *Landscape Ecol.* 7: 243-251.

Grant, W.E., French, N.R. & Folse Jr., L. J. 1980. Effects of pocket gopher mounds on plant production in shortgrass prairie ecosystems. *Southwest. Nat.* 25: 215-224.

Greig-Smith, P. 1979. Pattern in vegetation. *J. Ecol*. 67: 755-779.

Hart, R.H. & Ashby, M.M. 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. *J. Range Manage.* 51: 392-398.

Hobbs, N.T. 1999. Responses of large herbivores to spatial heterogeneity in ecosystems. In: Jung, H.G. & Fahey, G.C. (eds.) *Nutritional ecology of herbivores: Proceedings of the Vth international symposium on the nutrition of herbivores*, pp. 97-129. American Society of Animal Science, Savory, IL.

Hyder, D.N., Bement, R.F., Remmenga, E.E. & Terwilliger Jr., C. 1966. Vegetation-soils and vegetation-grazing relations from frequency data. *J. Range Manage.* 19: 11-17.

Kipple, G.E. & Costello, D.F. 1960. *Vegetation and cattle responses to different intensities of grazing on short-grass ranges on the central Great Plains*, Techn. Bull. 1216. United States Department of Agriculture, Washington, DC.

Klimeš L. 1999. Small-scale plant mobility in a species-rich grassland. *J. Veg. Sci.* 10: 209-218.

Legendre, P. & Fortin, M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio* 80: 107-138.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-67.

McNaughton, S.J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *Am. Nat.* 124: 863-886.

Milchunas, D.G. & Lauenroth, W.K. 1989. Three dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. *Oikos* 55: 82-86.

Milchunas, D.G., Lauenroth, W.K. & Burke, I.C. 1998. Livestock grazing: animal and plant biodiversity of shortgrass steppe and the relationship to ecosystem function. *Oikos* 83: 65-74.

Milchunas, D.G., Lauenroth, W.K. & Chapman, P.L. 1992. Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia* (*Berl.*) 92: 520-531.

Milchunas, D.G., Lauenroth, W.K., Chapman, P.L. & Kazempour, M.K. 1989. Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* 80: 11-23.

Milne, B.T. 1991. Heterogeneity as a multiscale characteristic of landscapes. In: Kolasa, J. & Pickett, S.T.A. (eds.) *Ecological heterogeneity*, pp. 69-84. Springer-Verlag, New York, NY.

Mitchell, G.C. 1971. *Spatial distribution and successional state of grassland vegetation related to grazing intensity treatment*s. U.S. International Biological Program Grassland Biome Techn. Report 101,Colorado State University, Fort Collins, CO.

Morton, A.J. 1974. Ecological studies of a fixed dune grassland at Newborough Warren, Anglesey. *J. Ecol*. 62: 261-278.

Oden, N.L. 1984. Assessing the significance of a spatial correlogram. *Geogr. Anal.* 16: 1-16.

Pacala, S.W. & Levin, S.A. 1997. Biologically generated spatial pattern and the coexistence of competing species. In: Tilman, D. & Kareiva, P. (eds.) *Spatial ecology*, pp. 233-249. Princeton University Press, Princeton, NJ.

Palmer, M.W. 1988. Fractal geometry: a tool for describing spatial patterns of plant commnities. *Vegetatio* 75: 91-102.

Pastor, J., Cohen, Y. & Moen, R. 1999. Generation of spatial patterns in boreal forest landscapes. *Ecosystems* 2: 439-450.

Pastor, J., Dewey, B., Moen, R., Mladenoff, D.J., White, M. & Cohen, Y. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. *Ecol. Appl.* 8: 411-424.

Pickett, S.T.A. & Cadenasso, M.L. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269: 331-334.

Reich, R.M., Czaplewski, R.L. & Bechtold, W.A. 1994. Spatial cross-correlation of undisturbed, natural shortleaf pine stands in northern Georgia. *Environ. Ecol. Stat.* 1: 201-217.

Reich, R. & Davis, R. 1998. *Quantitative spatial analysi*s. Unpubl. Course Notes, Colorado State University, Fort Collins, CO.

Riera, J.L., Magnuson, J.J., Vande Castle, J.R. & MacKenzie, M.D. 1998. Analysis of large scale spatial heterogeneity in vegetation indices among North American landscapes. *Ecosystems* 1: 268-282.

Sala, O.E., Oesterheld, M., Leon, R.J.C. & Soriano, A. 1986. Grazing effects upon plant community structure in subhumid grasslands of Argentina. *Vegetatio* 67: 27-32.

Sarnelle, O., Kratz, K.W. & Cooper, S.D. 1993. Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. *Oecologia* 96: 208-218.

Singh, J.S., Bourgeron, P. & Lauenroth, W.K. 1996. Plant species richness and species-area relations in a shortgrass steppe. *J. Veg. Sci*. 7: 645-650.

Smith, C.C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. *Ecology* 21: 381-397.

Sokal, R.R. & Oden, N.L. 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. *Biol. J. Linn.*

Soc. 10: 229-249.

ter Braak, C.J.F. & Šmilauer, P. (1998). *CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 4).* Centre for Biometry Wageningen (Wageningen, NL) and Microcomputer Power, Ithaca, NY.

Thompson, J.N. 1985. Within-patch dynamics of life histories, populations, and interactions: selection over time in small spaces. In: Pickett, S.T A. & White, P.S (eds.) *The ecology of natural disturbance and patch dynamics*, pp. 253-264. Academic Press, Inc, Orlando, FL.

Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75: 2-16.

Tracy, K.N., Golden, D.M. & Crist, T.O. 1998. The spatial distribution of termite activity in grazed and ungrazed Chihuahuan Desert grassland. *J. Arid Environ.* 40: 77-89.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20: 171-197.

Venables, W.N. & Ripley, B.D. 1994. *Modern applied statistics with S-Plus*. Springer-Verlag, New York, NY.

Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.

Wedin, D. A. & Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* (*Berl.*) 84: 433-441.

Whittaker, R.H. 1975. The design and stability of plant communities. In: van Dobben, W.H. & Lowe-McConnell, R.H. (eds.) *Unifying concepts in ecology*, pp. 169-181. Dr. W. Junk, The Hague.

Wiens, J.A., & Milne, B.T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecol.* 3: 87-96.

Yonker, C.M., Schimel, D.S., Paroussis, E. & Heil, R.D. 1988. Patterns of soil organic matter accumulation in a semiarid shortgrass steppe, Colorado. *Soil Sci. Soc. Am. J.* 52: 478-483.

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