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EFFECTS OF MIGRATORY GRAZERS ON SPATIAL HETEROGENEITY OF SOIL NITROGEN PROPERTIES IN A GRASSLAND ECOSYSTEM

DAVID J. AUGUSTINE[1] AND DOUGLAS A. FRANK

Department of Biology, Syracuse University, Syracuse, New York 13244 USA

Abstract. Large herbivores are known to respond to spatial heterogeneity in the distribution of forage resources, but how important herbivores are in creating those spatial patterns, how their influence may be scale dependent, and how herbivore-induced patterns affect ecosystem processes remain unclear. We examined the effects of native migratory ungulates on the spatial distribution of soil nitrogen and N-mineralization potential at scales ranging from 0.1–30 m in grasslands of Yellowstone National Park using geostatistical analyses of soils collected inside and outside long-term (36+-yr) exclosures.

At small spatial scales (0.1–2 m), ungrazed grasslands showed a high degree of patchiness in the distribution of soil N and N-mineralization potential (94% and 77% of sample variation explained by small-scale patchiness, respectively). For both variables, patches occurred at a consistent mean size of ~40 cm. In contrast, grazed grassland exhibited minimal spatial structure in the distribution of soil N and N-mineralization rates (<24% of variation for both variables spatially dependent) and no consistent patch size at a scale of 0.1–2 m. In grazed grassland, most variation was extremely fine grained, occurring across distances <10 cm. The high degree of fine-grained heterogeneity in grazed grassland was associated with greater plant diversity in small (20 × 20 cm) patches. Recycling of nitrogen through dung and urine is clearly important for maintaining long-term nitrogen balance of the system, but we estimated that only 2.5% of the grazed grassland sampled was recently affected by urine. Results conflict with predictions of increased heterogeneity in grazed communities based primarily on the deposition of dung and urine in discrete patches and suggest that the dominant mechanism(s) by which grazers alter N cycling in this ecosystem operates through the plant community. We hypothesize that grazers promote fine-scale heterogeneity by diversifying plant species effects on soils and/or increasing the spatial variability in plant litter inputs.

At larger spatial scales (5–30 m), large herbivores altered the distribution of soil N across a topographic gradient. In a grazed community, soil N properties were associated with the topographic gradient and exhibited increasing variance among sampling points separated by increasing distances from 5 to 30 m. Ungrazed grassland exhibited no spatial structure in soil N distribution and no correlation with topography. Collectively, our data show that grazers influence the distribution of soil N properties at every spatial scale from individual plants to landscapes.

Key words: biodiversity; geostatistics; grassland; herbivory; heterogeneity; nitrogen; ungulates; Yellowstone National Park, USA.

INTRODUCTION

In recent years, ecologists have recognized the central role that spatial patterns in nutrients, plants, and animals can play in determining species coexistence and population dynamics (Tilman 1988, 1994, Tilman and Kareiva 1997), successional patterns and the stability of plant communities (Robertson et al. 1988, Frelich and Reich 1995, Gross et al. 1995), and ecosystem processes (Robertson and Freckman 1995, Ettema et al. 1998, Burke et al. 1999, Turner and Carpenter 1999). Although the relationship between spatial pattern and scale has been identified as one of the unifying themes in ecology (Levin 1992), our understanding of how pattern is generated across spatial scales is extremely limited. Analyses of several terrestrial ecosystems have demonstrated a high degree of spatially structured, local variability in soil resources and nutrient fluxes (Robertson et al. 1993, 1997, Schlesinger et al. 1996, Fisher et al. 1998, Gorres et al. 1998). Abiotic factors such as topography, precipitation, and alluvial and fluvial processes are well known to create spatial heterogeneity in soil properties (e.g., Jenny 1980, Schimel et al. 1985*a*, *b*, Burke 1989, Fisk et al. 1998), but the role of biotic factors in creating spatial pattern, and the implications for community and ecosystem dynamics, are less clear. Plant individuals and plant community composition can affect the distribution of soil nutrients at a variety of spatial scales (Jackson and Caldwell 1993, Gonzalez and Zak 1994, Halvorson et al. 1994, Kelly and Burke 1997, Kleb and Wilson 1997). At the same time, coexistence of plant species may be pro-

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[1] E-mail: djaugust@mailbox.syr.edu

moted by soil heterogeneity at the scale of individual plants (Jackson and Caldwell 1996, Bonis et al. 1997, Ozinga et al. 1997, Reynolds et al. 1997). Despite increasing recognition of the high degree of soil nutrient heterogeneity within plant communities, biotic factors influencing the spatial structure of soil resources have been the subject of only limited experimental analysis.

One biotic component of grasslands that could exert strong effects on spatial patterning of soil processes is large mammalian herbivores. Ungulate herbivores regulate rates of primary production and nutrient cycling in a variety of ecosystems (reviewed by Augustine and McNaughton 1998, Ritchie et al. 1998). Moreover, herbivore distribution and consumption is well known to respond to spatial heterogeneity in plant communities at every scale from plant leaves to the landscape (Senft et al. 1987, McNaughton 1989). However, our understanding of how ungulates in turn may affect spatial heterogeneity is limited. Direct herbivore disturbances to the soil, such as wallowing, rooting, and burrowing, can have significant effects on spatial patterning (Huntly and Inouye 1988, Knapp et al. 1999). In addition, herbivores generate spatial pattern via inputs of excreta to the soil. Ungulates deposit nutrients that they consume from extensive areas into nutrient-enriched, 20–100-cm patches (Afzal and Adams 1992, Steinhauer and Collins 1995). Furthermore, herbivory may influence the pattern of litter inputs to the soil by (1) changing allocation patterns of carbon and nutrients to different plant tissues in response to grazing and (2) over longer time scales, altering the composition and spatial configuration of plant species. Research recognizing the potential for herbivore-induced spatial structure in soil–plant–herbivore interactions indicates that browsing by moose can create hectare-scale patchiness in soil nitrogen (N) and browse availability in southern boreal forests (Pastor et al. 1998) and that grazing by cattle can both increase (Afzal and Adams 1992) and decrease (Lavado et al. 1995) meter-scale patchiness of soil nutrients in pastures.

In Yellowstone National Park, USA, a close interaction has been documented between soil resources, grassland productivity, and grazing. The park supports one of the largest herds of native ungulates, including elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*), in North America (Houston 1982), providing an unusual opportunity to understand the role of unmanaged, migratory ungulates in ecosystem structure and functioning. Elk respond to heterogeneity in forage production by tracking a landscape-scale wave of grass production from low to high elevations across the growing season, by concentrating grazing in areas of high productivity (Frank and McNaughton 1992), and by exhibiting landscape-scale selection of winter grazing locations based on elevation and grassland type (Pearson et al. 1995). Current levels of grazing on Yellowstone's northern winter and associated summer ranges increase aboveground grassland productivity (Frank and McNaughton 1993) but have no effect on standing root biomass (Coughenour 1991). The stimulation of aboveground productivity may be closely linked to accelerated rates of N mineralization in the presence of grazers (Frank and Groffman 1998). Similarly, studies of graminoids from other ecosystems dominated by mammalian grazers emphasize the importance of soil N availability in maintaining high rates of plant productivity under intense grazing pressure (Wegener and Odasz 1997, Hamilton et al. 1998). Although previous studies in Yellowstone have quantified effects of grazers on mean rates of grassland production and soil N dynamics, the degree to which this biotic factor affects spatial patterns in the availability of soil N is unknown.

We sought to determine how Yellowstone's migratory ungulate populations may structure the spatial pattern of soil N properties. Specifically, we conducted an experiment combining a spatially explicit sampling design with geostatistical analyses (Robertson and Gross 1994, Goovaerts 1998) that enabled us to (1) quantify the magnitude of spatial heterogeneity of N dynamics in winter range grasslands of Yellowstone National Park at a broad range of scales relevant to individual plants and plant communities (0.1–30 m) and (2) measure the effects of Yellowstone's migratory ungulate populations on that spatial pattern.

Methods

Field methods

Plant-scale heterogeneity.—In May 1998, soil cores and plant biomass samples were collected at three study sites located on the northern winter range of Yellowstone National Park, USA (44°55′–45°10′ N and 110°10′–119°50′ W). Sites were located at Stephens Creek, Blacktail Plateau, and Lamar Valley and occurred at relatively low (1620 m), middle (2000 m), and high (2100 m) elevations on the winter range, respectively. Sites were selected to include a wide range of precipitation and soil conditions found on the northern winter range. A full description of site locations and characteristics is given by Frank and Groffman (1998). Mean annual precipitation increases with elevation from ~28 cm in the vicinity of Stephens Creek to 32 cm in the Lamar Valley (Houston 1982). Soils of Stephens Creek developed on a bentonite clay-rich substrate resulting from a late Pleistocene landslide. Soils at Blacktail Plateau and Lamar Valley were more characteristic of the northern winter range, having developed on glacial till (Frank and Groffman 1998). Sites were sampled in May, a month when rates of N mineralization had previously been shown to be the highest (Frank and Groffman 1998).

Each study site consisted of one plot placed within a 2-ha ungulate exclosure and a second, paired plot placed in an adjacent, unfenced area. Exclosures were established in 1958 and 1962. At each site, we selected

4 × 4 m plots inside and outside the exclosure with the same slope, aspect, and hill-slope position. Within both the fenced and grazed plots at each site, we established a grid of 111–112 sampling points distributed in a nested, systematic pattern as follows. In the largest systematic grid, points were established every 1 m (25 points). Within this grid, we randomly selected three 1 × 1 m plots, within which we established sampling points every 50 cm (5 additional sampling points within each 1 × 1 m grid). Finally, we randomly selected three 50 × 50 cm plots (in each of the 1 × 1 m grids), within which we established sampling points every 10 cm (24 additional points within each 50 × 50 cm grid). This stratified, nested design was selected to quantify heterogeneity across as broad a range of spatial scales as possible (Gross et al. 1995) and to include scales relevant to individual grassland plants. At each sampling point, we collected a 2 cm diameter × 15 cm depth soil core that was immediately placed in a 705-cm^3 polyethylene bag, stored in an ice-filled cooler, and then transported to a laboratory where cores were maintained at <5°C prior to analysis. We also collected all aboveground live plant biomass within a 5 cm radius of each sampling point. Soil and plant samples were collected from Blacktail Plateau on 16 May, from Lamar Valley on 21 May, and from Stephens Creek on 22 May. Shrubs were present within a small area of the sampling grids, primarily at the Lamar Valley study site inside the exclosure. At the time of sampling, we recorded whether a core was collected from beneath a shrub canopy.

At each site, we also measured local species diversity by placing 16 20 × 20 cm quadrats systematically across each 4 × 4 m plot and recording percentage of cover of each species in the quadrat. Species diversity measures were conducted in July 1998 when plants were larger and species could be more reliably distinguished. Percentage of cover of plant species in quadrats at each plot was used to examine four measures of species diversity. First, we calculated 20-cm scale alpha diversity as the mean of H' calculated for each quadrat (i.e., the mean of 16 H' values for each plot), where $H' = -\Sigma p_i \times \ln p_i$ and p_i is the proportional abundance of species i (Whittaker 1972). Secondly, we calculated 4-m scale alpha diversity by first averaging the percentage of cover of each species across the 16 quadrats and then calculating H', again following Whittaker (1972). Third, we calculated 4-m scale beta diversity as the dissimilarity of quadrats within each plot, which equals (1−PS) where PS refers to proportional similarity of species composition between pairs of quadrats (Beals 1969). Finally, we calculated 20-cm scale species richness as the mean of the number of species in each quadrat and 4-m scale species richness as the total number of species in the 16 quadrats.

Field-scale heterogeneity.—We also examined how grazers affect heterogeneity at a larger spatial scale at a single study site, Blacktail Plateau, by establishing a larger 60 × 30 m sampling grid with 5-m spacing between points (91 points per grid) both inside and outside the exclosure. Again, grids were the same in terms of slope, aspect, and hill-slope position. This site was selected for the field-scale study because it was one of the only long-term exclosures on the winter range where two topographically similar 60 × 30 m plots could be paired inside and outside the fence. The 60-m edge of both grids was oriented along a south-facing hill slope; points from 0 to 50 m north extended from a mid-hill slope to an upper bench, while sampling points at 55 and 60 m north were located on the gently sloping bench. Soils were sampled at each point on 11 May 1998, using the same methods described above. Plant biomass was not sampled at points in the large grids.

Laboratory methods

Aboveground plant samples were sorted into graminoids and nongraminoids, oven-dried at 60°C for at least 48 h, and weighed. Each soil core was hand-sorted to remove stones >2 mm diameter and plant roots. Roots were washed, dried at 60°C for at least 48 h, and weighed. Aboveground plant tissues and roots were ground with a Wiley mill (mesh opening = 1 mm^2), and total N and C content was determined for each sample by Dumas combustion using a CE Elantech 2100 soil analyzer (CE Elantech, Lakewood, New Jersey, USA).

For each soil core, a 10-g subsample (initial) was extracted with 50 mL of 1 mol/L KCl, shaken immediately and again at 12 h, and filtered into scintillation vials at 24 h. Extracts were frozen until analysis for NH_4^+-N and NO_3^--N by continuous flow colorimetry with a Lachat Quikchem Autoanalyzer (Lachat Instruments, Milwaukee, Wisconsin). An additional 10-g subsample was placed in a polyethylene bag, wetted to ~50% water-holding capacity, and incubated in the dark at 23°C for 10 d. Water-holding capacity was estimated for each site using eight additional cores collected the same day as grid sampling. Incubated soils were then extracted and analyzed for NH_4^+-N and NO_3^--N as for the initial subsamples. Gravimetric moisture content was measured using an additional 10-g subsample from each core. Total soil N and C was determined for each core by Dumas combustion using a CE Instruments CN Autoanalyzer. Potential N mineralization was measured as the difference in extractable N ($NH_4^+ + NO_3^-$) between incubated vs. initial subsamples from each core. Values for extractable N are corrected for initial soil moisture and reported on a soil dry mass basis.

Statistical analyses

We examined changes in the amount of variation among sampling points separated by a given distance as that distance increased (semivariance analysis; Robertson and Gross 1994, Goovaerts 1998) to characterize

patchiness in soil and plant N. Semivariograms were constructed for each sampling grid using GS+ (Gamma Design Software 1998). The pattern of semivariance vs. distance separating sampling points was then described by determining the best-fit model for each semivariogram. Parameters derived from these best-fit models were used to quantify three key aspects of patchiness in a variate's distribution: (1) the proportion of sample variance explained by small-scale patchiness (i.e., the degree to which patches are differentiated from the surrounding area by their distinct, within-patch homogeneity), (2) the mean diameter of those patches, and (3) the arrangement of patches across the plot. These measures depend on the type and shape of the model fitted to the semivariogram (see discussion of model types and ecological interpretations below). The proportion of sample variance explained by patchiness was measured as $1 - (C_0/(C + C_0))$ where C_0 is the y-intercept or "nugget" of the best-fit model and $(C + C_0)$ is the "sill" or level of semivariance where the fitted model reaches an asymptote (Robertson and Gross 1994). The mean diameter of patches, or "range," was measured by the distance separating sampling points at which semivariance reaches an asymptote (Robertson and Gross 1994). Finally, patch arrangement was determined by the presence of significant fluctuations in semivariance at spatial scales beyond the first peak, which indicates patches are arranged regularly across the plot. In contrast, a lack of significant fluctuations in semivariance at larger spatial scales indicates a random arrangement of patches (Pastor et al. 1998).

The type of model fitted to a semivariogram, and its specific shape, determine the description of spatial heterogeneity discussed above. Data exhibiting no patchiness across the spatial scales measured will be described by a random model, where the semivariogram is essentially flat. If patchiness does not occur at the scales sampled but may occur at a higher scale, semivariance will increase continuously with increasing distance between samples and be described by a linear model. If semivariance first increases across small spatial scales, then reaches an asymptote, data will be fit by a spherical model and indicate small-scale patches arranged randomly across the plot (Schlesinger et al. 1996). Finally, higher-order fluctuations beyond the first peak in semivariance indicate both small-scale patchiness and regular arrangement of those patches and can be described by models such as polynomial or harmonic functions that permit regular fluctuations in semivariance (Pastor et al. 1998).

For each variogram, we fitted random, linear, and spherical models. Spherical models were fit by least-squares estimation using GS+, while all others were fit by least-squares estimation using JMP IN (SAS Institute 1997). When analyzing the 4 × 4 m grids, we fitted higher order polynomial models if spherical and linear models showed a poor fit and the variogram clearly indicated fluctuations in semivariance at higher spatial scales in the study grid. For polynomial models, the sill and range were calculated from the first peak in semivariance. Because polynomial models do not meet constraints for kriging analysis (see Goovaerts 1998), these model fits could not be used in kriging and mapping of soil N distributions. We compared polynomial models to random, linear, and spherical models only if a polynomial model showed a statistically significant fit both for the overall test of model significance ($P < 0.05$) and for each of the parameter coefficients in the model ($P < 0.05$ for each coefficient). We compared random, linear, spherical, and statistically significant polynomial models by selecting the model with the lowest root mean squared error (RMSE), provided this was not at the expense of using many degrees of freedom (Appendix; Pastor et al. 1998). In one case where an exponential function fitted by GS+ showed a much lower RMSE than the spherical model, we used the exponential model (Appendix).

In the 4 × 4 m plots, we used a nested sampling design to provide a similar number of sample pairs at each separation distance used in constructing the semivariogram and to include separation distances spanning more than one order of magnitude (10–200 cm; 126 pairs for 10 cm separation distance and >200 pairs for larger separation distances). For the large, 60 × 30 m sampling grids at Blacktail Plateau, all points were spaced 5 m apart, so the semivariance analysis included a more narrow range of separation distances (5–30 m) but used a large number of sample pairs for constructing each point in the semivariogram (162 pairs for 5 m, 286–630 pairs for larger separation distances). In addition to the semivariance analysis, maps of soil N and N-mineralization potential were constructed for the 60 × 30 m grids with GS+ using ordinary block kriging (Robertson and Gross 1994) with 0.75-m^2 blocks. Maps were used to examine how the predicted distribution of soil N related to the topographical gradient in grazed vs. ungrazed grids. We also used ordinary block kriging to illustrate results from our comparison of extractable mineral N distribution in a plot likely influenced by urine input vs. a plot without such an influence.

To test for effects of grazing on both spatial and nonspatial measures of soil and plant properties, we used paired t tests comparing the mean value for the grazed vs. ungrazed plots across the three study sites. We also used paired t tests to compare the coefficients of variation from the three grazed vs. the three ungrazed plots for each of the soil and plant variables we measured and to compare diversity measures calculated for each plot.

Results

Plant-scale spatial heterogeneity (10–200 cm)

Soil properties and processes.—There were no consistent differences between grazed and ungrazed areas

TABLE 1. Soil and plant variables measured to examine small-scale (10–200 cm) spatial heterogeneity across grazed and ungrazed plots at three study sites in Yellowstone National Park, USA.

Treatment	Total soil N (%)	Extractable mineral N (μg·g dry soil)	N mineralization potential (μg·[g dry soil]$^{-1}$·[10 d]$^{-1}$)	Root biomass (g/m^2)	Aboveground biomass (g/m^2)	Total plant biomass (g/m^2)	Total plant N (g/m^2)
A) Means (1 SD)							
Grazed							
Blacktail	0.25 (0.05)	8.92 (6.17)	5.61 (7.85)	95.6 (73.8)	42.7 (32.7)	138.3 (87.6)	2.05 (1.43)
Lamar	0.20 (0.02)	4.26 (1.55)	6.28 (4.03)	78.2 (69.2)	32.4 (49.5)	110.5 (103.2)	1.59 (1.88)
Stephens Creek	0.10 (0.02)	2.73 (0.81)	5.37 (3.64)	36.4 (53.9)	38.0 (54.4)	74.5 (95.3)	0.86 (1.22)
Ungrazed							
Blacktail	0.18 (0.03)	5.03 (1.60)	3.52 (3.43)	55.6 (35.1)	44.0 (40.6)	99.6 (62.8)	1.26 (0.90)
Lamar	0.17 (0.05)	2.98 (0.98)	5.10 (3.69)	62.1 (54.8)	28.9 (34.2)	91.4 (67.9)	1.20 (0.97)
Stephens Creek	0.09 (0.03)	3.21 (1.36)	6.48 (4.50)	31.8 (29.1)	48.4 (87.5)	80.2 (106.0)	0.91 (1.31)
B) Coefficients of variation							
Grazed							
Blacktail	20.0	69.2	139.6	77.1	76.7	63.4	69.7
Lamar	10.8	36.3	70.5	88.5	153.0	93.4	118.4
Stephens Creek	18.0	29.7	67.8	147.9	142.9	128.0	141.4
Ungrazed							
Blacktail	19.7	31.8	97.4	63.0	92.1	63.0	71.4
Lamar	29.4	33.0	79.7	88.3	118.4	74.3	80.4
Stephens Creek	29.0	42.2	69.4	91.5	180.9	132.2	143.9

in mean values for total soil N ($t = 1.74$, df = 2, $P = 0.22$), total soil carbon ($t = 1.27$, df = 2, $P = 0.33$), extractable mineral N ($t = 1.23$, df = 2, $P = 0.34$), or N-mineralization potential ($t = 0.756$, df = 2, $P = 0.53$). These results are consistent with findings of Frank and Groffman (1998), with the exception that a promotion of in situ N-mineralization rates outside exclosures was detected in their study using a larger sample of seven sites. In this study, N-mineralization potential was higher in grazed plots at the Lamar Valley and Blacktail Plateau, but lower in grazed plots at Stephens Creek (Table 1), such that no overall difference was detected across sites.

Our focus in this study was spatial variation in plant and soil properties. Across the three sites, grazers did not alter the total amount of variation (coefficient of variation) in soil or plant properties (Table 1; $t \leq 1.78$, df = 2, $P \geq 0.21$ for all comparisons). However, with respect to total soil N and N-mineralization potential, this variance exhibited a dramatically greater degree of spatial structure across scales of 10–200 cm in ungrazed compared to grazed grassland. In particular, the proportion of sample variance explained by small-scale patchiness ($1-C_0/(C + C_0)$) was significantly greater in ungrazed vs. grazed grassland (Figs. 1 and 2, Table 2; total soil N: $t = 6.36$, $P = 0.024$; N-mineralization potential: $t = 12.97$, $P = 0.006$). This low degree of spatial structure in grazed grassland across scales of 10–200 cm indicates that ungulates greatly increased fine-grained variability (i.e., variation across distances <10 cm) in soil N properties. For N-mineralization potential in grazed plots, soil cores separated by 10 cm showed the same degree of variation as the total sample at Lamar Valley, only slightly less variation than the total sample at Stephens Creek, and more variability than the total sample at Blacktail Plateau (Fig. 2), such that semivariance at 10 cm was significantly greater in grazed vs. ungrazed plots (grazed, $\bar{X} = 1.0$; ungrazed, $\bar{X} = 0.69$; $t = 4.86$, df = 2, $P = 0.039$). For total soil N, semivariance at 10 cm was not different between grazed and ungrazed treatments (grazed, $\bar{X} = 0.75$; ungrazed, $\bar{X} = 0.43$; $t = 1.70$, df = 2, $P = 0.231$) because its value was the same for both treatments at Stephens Creek (Fig. 1).

In addition to ungrazed plots exhibiting a high degree of homogeneity within patches, the size of patches was consistent across sites. Patch size in ungrazed plots ranged from 39 to 55 cm diameter for total soil N and from 37 to 48 cm for N-mineralization potential (Figs. 1 and 2, Table 2). In contrast, semivariance in grazed plots either showed a linear pattern, indicating that homogenous patches did not occur within the 10–200 cm scale considered in this analysis, or minimal variation in semivariance at scales similar to the patch diameter of ungrazed plots. For example, the grazed plot at Lamar Valley had mean patch sizes of 56 cm and 38 cm for soil N and N-mineralization potential respectively, which were similar in size to patches in ungrazed plots, but the homogeneity of these patches in the grazed plot was low (proportion of variance explained by patchiness equal to 0.33 and 0.12, respectively). Semivariance patterns for N-mineralization potential at the other two sites suggested patches >188 cm diameter (Stephens Creek) or no patchiness (Blacktail Plateau).

Finally, grazing altered the distribution of homogenous patches, in particular with respect to N-mineralization potential. Semivariograms were characterized by two fluctuations best fit by fourth order polynomial

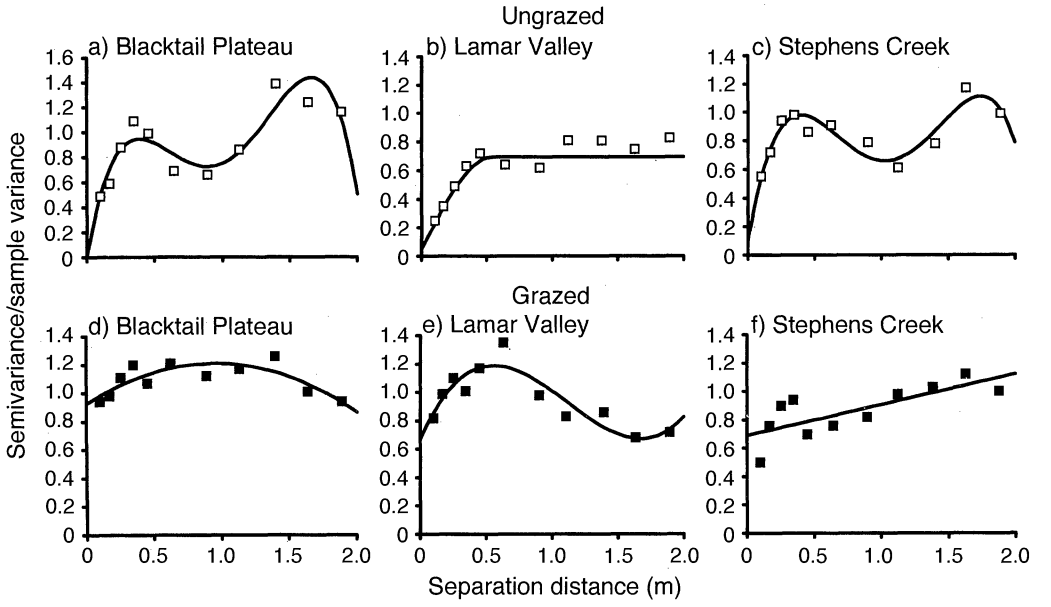

FIG. 1. Semivariograms for total soil N in ungrazed (a–c) and grazed (d–f) grassland plots at three sites in Yellowstone National Park, USA.

models at all three ungrazed study sites for N-mineralization potential and two of three sites for total soil N (Appendix), suggesting not only small-scale patchiness (first peak) but also regular patch spacing across the site (second peak). With the exception of total soil N for the Lamar Valley site, ungrazed grassland displayed a consistent patch separation distance of 1.5 m. Semivariograms for grazed sites indicated spacing between patches >2 m or no higher-order arrangement of patches (Figs. 1, 2).

At one study site (Lamar Valley, ungrazed), *Artemesia tridentata* shrubs were common and occurred on the study plot. This shrub is known to create islands of increased soil nutrient concentration beneath its canopy in some arid ecosystems (Jackson and Caldwell 1993, Halverson et al. 1994). We therefore reanalyzed

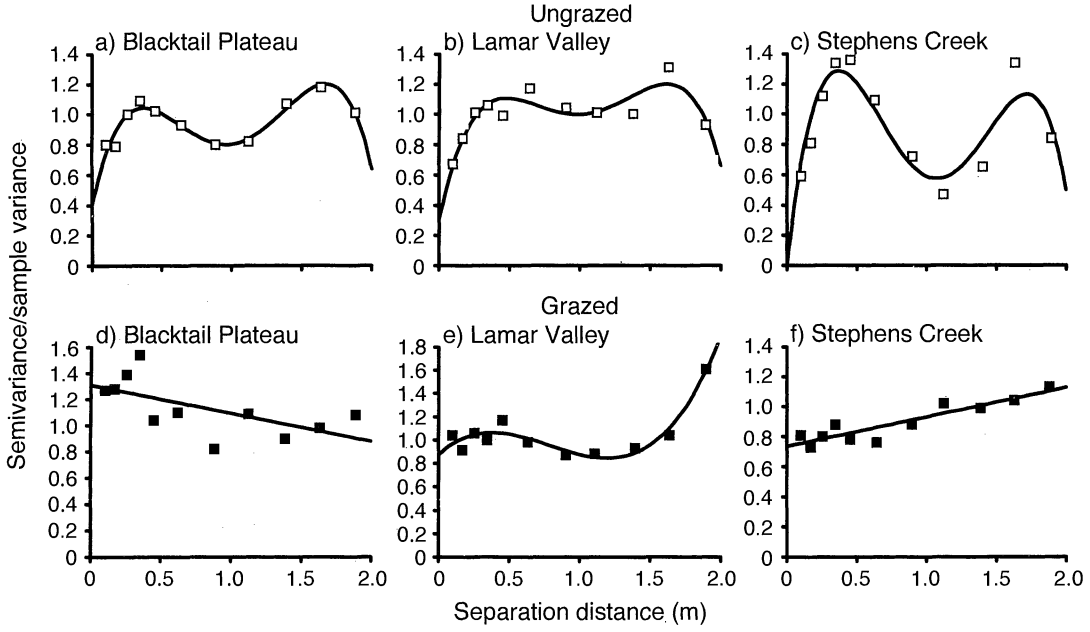

FIG. 2. Semivariograms for soil N-mineralization potential in ungrazed (a–c) and grazed (d–f) grassland plots at three sites in Yellowstone National Park, USA.

TABLE 2. Analysis of spatial structure of total soil N, N-mineralization potential, and plant biomass N based on the best-fit model for semivariance at each of three grazed and ungrazed study sites in Yellowstone National Park.

Site	Small-scale spatial structure: Nugget (C)	Sill ($C + C_0$)	Range (A)	Proportion	Existence and scale of higher-order arrangement of small, homogeneous patches
A) Total soil N (%)					
Ungrazed grassland					
Blacktail Plateau	0.00	0.95	0.39	1.00	regular patch spacing: ~1.0 m separation distance
Lamar Valley	0.05	0.69	0.55	0.93	none
Stephens Creek	0.10	0.98	0.41	0.90	regular patch spacing: ~1.1 m separation distance
Mean			0.45	0.94	
Grazed grassland					
Blacktail Plateau	0.92	1.21	0.95	0.08	none
Lamar Valley	0.67	1.19	0.56	0.33	possible regular patch spacing at scale 1.5–2.0 m
Stephens Creek	0.69	1.10	>1.88	0.31	none; possible patchiness at scale >2 m
Mean				0.24	
B) N-mineralization potential ($\mu g \cdot [g \text{ dry soil}]^{-1} \cdot [10 \text{ d}]^{-1}$)					
Ungrazed grassland					
Blacktail Plateau	0.40	1.04	0.37	0.60	regular patch spacing: ~1.0 m separation distance
Lamar Valley	0.30	1.11	0.48	0.70	regular patch spacing: ~1.1 m separation distance
Stephens Creek	0.00	1.29	0.37	1.00	regular patch spacing: ~1.2 m separation distance
Mean			0.41	0.77	
Grazed grassland					
Blacktail Plateau	1.31	0.90	<10	0.00	none
Lamar Valley	0.88	1.06	0.38	0.12	none; possible patchiness at scale >2 m
Stephens Creek	0.73	1.10	>1.88	0.27	none; possible patchiness at scale >2 m
Mean				0.13	
C) Extractable mineral N ($\mu \cdot [g \text{ dry soil}]^{-1} \cdot [10 \text{ d}]^{-1}$)					
Ungrazed grassland					
Blacktail Plateau	0.48	1.19	0.78	0.52	possible regular patch spacing at scale 1.5–2.0 m
Lamar Valley	0.85	0.85	<10	0.00	none
Stephens Creek	0.90	0.90	<10	0.00	none
Mean				0.17	
Grazed grassland					
Blacktail Plateau	0.00	2.50	139.6	1.00	none
Lamar Valley	1.00	1.00	<10	0.00	none
Stephens Creek	0.53	1.06	91.9	0.47	none
Mean				0.49	
D) Total plant N (g/m^2)					
Ungrazed grassland					
Lamar Valley	0.12	0.96	20.40	0.88	none
Blacktail Plateau	0.52	1.16	132.00	0.48	possible regular patch spacing at scale >2 m
Stephens Creek	0.50	1.70	>189.4	0.50	none; possible patchiness at scale >2 m
Mean				0.62	
Grazed grassland					
Lamar Valley	0.15	1.65	139.60	0.85	none
Blacktail Plateau	0.13	1.12	40.00	0.87	regular patch spacing: ~0.8 m separation distance
Stephens Creek	0.78	1.08	>187.8	0.22	none; possible patchiness at scale >2 m
Mean				0.65	

spatial patterns at this site excluding cores located beneath shrub canopies. The same semivariogram models were selected (spherical for soil N and fourth-order polynomial for N mineralization), and estimates of model nugget, range, and proportion of variance explained by patchiness were nearly identical to the models including soil cores from beneath shrubs. Parameter estimates of spatial structure for the ungrazed plot at Lamar Valley without beneath-shrub soil cores did not change our statistical comparison of patterns in grazed vs. ungrazed grassland. Therefore, differences in soil-N spatial heterogeneity between treatments do not appear to be the result of increased *Artemesia* cover in the absence of grazing.

Ungulate urine inputs.—To examine effects of ungulates on soil N via inputs of excreta, we analyzed the proportion of soil cores exhibiting unusually high levels of extractable mineral N. Based on studies of N dynamics beneath simulated cattle urine and dung patches, Afzal and Adams (1992) used an extractable mineral N level of 17 μg N/g dry soil or higher as indicative of the soil having been influenced by cattle excreta. In this study, extractable mineral N levels in ungrazed grassland varied from 0 to 19.5 μg/g with a

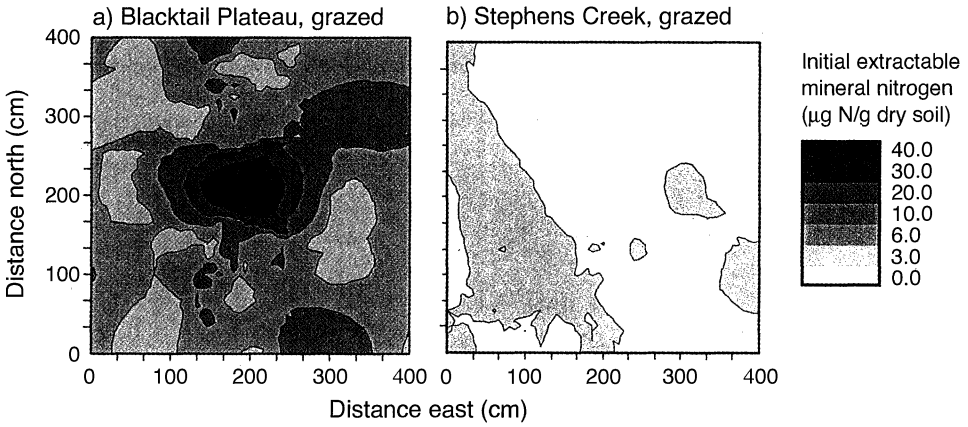

FIG. 3. Isopleths for extractable mineral N (a) across a 4 × 4 m grazed plot where the levels and distribution of mineral N indicate urine input and (b) across a 4 × 4 m grazed plot lacking any indication of urine input. Semivariance for both plots was best described by a spherical model indicating patches ~1 m in diameter (see Table 3), but the plot in (a) exhibited a higher mean and coefficient of variation compared to the other five plots (two grazed, three ungrazed) we examined (see Table 1). Note the nonlinear scale for isopleth values.

mean of 4.24 μg N/g dry soil. Of the 425 cores analyzed from grazed grassland, only three (all located in close proximity to one another at the Blacktail Plateau 4 × 4 m grid) contained mineral N levels >20 (28.2, 35.6, and 51.8 μg N/g dry soil). Such high values and their close proximity to one another strongly suggest urine input. Comparing semivariance and kriging analyses of initial extractable mineral N at all 4 × 4 m sampling grids suggested a urine-influenced patch at Blacktail Plateau (Fig. 3a). The other five grids (three ungrazed, two grazed) exhibited smaller-scale patches or no spatial structure at the 10–200 cm scale (e.g., Fig. 3b) and lower coefficients of variation in extractable mineral N (Table 1). Based on the kriged maps, an estimated 2.5% of grazed grassland contained levels >20 μg N/g dry soil. The estimated area affected by urine differed for the calculation based on cores (0.7%) vs. kriged maps (2.5%) because the urine patch occurred in an area of the plot with low sampling density.

Plant nitrogen and biomass.—The spatial distribution of N in plant biomass displayed no consistent differences between grazed vs. ungrazed plots (Table 2; $t \leq 0.15$, $P \geq 0.89$ for comparisons of range and proportion). Spatial patterns for plant biomass (below-, aboveground, and combined) also showed a similar lack of difference between grazed and ungrazed plots as for plant N ($t \leq 1.61$, $P \geq 0.25$ for all comparisons). All study grids exhibited a significant degree of small-scale heterogeneity. The semivariance analysis estimated that small-scale patchiness explained an average of 63% of the variation in plant N among sampling points, but the size of patches varied from 20 cm (Lamar Valley, ungrazed) to >188 cm (Stephens Creek, grazed and ungrazed; Table 2).

Plant diversity.—Ungulates influenced species diversity of the grasslands only at small spatial scales. Alpha diversity (calculated as H') measured at a scale of 20 × 20 cm was consistently higher in the three grazed plots compared to paired, ungrazed plots (Fig. 4; $t = 3.39$, $P = 0.077$). Species richness at a scale of 20 × 20 cm quadrats was also higher in grazed compared to ungrazed plots (Fig. 4; $t = 4.206$, $P = 0.052$). In contrast, grazing did not alter species diversity (H') or species richness at a scale of 4 × 4 m plots ($t < 1.592$, $P > 0.252$) or proportional dissimilarity among quadrats, a measure of beta diversity ($t = 0.628$, $P = 0.594$; Fig. 4).

Field-scale spatial heterogeneity (5–30 m)

We documented a dramatic difference in the spatial distribution of total soil N and soil N-mineralization potential across the 30 × 60 m grazed vs. ungrazed plots. No spatial pattern for soil N variables was observed inside the exclosure while semivariance was positively correlated with the distance between sampling points in the grazed field, indicating that homogenous patches occurred at a scale >30 m for soil N and at a scale of 27 m for N-mineralization potential (Table 3). Kriging analysis both for total soil N and N-mineralization potential showed that this spatial pattern in the grazed field corresponded to the topographic gradient across the plot; a gently sloping bench at the top of the field exhibited the highest levels, while the hill slope extending from the upper bench to the bottom of the plot showed decreasing levels (Figs. 5a and 6a). In addition to the topographically correlated variability in N mineralization, the grazed plot exhibited a midslope patch of high mineralization potential unrelated to topography (Fig. 6a). In contrast, although we sampled an area with identical topographic characteristics inside the exclosure, we found no correlation between the topographic gradient and soil N properties (Figs. 5b and 6b). Neither total soil N nor N-mineralization po-

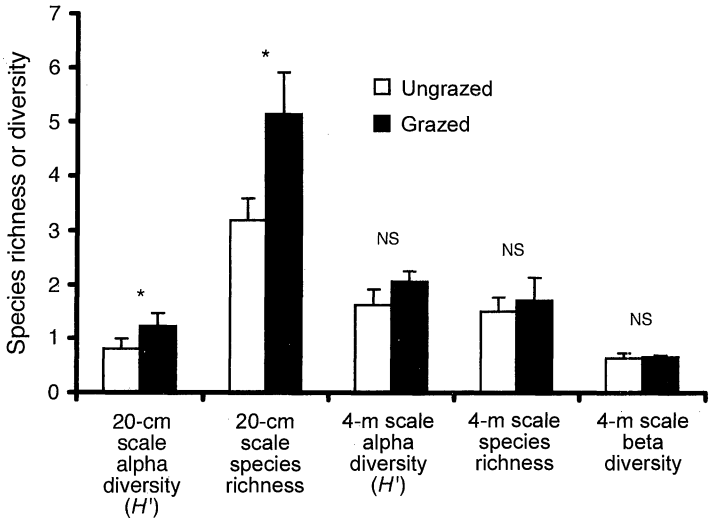

FIG. 4. Measures of plant species diversity at different spatial scales in grazed and ungrazed grassland at three sites in Yellowstone National Park. Asterisks indicate significant differences between grazed vs. ungrazed plots at the $\alpha = 0.05$ level. Species richness at the 20-cm scale is presented as the mean number of species per quadrat. Species richness at the 4-m scale is presented as the mean number of species per 4 × 4 m plot divided by 10. Beta diversity is the proportional dissimilarity among quadrats within a plot.

tential exhibited any significant spatial pattern at scales of 5–30 m inside the exclosure (Table 3).

DISCUSSION

Native, migratory ungulates inhabiting Yellowstone's northern winter range exert a strong effect on ecosystem dynamics by accelerating rates of primary productivity (Frank and McNaughton 1993) and nitrogen cycling (Frank and Groffman 1998). Our findings show that ungulate effects in Yellowstone also extend to the spatial patterning of soil N pools and N-mineralization potential. At small scales (10–200 cm), removal of grazers increased patchiness in soil N and N-mineralization potential, while grazed grassland exhibited extremely fine-grained (<10 cm) variability. At larger spatial scales extending across a topographic gradient, soil N properties exhibited no spatial structure in ungrazed grassland, while soil N and N-mineralization potential in grazed grassland exhibited >27 m diameter patches associated with the topographic gradient extending from an upper bench to a mid-hill-slope position. These results demonstrate that, in addition to the effects of topography and vegetation on spatial patterning of resource availability, biotic components of ecosystems such as large herbivores not only respond to resource heterogeneity, but also play a significant role in generating observed patterns.

Plant-scale spatial heterogeneity

While recent studies have demonstrated plant-level (presence or absence) and species-level effects on soil heterogeneity in a variety of ecosystems (Jackson and Caldwell 1993, Halverson et al. 1994, Kleb and Wilson 1997, Reynolds et al. 1997), our findings show herbivory also modifies soil heterogeneity at small spatial scales, increasing the amount of variability in the soil environment experienced by a plant individual. Potential mechanisms by which large grazers could alter heterogeneity relative to ungrazed grassland include (1) inputs of dung and urine (Floate 1981, Ruess and McNaughton 1987, Afzal and Adams 1992), (2) altered patterns of resource allocation by individual plants and hence changes in inputs to soil via root turnover/exudation and leaf litter, (3) long-term effects on the spatial pattern of plant species composition and hence the spatiotemporal distribution of litter quality and input (Lavado et al. 1995, Pastor et al. 1998), and (4) indirect interactions with other grassland components, such as

TABLE 3. Analysis of spatial structure of total soil N and N-mineralization potential based on the best-fit model for semivariance within grazed and ungrazed 60 × 30 m sampling grids sites at Blacktail Plateau.

		Field-scale spatial structure			
Treatment	Model	Nugget (C)	Sill ($C + C_0$)	Range (A)	Proportion
Total soil N (%)					
Ungrazed	random	0.87	0.87	<5	0.00
Grazed	linear	0.51	0.86	>30	0.41
N-mineralization potential					
Ungrazed	random	0.82	0.82	<5	0.00
Grazed	exponential	0.53	1.07	26.7	0.51

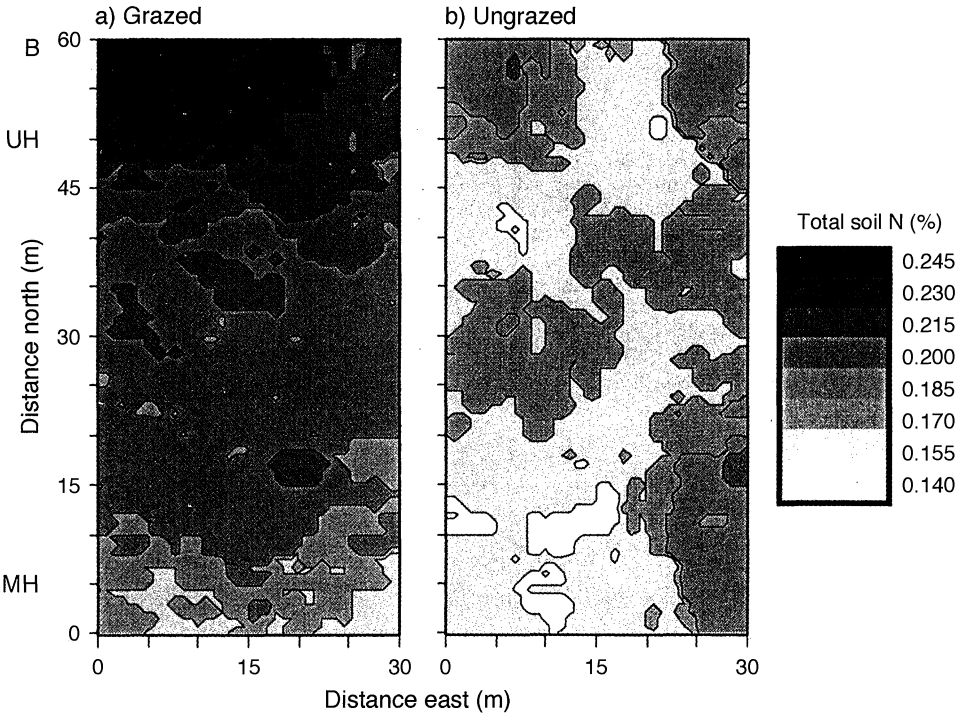

FIG. 5. Isopleths for total soil N (as a percentage of dry mass) across a grazed and an ungrazed 60 × 30 m plot at Blacktail Plateau in Yellowstone National Park. Letters along the *y*-axis denote the topographical gradient along this axis (B = bench, UH = upper hill slope, and MH = mid-hill slope).

the small mammal or insect community, which in turn affect soil patterns.

Inputs of excreta are clearly expected to increase soil nutrient patchiness at small spatial scales. In pastures grazed by cattle, urine creates nitrogen-enriched patches on the order of 80 cm in diameter, while dung inputs can create smaller patches on the order of 20 cm diameter in the surface soil layer (Afzal and Adams 1992). In Yellowstone grasslands, ungulate dung and urine comprise a major input of N to the ecosystem, representing an amount equivalent to 27% of the N mineralized annually (Frank et al. 1994). However, in contrast to the expected effect of grazers via excreta, we found the dominant effect of grazers on Yellowstone's northern range grasslands was reduced heterogeneity in both soil N and N-mineralization potential at a scale of 10–100 cm.

Several factors may explain the general lack of small-scale patchiness in soil N properties in the grazed plots. Because we only examined three sites and a total of 425 soil cores from grazed grassland, plots by chance may not have been recently affected by dung or urine inputs. Elk were observed in the immediate vicinity of grazed study grids at all sites during the May sampling period, but their presence on the specific plots used in this study was not measured. To look for urine-affected patches in the 4 × 4 m grazed plots, we analyzed spatial variation in levels of initial, extractable mineral N of soil samples and examined extractable N levels from the large grid at Blacktail Plateau that included a range of topographic positions. The presence of one urine patch, covering 2.5% of the total grazed area sampled and containing mineral N levels up to 51 mg/g dry soil, is consistent with the expectation that ungulate urine inputs induce 100-cm scale patches in soil N. The elevated levels of mineral N in urine-affected cores did not influence the rate of N mineralized during the laboratory incubations and hence did not affect patchiness in N-mineralization potential. Extractable mineral N from all other areas of both grazed and ungrazed plots, including the large grid at Blacktail Plateau, did not exceed 19.5 mg N/g soil. Urine patches are visible later in the growing season as discrete areas of extremely green vegetation and represent an important N input when accumulated over long time periods, but our results indicate that urine affects only a small proportion of the winter range at any given time.

In contrast, Afzal and Adams (1992) estimated that 27% of a pasture containing 3 cattle/ha over a 200-d period was influenced by urine. Elk densities on Yellowstone winter range in the late 1970s varied from 0.17 to 0.25 elk/ha (Houston 1982). The northern elk herd's numbers nearly doubled by 1986, remaining near an average of 21 070 during 1986–1991 (Mack and Singer 1993, Coughenour and Singer 1996). During this period, elk were distributed over an expanded winter range area of 148 893 ha (Coughenour and Singer 1996), suggesting densities of 0.11 to 0.16 elk/ha. Both

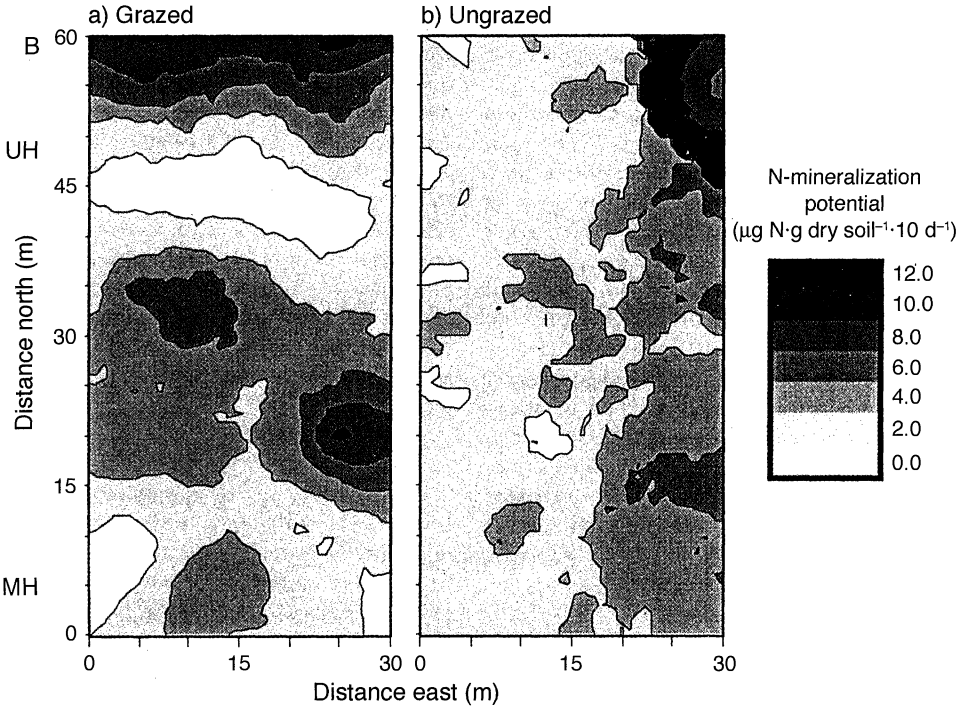

FIG. 6. Isopleths for N-mineralization potential across a grazed and an ungrazed 60 × 30 m plot at Blacktail Plateau in Yellowstone National Park. Letters along the *y*-axis denote the topographical gradient along this axis (B = bench, UH = upper hill slope, and MH = mid-hill slope).

estimates of elk density and areal coverage of urine are <1/10 that of cattle density and urine inputs for the pasture studied by Afzal and Adams (1992), suggesting ungulate density may be a key factor in determining the mechanisms by which herbivores induce heterogeneity in natural vs. more intensively managed systems.

With respect to dung inputs, all grazed study plots contained fecal pellets on the soil surface. Dung can affect mineral N concentrations in surface soil (0–2 cm layer), but analyses of cattle dung patches found that effects did not extend deeper, and dung added during winter had no effect on spring N-mineralization rates of cores to 6 cm depth (Afzal and Adams 1992). In addition, many elk pellets did not occur in discrete patches. Dung deposited in the snow layer during winter may be redistributed during spring snowmelt and by trampling, which would reduce small-scale patchiness of inputs to the soil. Although our results indicate dung and urine inputs are not the primary effect of ungulates on soil N heterogeneity, the return back to the soil of N consumed by grazers is still clearly of major importance in maintaining the overall N balance in this ecosystem (Frank et al. 1994).

In contrast to effects via excreta, ungulates could promote fine-grained soil heterogeneity by altering the pattern of plant litter inputs to the soil. At the level of plant populations, grazing can increase population turnover in grasslands (Pyke 1987, O'Connor 1994) and the death of an individual grass cluster can increase soil carbon mineralization rates beneath the plant (Kelly and Burke 1997). At the level of plant individuals, loss of aboveground tissue can affect soil carbon inputs from root exudation (Bokari and Singh 1974, Dyer and Bokari 1976, Holland et al. 1996) and root mortality (Richards 1984). Root dynamics may be a particularly important determinant of soil N distribution in Yellowstone grasslands because root biomass was much greater and more evenly distributed than aboveground plant biomass. Localized inputs of labile carbon to the soil, for example from exudation or fine-root mortality in grazed plants, in turn could stimulate microbial activity and N-mineralization rates (Frank and Groffman 1998). In other grassland systems, soil nutrient heterogeneity is primarily associated with the presence or absence of bunchgrass individuals (Gibson 1988, Burke et al. 1999). We did not observe grazer effects on the spatial distribution of above- or belowground plant biomass that correlated with soil N properties, suggesting that grazing effects were more closely linked to soil heterogeneity than to the distribution of live plant individuals at a given point in time. However, an important caveat in interpreting our results is that we measured biomass early in the growing season, ~2 mo before peak standing crop, and we did not include standing dead material, which is a significant input to the soil inside exclosures (Coughenour 1991) and could contribute to small-scale patchiness in ungrazed grassland.

At the community level, grazers could also promote fine-scale heterogeneity by increasing the number and evenness of plant species within a small area, and, therefore, the potential for species effects to contribute to soil heterogeneity. Consistent with this hypothesis, grazing altered the pattern of plant species coexistence at a small spatial scale by increasing species richness and diversity within 20 × 20 cm quadrats. At a larger spatial scale (4 × 4 m plots) species diversity was similar in grazed and ungrazed grassland, consistent with a previously reported lack of grazer effects on species composition in Yellowstone grassland (Houston 1982, Coughenour 1991). Similarly, for a larger sample of 26 long-term exclosures located in grasslands of Colorado, Wyoming, Montana, and South Dakota, Stohlgren et al. (1999) found greater species richness in 1-m^2 plots for grazed compared to ungrazed communities, while grazing had no effect on species richness at the community (1000-m^2) level. Although the causal relationship between species diversity and soil heterogeneity could not be addressed in this study, our findings suggest a link between fine-grained resource heterogeneity and species richness at small spatial scales in grazed communities.

Field-scale heterogeneity

Across landscapes, topography is well known to have major effects on spatial variability in soil processes (Jenny 1980, Schimel et al. 1985*a, b,* Burke 1989, Frank et al. 1994, Fisk et al. 1998). Recently, Frank and Groffman (1998) demonstrated that grazers also have a major influence on N-mineralization rates in Yellowstone's grasslands that exceeds the variability associated with topography. At seven sites distributed across Yellowstone's northern winter range, annual N mineralization at topographically diverse sites varied from 0.8 to 2.9 g N/m^2 inside long-term exclosures, while mineralization rates ranged from 1.3 to 7.8 g N/m^2 among grazed sites. These results indicate that grazers increase the heterogeneity of N cycling at the landscape scale (Frank and Groffman 1998).

Our field-scale analysis at the Blacktail Plateau site also showed that within a site (i.e., within a 60 × 30 m area), grazing can alter the spatial distribution of soil N properties across a topographic gradient. Variation in soil N and N-mineralization potential was spatially dependent up to a scale of 27 m for N-mineralization potential and >30 m for total soil N. In particular, the grazed community exhibited a pattern of increasing soil N and N-mineralization rates from the lower, steep slope at the bottom of the sampling grid toward the upper bench at the top of the grid, while variation in the ungrazed community showed no relationship to topography. Although unreplicated, this contrast indicates that within a site, grazing increases topographic variation in soil properties and increases patchiness at a scale of ≥30 m. Because the sites analyzed by Frank and Groffman (1998) consisted of 10 × 10 m plots, sites in grazed communities were more likely to fall within a 30 m diameter patch of high or low N mineralization rates than sites in ungrazed communities. Such variation in soil nitrogen across topographic gradients could be caused by variation in grazing intensity and bedding-site selection, particularly as a response by grazers to gradients in productivity (Frank and McNaughton 1992) and winter snow cover. Dung inputs measured previously, across a variety of topographic positions on winter range grassland were substantially greater at ridgetop and upper bench locations relative to hill slopes (Frank et al. 1994), consistent with the spatial pattern of total soil N we documented in the grazed site.

Conclusions

Collectively, our results show that grazers in Yellowstone alter the spatial distribution of soil N properties at every scale from individual plants (<10 cm) to plant communities (30 m) to topographically variable landscapes. Small-scale patterns suggest that the major effect of ungulates on spatial variation is not a consequence of fluxes of urine and dung to the soil. Instead, grazers primarily alter spatial structure by increasing <10 cm soil variation, which we hypothesize is caused by herbivores promoting greater fine-scale plant species diversity and/or variation in plant turnover. However, N returned to the soil in urine and dung is still important through its long-term effect on soil N stocks and its short-term effect on small areas of the grassland.

To our knowledge, this study is the first description of spatial patterns of soil N across such a broad range of spatial scales in grassland supporting native herbivores and hence provides a baseline for understanding the role of herbivores in more intensively managed systems (Arcese and Sinclair 1997). In other arid systems, grazing by cattle has been linked to increased soil nutrient patchiness via effects on grass community composition (Lavado et al. 1995) or shrub encroachment leading to islands of fertility surrounded by barren soil (Schlesinger et al. 1996). Increased nutrient patchiness associated with shrub encroachment has also been implicated as a potential feedback to grassland desertification (Schlesinger et al. 1990, 1996). Our findings that native ungulates exert the opposite effect on nutrient heterogeneity in Yellowstone could be linked to the unique temporal pattern of herbivory due to migration of elk to higher elevation grassland in spring and summer (Frank and McNaughton 1992), differences in ungulate density among systems discussed previously, and the relatively nitrogen-rich soils underlying winter range grasslands (Frank et al. 1994). Identifying the importance of grazing seasonality and intensity in determining soil nutrient patterns will require comparisons with similar measures of spatial heterogeneity in a variety of grassland systems supporting different grazing regimes.

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LITERATURE CITED

Afzal, M., and W. A. Adams. 1992. Heterogeneity of soil mineral nitrogen in pasture grazed by cattle. Soil Science Society of America Journal **56**:1160–1166.

Arcese, P., and A. R. E. Sinclair. 1997. The role of protected areas as ecological baselines. Journal of Wildlife Management **61**:587–602.

Augustine, D. J., and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management **62**:1165–1183.

Beals, E. W. 1969. Vegetational change along altitudinal gradients. Science **165**:981–985.

Bokari, U. G., and J. S. Singh. 1974. Effects of temperature and clipping on growth, carbohydrate reserves, and root exudation of western wheatgrass in a hydroponic culture. Crop Science **14**:790–794.

Bonis, A., P. J. Grubb, and D. A. Coomes. 1997. Requirements of gap-demanding species in chalk grassland: reduction of root competition versus nutrient-enrichment by animals. Journal of Ecology **85**:625–633.

Burke, I. C. 1989. Control of nitrogen mineralization in a sagebrush steppe landscape. Ecology **70**:1115–1126.

Burke, I. C., W. K. Lauenroth, R. Riggle, P. Brannen, B. Madigan, and S. Beard. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems **2**:422–438.

Coughenour, M. B. 1991. Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. Journal of Applied Ecology **28**:71–82.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications **6**:573–593.

Dyer, M. I., and U. G. Bokari. 1976. Plant–animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology **57**:762–772.

Ettema, C. H., D. C. Coleman, G. Vellidis, R. Lowrance, and S. L. Rathbun. 1998. Spatiotemporal distributions of bacterivorous nematodes and soil resources in a restored riparian wetland. Ecology **79**:2721–2734.

Fisher, E., B. Thornton, G. Hudson, and A. C. Edwards. 1998. The variability in total and extractable soil phosphorus under a grazed pasture. Plant and Soil **203**:249–255.

Fisk, M. C., S. K. Schmidt, and T. R. Seastedt. 1998. Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. Ecology **79**:2253–2266.

Floate, M. J. S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural systems. *In* F. E. Clark and T. Rosswall, editors. Terrestrial nitrogen cycles. Ecological Bulletins-NFR **33**:585–601.

Frank, D. A., and P. M. Groffman. 1998. Ungulate versus topographic control of soil carbon and nitrogen processes in grasslands of Yellowstone National Park. Ecology **79**: 2229–2241.

Frank, D. A., R. Inouye, N. Huntly, G. Minshall, and J. Anderson. 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry **26**:163–188.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology **73**:2043–2058.

Frank, D. A., and S. J. McNaughton. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia **96**:157–161.

Frelich, L., and P. Reich. 1995. Spatial patterns and succession in a Minnesota southern- boreal forest. Ecological Monographs **65**:325–346.

Gamma Design Software. 1998. GS+: geostatistics for the environmental sciences. Version 3.07. Gamma Design Software, Plainwell, Michigan, USA.

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

Gonzalez, O. J., and D. R. Zak. 1994. Geostatistical analysis of soil properties in a secondary tropical dry forest. Plant and Soil **163**:45–54.

Goovaerts, P. 1998. Geostatistical tools for characterizing the spatial variability of microbiological and physico-chemical soil properties. Biology and Fertility of Soils **27**:315–334.

Gorres, J. H., M. J. Dichiaro, J. B. Lyons, and J. A. Amador. 1998. Spatial and temporal patterns of soil biological activity in a forest and an old field. Soil Biology and Biochemistry **30**:219–230.

Gross, K. L., K. S. Pregitzer, and A. J. Burton. 1995. Spatial variation in nitrogen availability in three successional plant communities. Journal of Ecology **83**:357–367.

Halverson, J. J., H. Bolton, J. L. Smith, and R. E. Rossi. 1994. Geostatistical analysis of resource islands under *Artemesia tridentata* in shrub-steppe. Great Basin Naturalist **54**:313–328.

Hamilton, E. W., M. S. Giovannini, S. J. Moses, J. S. Coleman, and S. J. McNaughton. 1998. Biomass and mineral element responses of a Serengeti short grass species to nitrogen supply and defoliation: compensation requires a critial [N]. Oecologia **114**:407–418.

Holland, J. N., W. Cheng, and D. A. Crossely. 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground C fluxes using carbon-14. Oecologia **107**:87–94.

Houston, D. B. 1982. The northern Yellowstone elk. Macmillan, New York, New York, USA.

Huntly, N., and R. Inouye. 1988. Pocket gophers in ecosystems: patterns and mechanisms. Bioscience **38**:786–793.

Jackson, R. B., and M. M. Caldwell. 1993. Geostatistical patterns of soil heterogeneity around individual perennial plants. Journal of Ecology **81**:683–692.

Jackson, R. B., and M. M. Caldwell. 1996. Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment. Journal of Ecology **84**:891–903.

Jenny, H. 1980. The soil resource: origin and behavior. Ecological Studies 37. Springer-Verlag, New York, New York, USA.

Kelly, R. H., and I. C. Burke. 1997. Heterogeneity of soil organic matter following death of individual plants in shortgrass steppe. Ecology **78**:1256–1261.

Kleb, H. R., and S. D. Wilson. 1997. Vegetation effects on soil resource heterogeneity in prairie and forest. American Naturalist **150**:283–298.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. Bioscience **49**:39–50.

Lavado, R. S., J. O. Sierra, and P. N. Hashimoto. 1995. Impact of grazing on soil nutrients in a Pampean grassland. Journal of Range Management **49**:452–457.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**:1943–1967.

Mack, J. A., and F. J. Singer. 1993. Population models for elk, mule deer, and moose on Yellowstone's norther winter range. Pages 270–305 *in* R. Cook, editor. Ecological issues on reintroducing wolves into Yellowstone National Park. Scientific Monograph NPS/NRYELL/NRSM-93/22. United States Department of Interior, Washington, D.C., USA.

McNaughton, S. J. 1989. Interactions of plants of the field layer with large herbivores. Symposium of the Zoological Society of London **61**:29–51.

O'Connor, T. G. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. Journal of Applied Ecology **31**:155–171.

Ozinga, W. A., J. Van Andel, and M. P. McDonnell-Alexander. 1997. Nutritional soil heterogeneity and mycorrhiza as determinants of plant species diversity. Acta Botanica Neerlandica **46**:237–254.

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

Pearson, S. M., M. G. Turner, L. L. Wallace, and W. H. Romme. 1995. Winter habitat use by large ungulates following fire in northern Yellowstone National Park. Ecological Applications **5**:744–755.

Pyke, D. A. 1987. Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals. The influence of grazing frequency and plant age. Journal of Ecology **75**:825–835.

Reynolds, H. L., B. A. Hungate, F. S. Chapin, III, and C. M. D'Antonio. 1997. Soil heterogeneity and plant competition in an annual grassland. Ecology **78**:2076–2090.

Richards, J. H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. Oecologia **64**:21–25.

Ritchie, M. E., D. Tilman, and J. M. H. Knops. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology **79**:165–177.

Robertson, G. P., J. R. Crum, and B. G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. Oecologia **96**:451–456.

Robertson, G. P., and D. W. Freckman. 1995. The spatial distribution of nematode trophic groups across a cultivated ecosystem. Ecology **76**:1425–1432.

Robertson, G. P., and K. L. Gross. 1994. Assessing the heterogeneity of below-ground resources: quantifying pattern and scale. Pages 237–253 *in* M. M. Caldwell and R. W. Pearcy, editors. Plant exploitation of environmental heterogeneity. Academic Press, New York, New York, USA.

Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology **69**:1517–1524.

Robertson, G. P., K. M. Klingensmith, M. J. Klug, E. A. Paul, J. R. Crum, and B. G. Ellis. 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. Ecological Applications **7**:158–170.

Ruess, R. W., and S. J. McNaughton. 1987. Grazing and the dynamics of nutrient and energy regulated microbial processes in the Serengeti grasslands. Oikos **49**:101–110.

SAS Institute. 1997. JMP IN, version 3. 2.1. SAS Institute, Cary, North Carolina, USA.

Schimel, D. S., D. C. Coleman, and K. A. Horton. 1985*a*. Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. Geoderma **36**:201–214.

Schimel, D. S., M. A. Stillwell, and R. G. Woodmansee. 1985*b*. Biogeochemistry of C, N, and P on a catena of the shortgrass steppe. Ecology **66**:276–282.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364–374.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and G. G. Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Senft, R. L., M. B. Coughenour, D. W. Bailey, and L. R. Rittenhouse. 1987. Large herbivore foraging and ecological hierarchies. Bioscience **37**:789–799.

Steinhauer, E. M., and S. L. Collins. 1995. Effects of urine deposition on small-scale patch structure in prairie vegetation. Ecology **76**:1195–1205.

Stohlgren, T. J., L. D. Schell, and B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications **9**:45–65.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, New Jersey, USA.

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

Tilman, D., and P. Kareiva, editors. 1997. Spatial ecology. Princeton University Press, Princeton, New Jersey, USA.

Turner, M. G., and S. R. Carpenter. 1999. Spatial variability in ecosystem function. Introduction to special feature. Ecosystems **2**:383.

Wegener, C., and A. M. Odasz. 1997. Effects of laboratory simulated grazing on biomass of the perennial Arctic grass *Dupontia fisheri* from Svalbard: evidence of overcompensation. Oikos **79**:496–502.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon **21**:213–251.

APPENDIX

A table presenting the residual mean squared error (RMSE) and tests of statistical significance for models fitted to semivariograms of soil nitrogen properties measured in grazed and ungrazed grassland in Yellowstone National Park, USA, is available in ESA's Electronic Data Archive: *Ecological Archives* E082-035.