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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Spatial pattern of grazing affects influence of herbivores on spatial heterogeneity of plants and soils

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Abstract With our enhanced understanding of the factors that determine biodiversity and assemblage structure has come increasing acknowledgment that the use of an appropriate disturbance regime to maintain spatial heterogeneity is an effective conservation technique. A herbivore's behavior affects its disturbance regime (size and intensity); this, in turn, may modify the associated spatial heterogeneity of plants and soil properties. We examined whether the pattern of spatial disturbance created by the Siberian marmot (*Marmota sibirica*) affects the spatial heterogeneity of vegetation and soils at a colony scale on the Mongolian steppe. We expected that the difference in management between two types of area (protection against hunting marmots vs. hunting allowed) would result in different behavioral patterns; therefore, we estimated the patterns of spatial disturbance separately in protected and unprotected areas. We then surveyed plant communities and soil nutrients in these areas to assess their spatial heterogeneity. We found that disturbance of both vegetation and soil was more concentrated near marmot burrows in the unprotected area than in the protected area. In addition, the degrees of spatial heterogeneity of vegetation and soil NO_3-N were greater in the unprotected area than in the protected area, where disturbance was more widely distributed. These results indicate that the spatial pattern of disturbance by herbivores affects the spatial heterogeneity of vegetation and soil properties through changes in the disturbance regime. Our findings also suggest that the intensity of disturbance is more important than its size in determining community structure in Mongolian grasslands.

Keywords Disturbance intensity · Disturbance size · Disturbance regime · Marmots · Mongolian grassland

Introduction

Disturbance-induced environmental heterogeneity has been positively associated with species diversity in both natural and managed ecosystems (Benton et al. 2003). Warren et al. (2007) suggested that biodiversity is maximized where multiple kinds, frequencies, severities, periodicities, sizes, shapes, or durations of disturbance, or a combination of these factors, occur concomitantly in a spatially and temporally distributed fashion (White and Harrod 1997). Where a heterogeneous disturbance regime exists, species partition the varied conditions that result from disturbance so that a multitude of species can coexist along gradients of disturbance and succession.

On the Mongolian steppe, Siberian marmots (*Marmota sibirica*) modify plant communities and the physical and chemical properties of soil through activities such as

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burrowing, grazing, defecating, and urinating (Van Staalduinen and Werger 2007; Yoshihara et al. 2009). As a result of marmot disturbance, grass-dominated steppe vegetation is locally replaced by patchily distributed forb-dominated communities.

Because marmot burrows serve as focal points for marmot activity (Branch 1993), the relative intensity of this activity decreases with increasing distance from the burrows (Karels et al. 2004). However, burrowing rodents change their activity ranges when there is a risk of intruders (such as humans) approaching the burrows (Magle et al. 2005). Compared with the marmots at sites with low levels of human contact, marmots at high-use sites (e.g., in tourist areas) display reduced responses to human approach; this could be construed as either successful accommodation of disturbance or a decrease in predator awareness (Griffin et al. 2007).

The creation of disturbance patches by herbivores can alter the spatial heterogeneity of vegetation and soil properties, depending on how that behavior affects the disturbance regime (Gurney and Lawton 1996). A herbivore's activity range and the spatial extent and intensity of the disturbances caused by the herbivore might interact. A large activity range likely results in a large area being disturbed, but at a lower intensity than when the same level of disturbance is concentrated within a smaller range. These theoretical findings, however, have yet to be tested empirically under field conditions. In light of these previous research findings, it is reasonable to hypothesize that the effects of disturbance by Siberian marmots on the spatial heterogeneity of vegetation and soil properties reflect the marmots' spatial grazing patterns. Therefore, if disturbance intensity were more important than disturbance size in determining plant community structure, then the landscapes created by marmots with a small activity range would be more spatially heterogeneous than those created by marmots with a large activity range (Fig. 1, Hypothesis 1). This is because disturbance-dependent plant species would become established in the intensively disturbed patches and thus be able to coexist with competitively dominant species in a spatially partitioned manner. In contrast, if the size of a disturbance were more important than its intensity in determining plant community structure, then the landscapes created by marmots with a large activity range would be more spatially heterogeneous than those created by marmots with a small activity range (Fig. 1, Hypothesis 2). In this scenario, disturbance-dependent species would become established only in the larger disturbance patches, leading to spatial partitioning of the coexisting competitively dominant species. Although we recognize that disturbance frequency is another important aspect of the disturbance regime (Turner et al. 1998), in this study we focused on the relative importance of disturbance intensity and size.

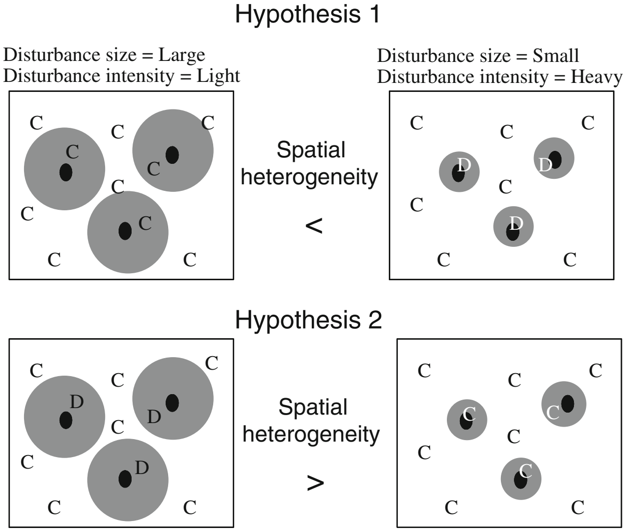

Fig. 1 Conceptual framework of our two hypotheses. *Black dots* indicate the positions of burrows and *gray circles* show disturbance patches. *Patch size* is proportional to disturbance size and *darkness* is proportional to disturbance intensity. *c* Competitively dominant plant species, *d* disturbance-dependent plant species

Historically, marmots have suffered from hunting in Mongolia and have learned to be wary of humans (Wingard and Zahler 2006). We, therefore, expected that the difference in management between two types of area (protection against hunting vs. hunting allowed) would result in different behavioral patterns. As we compared the behavior of marmots in protected and unprotected areas, we expected that, in areas where hunting is allowed, marmots would remain closer to their burrows.

The purpose of this paper is to examine how behavioral decisions by marmots affect the spatial heterogeneity of plants and soil properties and, if hunting alters their behavior, does it do so sufficiently to alter plants and soil properties. Specifically, we aimed to reveal: (1) the importance of considering the spatial pattern of grazing when studying the dynamics of spatial heterogeneity of plants and soil (2) the relative importance of disturbance size versus intensity, and (3) an appropriate disturbance regime for maintaining the spatial heterogeneity of vegetation and soil properties in Mongolian grasslands.

Materials and methods

Site description

Our study was conducted within Hustai National Park (HNP), which covers 60,000 ha and is located 100 km west of Ulaanbaatar, Mongolia (47°50′N, 106°00′E, elevation 1,100–1,840 m a.s.l.). HNP receives 232 mm of precipitation annually and is situated in the forest steppe region of Mongolia. We conducted our field survey in protected areas, located close to the headquarters of HNP, and in unprotected areas, located 15 km northwest of the boundary of HNP's core zone.

Spatial pattern of disturbance

We quantified the spatial pattern of marmot disturbance to verify whether the frequency of spatial disturbance classes differed between areas. Because dung density is considered to be a good indicator of the degree of marmot disturbance (Karels et al. 2004), in 2007 we used a global positioning system (Garmin, Taiwan) to identify the locations of marmot burrows and dung within a 25-ha area (500 × 500 m).

In June and July 2007, we established three 4-ha (200 × 200 m) plots that included marmot burrows in the protected areas and another three 4-ha plots in the unprotected areas (i.e., $n = 6$ plots in total). Each plot was then subdivided into 1,600 adjacent 25-m^2 (5 × 5 m) square grid cells. We chose a single focal adult, which we identified by specific characteristics (e.g., body size, color), in each of the six plots (i.e., $n = 6$ individuals). Each individual's feeding behavior was observed from behind a rock to minimize disturbance. We noted the grazing frequency in each grid cell, considering each series of grazing activities as a single instance. These focal observations were conducted continuously for an 8-h period for 5 days in each plot from the end of June to mid-July.

Vegetation survey

We established three 0.25-ha (50 × 50 m) plots that included marmot burrows within the 4-ha plots in the protected area (plots P1–P3) and three 0.25-ha plots that included the same number of burrows in the unprotected area (plots UP1–UP3). In addition, we established a 0.25-ha control plot without marmot burrows in each area. Each plot was subdivided into 625 adjacent 4-m^2 (2 × 2 m) quadrats, giving a total of 5,000 quadrats. In 2006, we recorded the presence or absence of plant species in each quadrat of plots P1 and UP1. Because the comparative analysis of multiple types of measurements is more likely to yield an accurate outcome (Tews et al. 2004), we also recorded the area of ground covered by each species in each quadrat of P2 and UP2 in 2007 and in each quadrat of P3 and UP3 in 2008, using a modified Daubenmire percentage cover scale (Collins and Smith 2006).

Soil nutrition survey

To investigate the soil properties, we extracted 64 core samples (10-cm diameter × 15-cm depth) from 40 × 40-m areas situated at the centers of plots P2, UP2, and the controls, with 5-m spacing between points. At each point, we extracted three core samples (a three-point replication method) from bare ground (between plants) and homogenized the samples. We extracted an additional eight samples at the center of the 64 points, with 2.5-m spacing. The survey was conducted in a focal plot in each area to optimize sampling effort.

The soil samples were dried in an oven at 70°C for 48 h and weighed. Dry combustion of decalcified soil samples was used to measure total nitrogen (TN), digestion with a salicylic acid mixture was used to determine NO_3-N, and the Bray and Kurtz method was used to measure K (Sparks et al. 1996).

Data analysis

To detect spatial relationships between burrows and feces, we used bivariate point-process analysis (Fortin and Dale 2005). We adopted an antecedent condition (sensu Wiegand and Moloney 2004) in which we kept the locations of burrows fixed and randomized only the locations of the feces. The pair-correlation function (g) is the probability-density function for the distances (r) between pairs of points and the noncumulative version of Ripley's K-function satisfying

$$g(r) = (1/2\pi r)\mathrm{d}K(r)/\mathrm{d}r,$$

(Stoyan and Penttinen 2000). The pair-correlation was computed by using the point-process analysis program of Takenaka (2008). A χ^2-test was used to analyze differences in the pair-correlation function (g) between areas at each distance from the burrows.

The total grazing frequency obtained from the behavioral observations was counted in each grid cell. In each plot, we calculated the relative frequency of grazing at a given grid distance from the nearest grid cell that included burrows. Non-parametric analysis (χ^2-tests and Mann–Whitney U-tests) were used to analyze differences in grazing frequency between areas at each distance from the burrows (Zar 1996).

Spatial heterogeneity of vegetation was calculated as the mean dissimilarity in community species composition among different sample points within a given field (Collins and Smith 2006). We used a 1 − Sørensen's QS index for presence or absence measurements of heterogeneity and a 1 − Bray–Curtis and a Euclidian distance index for quantitative measurements of heterogeneity. Because the effect of grazing on the spatial heterogeneity of vegetation is scale dependent (Adler et al. 2001), we evaluated the spatial heterogeneity of vegetation at three spatial scales: fine (4 m^2), intermediate (16 m^2), and coarse (100 m^2). For spatial heterogeneity of vegetation at the intermediate and coarse scales, we averaged species abundances among four

(2 × 2) and 25 (5 × 5) adjacent quadrats in each plot, respectively. We defined the single quadrat at the fine scale, the four adjacent quadrats at the intermediate scale, and the 25 adjacent quadrats at the coarse scale as a unit in the context of this analysis. For each dissimilarity index, we calculated the average heterogeneity value of all possible pairwise comparisons of the units within each plot at a fine scale ($n = 195{,}000$), intermediate scale ($n = 10{,}296$), and coarse scale ($n = 300$).

Plant dispersal into a patch is controlled primarily by factors relating to the patch's position in the landscape (Wright et al. 2003). Because the protected and unprotected areas were geographically separated, we expected the vegetation response to disturbance to differ substantially between the areas because of factors such as differences in the invasion process after disturbance events. Thus, we calculated the differences in spatial heterogeneity of vegetation between undisturbed and disturbed plots in each area and compared the heterogeneities. We calculated the difference (D_{ds}) between the dissimilarity values in the colony plots (i.e., plots that contained marmots) in both the protected and unprotected areas and the dissimilarity values in the control plot (with no burrows) for 1 − Sørensen's QS index in each area (Questad and Foster 2007):

$$D_{\mathrm{ds}} = \mathrm{DS}_{\mathrm{colony}} - \mathrm{DS}_{\mathrm{control}}.$$

The value of D_{ds} indicates the degree of the contribution made by marmots to increasing or decreasing the spatial heterogeneity of vegetation in an area. In order to statistically compare the D_{ds} values in the 1 − Sørensen's QS index between the protected and unprotected areas, we used the Mann–Whitney *U*-test.

To permit a detailed comparison of the changes in the plant community around burrows in the different plots, we pooled the vegetation coverage data from the eight quadrats adjacent to a quadrat that included a burrow and the 16 quadrats that were two quadrats distant from the quadrat that included a burrow to produce a single average value per burrow. Plant species were classified into competitively dominant species or disturbance-dependent species according to descriptions in the literature (e.g., Yoshihara et al. 2008).

We input all the soil data (P2 and UP2) in version 9.2 of the ArcGIS software and used kriging to predict values at unsampled locations. In the first step, we examined changes in the amount of variance among sampling points separated by a given distance (*h*, the spatial lag) at increasing distances to quantify the spatial structure of the data (i.e., to create an experimental variogram). Second, we fit several models for each variogram to construct a theoretical variogram. We then compared the root-mean-square errors (RMSEs) of five practical models: random, spherical, exponential, Gaussian, and J-Bessel. We selected the model with the lowest RMSE as the best-fit model (Augustine and Frank 2001). Finally, we used the best-fit models to construct maps of soil TN, NO_3-N, and K in each plot for the 40 × 40-m sample areas.

Results

Distribution of burrows and feces

The value of *g* in the unprotected area was approximately 120% of that in the protected area at scales of 0–2 m, but it was only about 70% of the value for the protected area at scales from 10–20 m (Fig. 2). The distribution of feces differed significantly between the two areas ($\chi^2 = 66.71$, $df = 49$, $P < 0.05$). These results indicate that the spatial relationship between burrows and feces in the unprotected area was more attractive than in the protected area: that is, in the unprotected area marmot activity was more concentrated around burrows.

Spatial grazing pattern

The distribution of grazing frequencies differed significantly between the two areas ($\chi^2 = 14.48$, $df = 6$, $P < 0.05$) at grid distances of zero and two cells from the

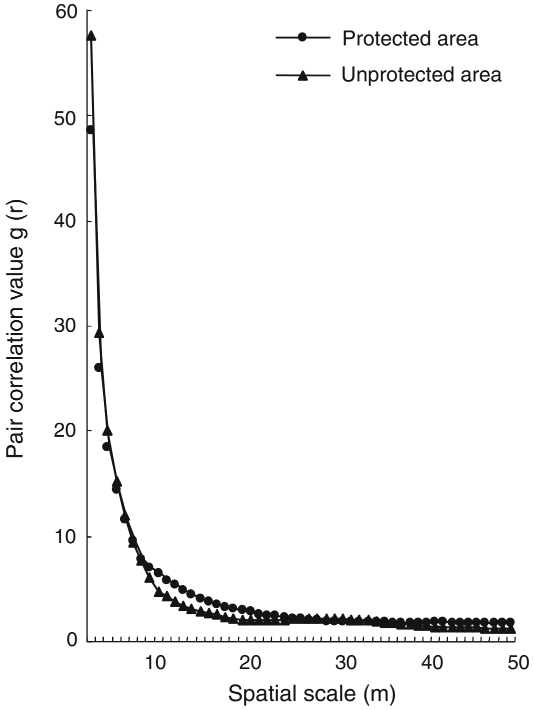

Fig. 2 Spatial relationships between burrows and feces in the protected and unprotected areas using the pair-correlation function (*g*) as a function of spatial scale (*r*). *g* is the probability-density function for the distances (*r*) between pairs of points

nearest grid cell that contained a burrow (*U*-test, $P < 0.05$; Appendix A). These results indicate that marmots in unprotected areas grazed more heavily near their burrows (distance of zero cells) than those in protected areas. At a distance of two cells, grazing was heavier in the protected area, and at all other distances it did not differ between areas.

Spatial heterogeneity of vegetation

The difference in the 1 − Sørensen's similarity index between the colony plots and control plot (D_{ds}) in the protected area was significantly greater than in the unprotected area at a fine scale (protected, mean $D_{\mathrm{ds}} = -0.048$; unprotected, mean $D_{\mathrm{ds}} = 0.065$; $P < 0.05$) and at an intermediate scale (protected, $D_{\mathrm{ds}} = 0.043$; unprotected, $D_{\mathrm{ds}} = 0.129$; $P < 0.05$), but it did not differ significantly at the coarse scale (protected, $D_{\mathrm{ds}} = 0.058$; unprotected, $D_{\mathrm{ds}} = 0.070$; $P = 0.827$; Fig. 3). Across all scales, the effects of the disturbance pattern on the spatial heterogeneity of vegetation were much clearer in the quantitative evaluation of the vegetation (Bray–Curtis) than in the qualitative evaluation (Sørensen's QS). In the unprotected area, plant composition changed more dramatically around the burrows than in the protected area (Appendix B). The coverage of competitively dominant species increased gradually with increasing distance from a burrow, whereas disturbance-dependent species became more abundant with decreasing distance. We noted a correspondence between the spatial scale of the disturbance patch and the vegetation heterogeneity. We identified clear differences in grazing frequency between protected and unprotected areas (at a distance of zero grid cells, or 25 m^2 around the burrow; Appendix B), and the largest difference in the degree of increase of spatial heterogeneity due to marmot disturbance occurred at the intermediate scale (16 m^2; Fig. 3).

Spatial heterogeneity of soil nutrition

The mean and coefficient of variation (CV) of TN were comparable in the protected and unprotected areas (Table 1). For all soil nutrients, the nugget values were lowest in the unprotected area. In the unprotected area, the mean and CV of NO_3-N were approximately 163 and 236%, respectively, of the corresponding values in the protected area. The semivariance at a lag of 2.5 m in the unprotected area was nearly 3 times greater than that in the protected area, indicating that the unprotected area had greatly increased fine-grain variability (Figs. 4, 5). For soil NO_3-N, the protected area showed no spatial pattern, but the unprotected area showed an oscillating spatial pattern. For K, the mean and CV in the unprotected area were 62 and 53% of the corresponding values in the protected area.

Similar to the pattern between the spatial scale of the disturbance patch and the vegetation heterogeneity, we found a correspondence between the spatial scale of the disturbance patch and the soil heterogeneity. The differences in soil heterogeneity of NO_3-N between protected and unprotected areas at a lag of 2.5 may reflect the disturbance frequency at scales of 0–2 m (Figs. 2, 5).

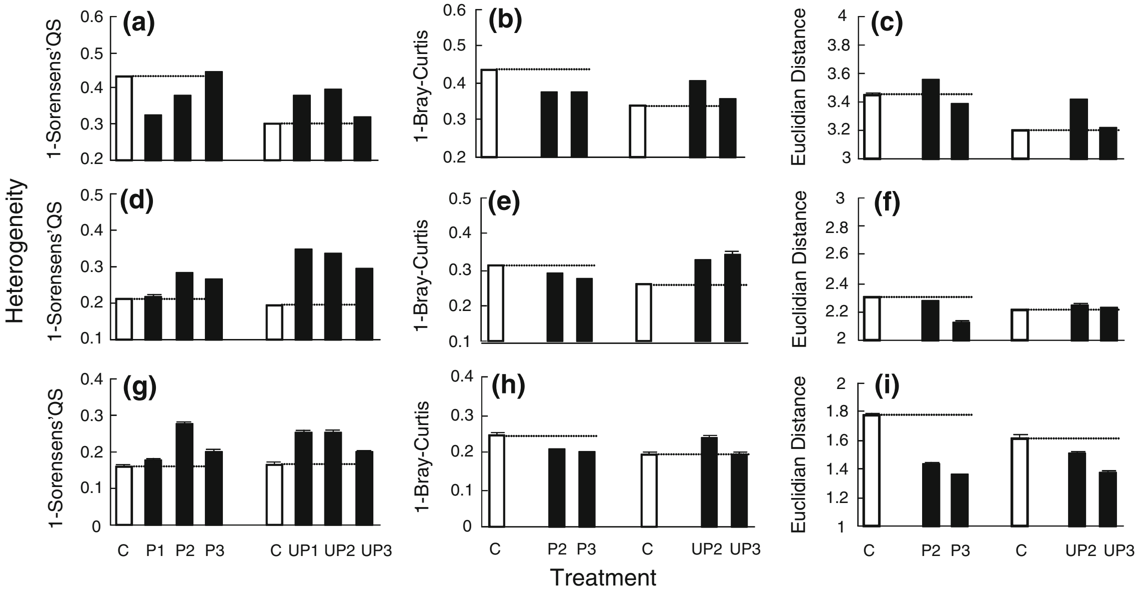

Fig. 3 Spatial heterogeneity of vegetation in each plot at **a–c** fine, **d–f** intermediate, and **g–i** coarse spatial scales. Heterogeneities were calculated over all possible pairs of quadrats within a plot using the three metrics and then averaged values are means ± SE (see text for details). *C* control plot, *P* plots in protected area, *UP* plots in unprotected area

Table 1 Statistical characteristics of soil nutrient parameters, the spatial structure of soil nutrient properties, and the root-mean-square errors (*RMSE*) based on the best-fit model for semivariance in each area

Soil properties	Treatment	Mean	CV	Model	Nugget (C)	Sill ($C + C_0$)	Proportion $1 - (C/C + C_0)$	Range	RMSE
Total N (%)	Control	0.20	0.13	Exponential	0.006	0.007	0.15	19.63	0.03
	Protected area	0.16	0.19	Exponential	0.007	0.008	0.13	25.38	0.03
	Unprotected area	0.15	0.17	Spherical	0.003	0.006	0.41	28.68	0.02
NO_3 (mg g^{-1})	Control	0.62	0.58	Spherical	0.09	0.15	0.38	19.59	0.36
	Protected area	0.62	0.61	Gaussian	0.14	0.15	0.04	14.16	0.37
	Unprotected area	1.01	1.44	J-Bessel	0.00	0.21	1.00	8.94	1.24
K (mg g^{-1})	Control	12.52	0.15	Gaussian	2.13	4.37	0.51	38.39	0.52
	Protected area	21.38	0.43	J-Bessel	3.91	7.97	0.51	5.13	8.45
	Unprotected area	13.38	0.23	J-Bessel	0.00	7.02	1.00	8.66	2.12

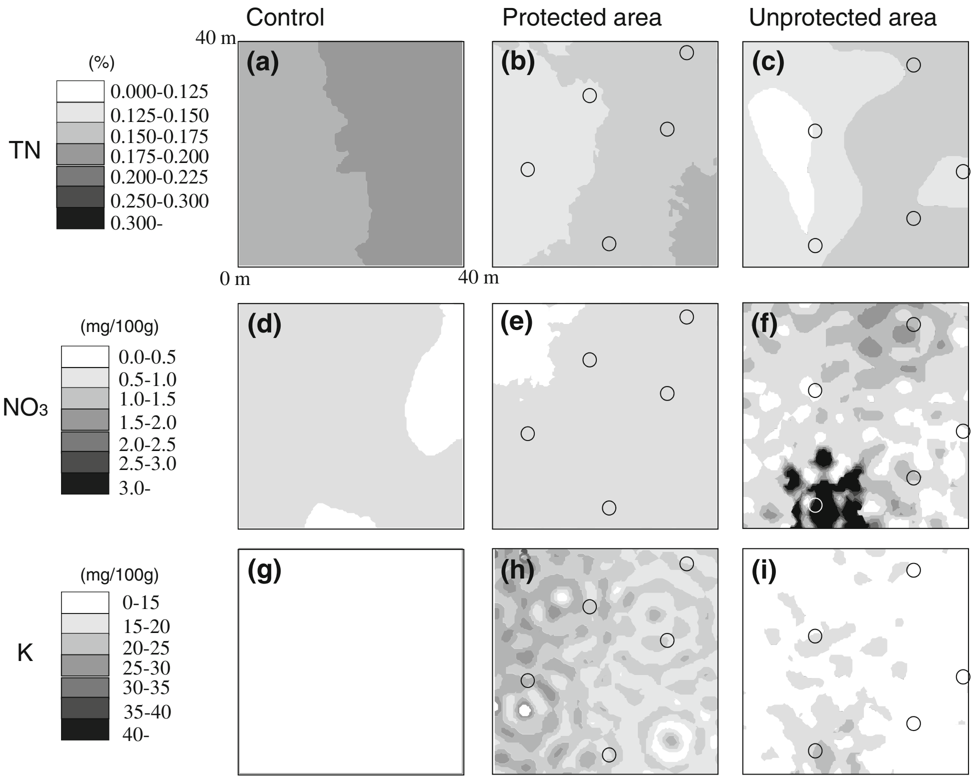

Fig. 4 Maps of soil nutrient properties determined using interpolation from best-fit semivariograms, **a-c** total N (*TN*), **d–f** NO_3, and **g–i** K.

Circles indicate the positions of marmot burrows

Discussion

Spatial pattern of grazing controls the influence of herbivores

Disturbance by marmots was more concentrated near the burrows in the unprotected area than in the protected area. The degrees to which the spatial heterogeneity of vegetation and soil NO_3-N increased as a result of disturbance by marmots were greater in the unprotected area, where disturbance was less widely dispersed. The greater spatial heterogeneity of vegetation in the unprotected area resulted from the emergence of disturbance-dependent plant species in intensively disturbed patches near the burrows; this divided the space into patches dominated by competitively dominant species and patches dominated by disturbance-dependent species.

Although both the herbivore species and measurement scale are known to modify the calculated effects of herbivory on the spatial heterogeneity of vegetation (Adler et al. 2001; Davidson and Lightfoot 2006; Yoshihara et al. 2009), our understanding of how the spatial grazing patterns of an individual herbivore control these effects remains unclear. However, we did note a correspondence

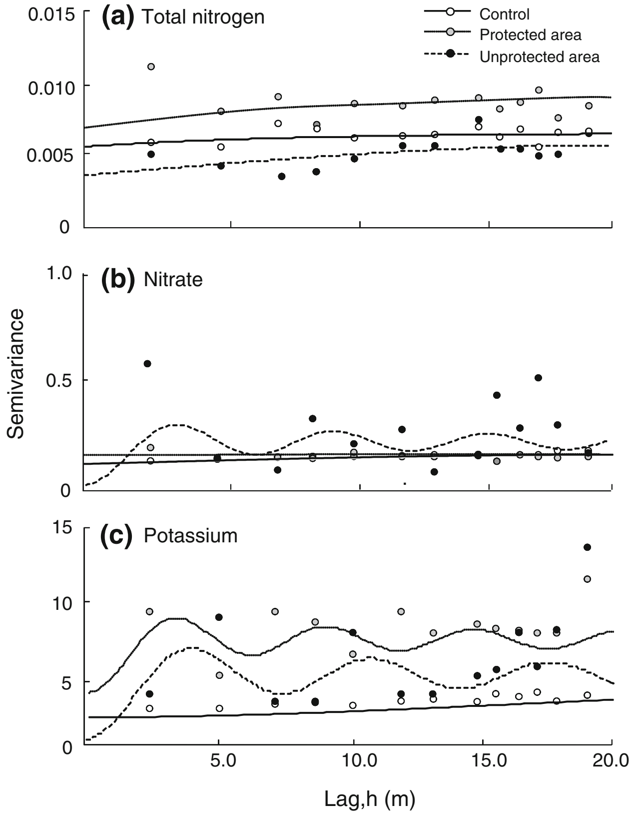

Fig. 5 Best-fit semivariograms in the three treatment areas for **a** TN, **b** NO_3, and **c** K

between the spatial scale of the disturbance patch and the vegetation heterogeneity. Thus, these results emphasize the importance of considering the behavior of herbivores within an area (i.e., the spatial pattern of grazing) in grazing studies that examine the dynamics of spatial heterogeneity of plants and soil properties.

Importance of intensity in the disturbance regime

Marmots with a small activity range increased the spatial heterogeneity of vegetation at the landscape level more than those with a large activity range. This finding supports hypothesis 1 in Fig. 1, thereby indicating that disturbance intensity is more important than disturbance size in determining the plant community structure on the Mongolian steppe.

In forests, the importance of disturbance size has generally been recognized. A larger disturbance patch includes a greater amount of interior habitat that is far from intact (undisturbed) patches. These interior patches have a strong impact on plant succession or species composition (Bergeron and Dansereau 1993; Shure et al. 2006), because they experience quite different physical conditions from those of edge and undisturbed habitats; for instance, they may have greater light availability, higher air temperatures, greater wind speeds, and lower humidity (Denslow 1987). In contrast, in arid grasslands, intact patches and the edges of disturbed patches may have similar physical conditions because the disturbed patches are surrounded by low grasslands and sparse shrubs. Thus, disturbance size may play a minor role in changing the composition of these communities. For instance, Morgan (1998) reported that the emergence of forbs in an Australian grassland was largely independent of gap size. Alternatively, the observed pattern may simply reflect the fact that low-intensity disturbance does not result in the replacement of plant species even if it produces a reduction in plant height.

Spatial pattern of grazing and soil heterogeneity

Unlike our clear results for vegetation heterogeneity, the relationship between the spatial pattern of grazing and the spatial heterogeneity of soil properties was somewhat vague (Fig. 4). However, the high NO_3-N concentration near some burrows in the unprotected area could have resulted from a combination of high deposition of dung and urine in these small areas and a high net mineralization rate of NO_3-N (Fig. 2). Such contrasting patterns of nutrient cycling on and near animal burrows have been widely observed in several grassland–grazer systems (Holland and Detling 1990; Van Staalduinen et al. 2007; Wesche et al. 2007). The oscillatory semivariograms for K showed repeated patterns, probably because the burrows/fecal piles are regularly arranged across the landscape.

Applications

The higher level of spatial heterogeneity of vegetation in plots with intensive but patchily distributed small disturbances suggests that such a heterogeneous disturbance regime is appropriate for maintaining rich biodiversity in the Mongolian steppe. Yoshihara et al. (2008) reported that intensive disturbance often increases the abundance of species that are less palatable to livestock and decreases edible plant biomass, thus promoting degradation of the land in this region. Where the disturbances were localized, however, these harmful influences could be minimized. Our field research was conducted in livestock-free areas, but marmots are distributed throughout the Mongolian steppe, where they coexist with livestock and create unique communities. The challenge for future field experiments on the steppe will be to design studies that can generate a range of disturbance regimes under the joint effects of marmot and livestock grazing.

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