

Clustered animal burrows yield higher spatial heterogeneity

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Abstract An understanding of the relationships between spatial heterogeneity and disturbance regime is important for establishing the mechanisms necessary to maintain biodiversity. Our objective was to examine how the configuration of disturbance by burrowing rodents (Siberian marmot) affected the spatial heterogeneity of vegetation and soil nutrient properties. We established three 2500-m² (50 m × 50 m) isolated-burrows plots and three 2500-m² clustered-burrows plots in a Mongolian grassland. Each plot was subdivided into 4-m² quadrats, and the plant species richness, percent coverage, and soil nutrient properties in the quadrats were surveyed. Spatial heterogeneity was calculated for vegetation using the mean dissimilarity of species composition among sample quadrats, and geostatistical analysis was used to calculate soil properties. Heterogeneous patches of plants such as *Achnatherum splendens* and higher nutrient concentrations were found only near the clustered burrows. As a

result, spatial heterogeneities of vegetation and soil nutrient properties were higher in the clustered colony than those in the isolated colony. The configuration of disturbance patches affected the spatial heterogeneity at the landscape level through the spatial pattern of disturbance frequency.

Keywords Patch configuration · Disturbance regime · Mongolia · Siberian marmot · Soil nutrition · Plant composition

Introduction

Understanding the patterns, causes, and consequences of spatial heterogeneity is a research frontier in the landscape ecology, population ecology, and ecosystem ecology (Hanski and Simberloff 1997; Turner et al. 2001; Wu 2004). Spatial heterogeneity has been recognized as a key focus in biodiversity from the individual to the species, community, and ecosystem levels (Huston 1994; Tilman 1999; Tews et al. 2004; Dufour et al. 2006; North and Ovaskainen 2007) through its effects on survival rate (Corlett 2000), competition (Fransen et al. 2001; Day et al. 2003), dispersal success (Rees et al. 2000), lateral flux of matter or energy (Reiners and Driese 2001), and ecosystem functions (Lovett et al. 2005).

Disturbance is the one of main factors generating spatial heterogeneity (Levin 1992; White and Jensch 2001). Species respond differently to disturbance

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according to their various abilities to tolerate or thrive under disturbed conditions. These various responses are related to species' life-history traits; for instance, generally annual plants do better in disturbed areas than do perennials; plants propagated clonally regenerate better in disturbed areas than do those propagated by seed (Halpern 1988; 1989; Turner et al. 1997; White and Harrod 1997; Dorrough et al. 2004). If we consider nonspatial components of disturbance at the patch scale, different types of patches (succession stage) will form according to the disturbance magnitude gradient. Recent studies have examined the importance of the spatial and temporal components of individual disturbances (e.g., Halpern 1989; Moloney and Levin 1996; Platt and Connell 2003). In the context of communities at the landscape scale, because the disturbance regime (e.g., size, frequency, and proportion of disturbed area; temporal variation) controls the proportion of the landscape at each succession stage (Wu and Levin 1994; Moloney and Levin 1996; White and Harrod 1997; Platt and Connell 2003), it is essential to consider the disturbance regime when examining the dynamics of spatial heterogeneity.

Romme et al. (1998) suggested that some unusually frequent or intense disturbances produce qualitatively different responses as compared with similar disturbances of lesser magnitude; such events cause dramatic changes in impact at some point along the disturbance intensity or frequency gradient (threshold responses). Similarly, compounded disturbances within the normative recovery time of a community appear to cause that community to enter new domains or produce alternative stable states that are ecologically surprising (Paine et al. 1998). For example, in Jamaican coral reefs, three sequential disturbances failed to allow coral recovery, which would have developed, had the disturbance events occurred individually (Hughes 1994; Andres and Witman 1995). These findings indicate that the effects of compounded disturbances on a community are not simply additive but multiplicative. If such emergent patches are generated within a spatial extent, spatial heterogeneity at the landscape scale will be affected. In a tallgrass prairie ecosystem, frequent fires modified the species composition of vegetation to a greater extent than did a single fire (Collins 2000) and, consequently, affected spatial heterogeneity (Knapp et al. 1999, Collins and Smith 2006).

The configuration of disturbance patches should affect spatial heterogeneity by changing the spatial pattern of the disturbance frequency. Assuming that each disturbance patch is spatially concentrated, these patches may overlap in some areas. Different communities will be created in these frequently disturbed overlapping patches, resulting in an increase of spatial heterogeneity at the landscape scale. Simulation models have evaluated the effects of disturbance configuration (spatial autocorrelation among individual disturbances) on the distribution and abundance of species at the landscape scale (Green 1989; Moloney and Levin 1996); however, empirical work designed to characterize the effects at the landscape scale has not been conducted.

Herbivores affect the spatial patterns of vegetation and soil nutrition through defoliation, trampling, excavating, and excretion. For instance, prairie dogs, rabbits, and voles in grasslands increase the spatial heterogeneity of biomass at the landscape scale (Bangert and Slobodchikoff 2000; Questad and Foster 2007; Olofsson et al. 2008). Urination by cattle creates nitrogen-enriched patches on the order of 80 cm in diameter (Stillwell et al. 1983), resulting in an increased late-succession species such as C4 plants and increased β diversity (Steinauer and Collins 1995). These influences are mitigated by grazing, however. Since such high nutrient patches attract grazers, urine appears to impact spatial heterogeneity of vegetation to a larger scale via defoliation by grazers than do by urine alone (Steinauer and Collins 2001).

In Mongolian grasslands, Siberian marmots (*Marmota sibirica*; “tarbagan” in Mongolian) modify plant communities and soil physical and chemical properties through activities such as burrowing, herbivore, and urinating (Adiya 2000; Van Staaldunen and Werger 2007). In order to minimize their predation risk (Holmes 1984), marmots return frequently to their burrows. Because their burrows serve as focal points for their activities (Behrends et al. 1985; Branch 1993), the relative frequency of marmot activity decreases with increasing distance from their shelters (Karels et al. 2004). Therefore, the compositional heterogeneity of vegetation increases in areas closer to marmot burrows (English and Bowers 1994; Yoshihara et al. 2009).

The isolated-burrows plot includes two patch types that differ in disturbance frequency: an undisturbed patch and frequently disturbed patches (A and B in

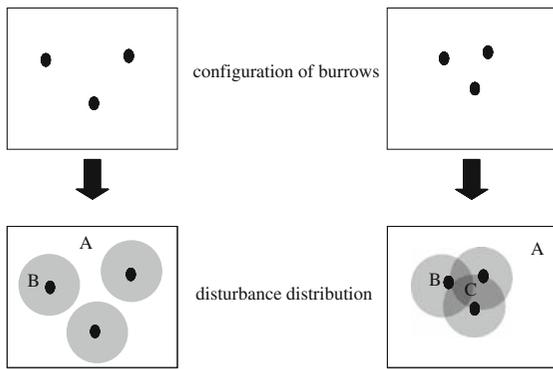


Fig. 1 Conceptual framework of our hypothesis. *Black dots* indicate burrows. Space is divided in relation to disturbance frequency: *A* absence of disturbance; *B* disturbed by an individual animal (infrequent); *C* disturbed by multiple animals (frequent). Clustered burrows create a frequently disturbed patch (*C*), which is expected to increase spatial heterogeneity in the area

Fig. 1). The clustered-burrows plot includes three types of patches: an undisturbed patch, frequently disturbed patches, and an extremely frequently disturbed patch near the center of the cluster (*C* in Fig. 1). In this grassland, we predict that the disturbance-free patches (*A*) would be dominated by perennial graminoids, the disturbed patches (*B*) would be dominated by annual forbs, and unexpected communities would be established in the extremely frequently disturbed patch (*C*), which should contribute to a greater degree of landscape level heterogeneity in the clustered-burrows plot. The aim of this study was to investigate the effects of the spatial configuration of disturbance patches on spatial heterogeneity at the landscape level by comparing areas with isolated marmot burrows versus those with clustered burrows. At the colony scale (contain multiple burrows), we expected that the spatial heterogeneities of vegetation and soil nutrients in the clustered-burrows plot would be higher than that in the isolated-burrows plot (Fig. 1).

Materials and methods

Study areas

We selected study sites in Hustai National Park (HNP), which is located 100 km west of Ulaanbaatar, Mongolia (47°50'N, 106°00'E, elevation 1100–1840 m).

HNP occupies $\sim 600 \text{ km}^2$ of the forest steppe region of Mongolia and receives an average annual precipitation of 232 mm. The annual average temperature is 0.2°C and average monthly temperatures vary between -23°C (in January) and $+20^\circ\text{C}$ (in July). About 88% of the area of HNP is covered by grassland and shrubland steppe and about 5% is covered by birch-dominated forest (Wallis de Vries et al. 1996).

The types of vegetation that grow on the mounds created by Siberian marmots (*M. sibirica*) can differ greatly from those on the surrounding, comparatively homogeneous, grasslands, which are dominated by a few graminoids (Van Staalduinen and Werger 2007). When this study was conducted, livestock had been excluded from the HNP's core areas for 15 years. HNP is thus a suitable site for detecting the effect of marmots on landscape heterogeneity in grasslands.

Sampling design

Because dung density is considered a good indicator of marmot disturbance (Karels et al. 2004), we located and noted the position of marmot burrows and dung within a 25-ha area ($500 \text{ m} \times 500 \text{ m}$) using a global positioning system receiver (Garmin Inc., Taiwan). Based on these data, we identified an area with clustered burrows and an area with isolated burrows.

Our field surveys were conducted in July and August in 2006 and 2007. According to Addicott et al. (1987), the spatial extent that encompasses most of an organism's activity relevant to some process (and over a relevant amount of time) is the appropriate scale for investigating this process. Thus, the effect of grazing by marmots at the colony scale was investigated by comparing the 2500-m^2 plots. We established three 2500-m^2 ($50 \text{ m} \times 50 \text{ m}$) plots including some isolated marmot burrows (isolated colony, ISO) and three 2500-m^2 plots including the same number of clustered burrows (clustered colony, CLU). Each plot was subdivided into 625 adjacent 4-m^2 ($2 \text{ m} \times 2 \text{ m}$) quadrats (total = 3750 quadrats), because the 4-m^2 quadrat size is a suitable grain size to reflect marmot disturbances (Yoshihara et al. 2009).

The plots were separated by $\sim 300 \text{ m}$ within the same landscape (valley foot slope); all plots had the same soil type (Haplic Kastanozems) according to the soil-type layer in the GIS database produced by the HNP and were dominated by *Stipa krylovii*.

In 2006, we recorded the absence/presence of each plant species in each quadrat of plots ISO1 and CLU1. In many studies on heterogeneity, the comparative analysis of multiple types of measurements most likely yields accurate outcome (Tews et al. 2004). We therefore recorded the area of ground covered by each species in each quadrat of ISO2 and CLU2 in 2007, and ISO3 and CLU3 in 2008, using a modified Daubenmire percent cover scale (Daubenmire 1959; Collins and Smith 2006): 0, absent; 1, <1%; 2, 2–5%; 3, 6–25%; 4, 26–50%; 5, 51–75%; 6, 76–95%; and 7, >95%.

In order to investigate soil properties, we extracted soil core samples (10-cm diameter \times 15-cm depth) from 40 m \times 40 m areas situated at the centers of plots ISO2 and CLU2, with 5-m spacing between points (64 points). At each point, we extracted three replications (three-point method) and the samples were homogenized. In addition, we extracted an extra eight random samples at the center of the 64 points, at a 2.5-m spacing. For comparison, we performed the same soil sampling in an area without marmot burrows (off-colony plot). This nested design was well suited for quantifying heterogeneity across as broad a range of spatial scales as possible (Gross et al. 1995; Augustine and Frank 2001).

In the laboratory of the Department of Ecosystem Studies of the Mongolian State University of Agriculture, soil samples were dried in an oven at 70°C for 48 h and weighed. Dry combustion with decalcified soil samples (Matejovic 1993) was used to measure total nitrogen (TN), digestion with a mixture of salicylic acid was used to determine nitrate nitrogen (NO₃-N), and Colwell methods were used to measure potassium (K).

Data analysis

On a map of the plots generated in ArcMAP 9.2 (ESRI 2007), we radiated out 11.6-m buffers from each burrow, where the 11.6 m equals the normal activity range (X) based on a study of hoary marmots (*Marmota caligata*) by Karels et al. (2004). With the aid of spatial analysis, we divided the 25-ha area into three patch types: outside the buffers (analogous to A in Fig. 1), within single buffer (B in Fig. 1), and within overlapped buffers (C in Fig. 1). Dung density was calculated in each patch type. We performed the same methods with changing buffer size (i.e., activity

range), radiated out 5.8-m (1/2 X) and 23.2-m (2 X) buffers from each burrow.

In order to compare plant species composition between the isolated-burrows plots and the clustered-burrows plots, we calculated the species richness for each quadrat. Spatial heterogeneity for each plot was calculated as the mean dissimilarity in community species composition among sample points in space (Collins and Smith 2006). We used a 1-Sorensen's quotient of similarity (1-Sorensen's QS) index for the absence/presence measurements of vegetation heterogeneity and a Euclidian distance index for quantitative measurement of vegetation heterogeneity: a greater value of each index indicates higher spatial heterogeneity. We calculated the heterogeneity over all possible pairs of quadrats within a plot. We used Euclidian distance because it is less affected by species richness and therefore more accurately measures community heterogeneity (Collins 2000).

In order to statistically compare the vegetation heterogeneity between in the clustered-burrows plots and in the isolated-burrows plots, we used the three values of 1-Sorensen's QS index in each plots with a t test. If the P value was smaller than 0.05, we concluded that the dissimilarity index between the plots was significantly different.

We input all the soil data (ISO2 and CLU2) and used kriging in ArcGIS to predict values of unsampled locations. In a first step, to predict an unknown value for a specific location, the kriging technique requires the values of the measured sample points around the prediction location and the spatial data configuration. We input all soil data and related locations using the geostatistical analysis extension of ArcGIS. Then, we examined changes in the amount of variance among sampling points separated by a given distance (h , spatial lag) at increasing distances to quantify the spatial structure of the data (experimental variogram).

Second, we fit several models for each variogram to construct a theoretical variogram. Then we compared the root mean squared errors (RMSEs) of practical models: spherical, exponential, Gaussian, and J-Bessel (Ella et al. 2001; Sarangi et al. 2006). We then selected the model with the lowest RMSE as the best-fit model (Pastor et al. 1998; Augustine and Frank 2001). Parameters derived from the best-fit model were used to quantify the spatial pattern of patchiness in a variate's distribution. Parameter C_0 ,

the y intercept of the best-fit model in a variogram, is called the “nugget” and indicates local random effects or measurement error at a short distance. Parameter $(C + C_0)$, where the fitted model reaches an asymptote, is called the “sill” or semivariance and indicates the intensity of the spatial pattern (Robertson and Gross 1994). The proportion of sample variance explained by patchiness was calculated as $1 - [C_0/(C + C_0)]$. The “spatial range” was measured as the distance separating sampling points at which semivariance reaches an asymptote (Robertson and Gross 1994), which indicates the maximum distance at which the variable is spatially autocorrelated.

Finally, maps of soil TN, $\text{NO}_3\text{-N}$, and K in each plot (off-colony plot, ISO2, CLU2) were constructed for the $40\text{ m} \times 40\text{ m}$ sample areas using the best-fit models. Based on these maps, soil properties were compared among the off-colony, isolated-burrows, and clustered-burrows plots.

Results

Marmot disturbances

Marmot dung density in the clustered-burrows plots was ~ 2.3 , 1.8, and 3.2 times greater than in the isolated-burrows plots when 5.8-, 11.6-, and 23.2-m buffers were radiated out from each burrow, respectively (Fig. 2). This indicated that the clustered-burrows plot was extremely frequently disturbed by marmots.

Plant communities and spatial heterogeneity

In plots ISO1, ISO2, and ISO3, a total of 52, 40, and 49 plant species were recorded, and in plots CLU1, CLU2, and CLU3, 48, 49, and 51 species were recorded.

Spatial heterogeneity was significantly higher in the clustered burrows than in the isolated-burrows plots (Fig. 3, $t = -3.59$, $df = 4$, $P < 0.05$). The mean Euclidian distances were 3.47 in the isolated-burrows plots and 3.71 in the clustered-burrows plots. At the clustered-burrows plots, the positions of the highly heterogeneous patches roughly overlapped those of the marmot burrows (Figs. 4, 5, 6). Large, highly heterogeneous patches were apparent in the

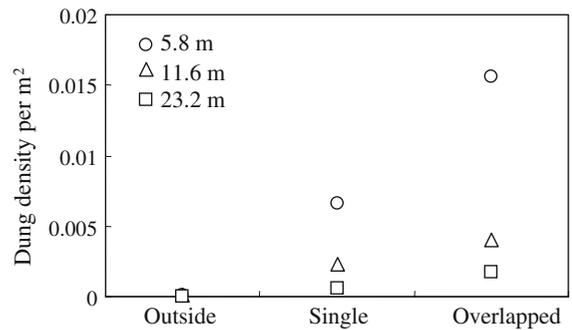


Fig. 2 Dung density of outside of the buffers (off-colony), within the single buffers (isolated-burrows plot), and the overlapped buffers (clustered-burrows plot) patches. Disturbance ranges radiated out 5.8 (1/2X), 11.6 (X), and 23.2 (2X) m from each burrow, where 11.6 (X) m indicates the normal activity range of marmots

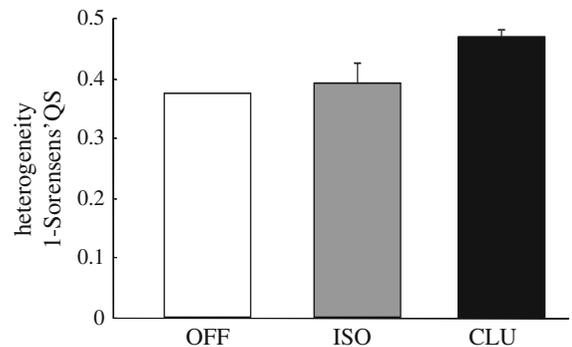


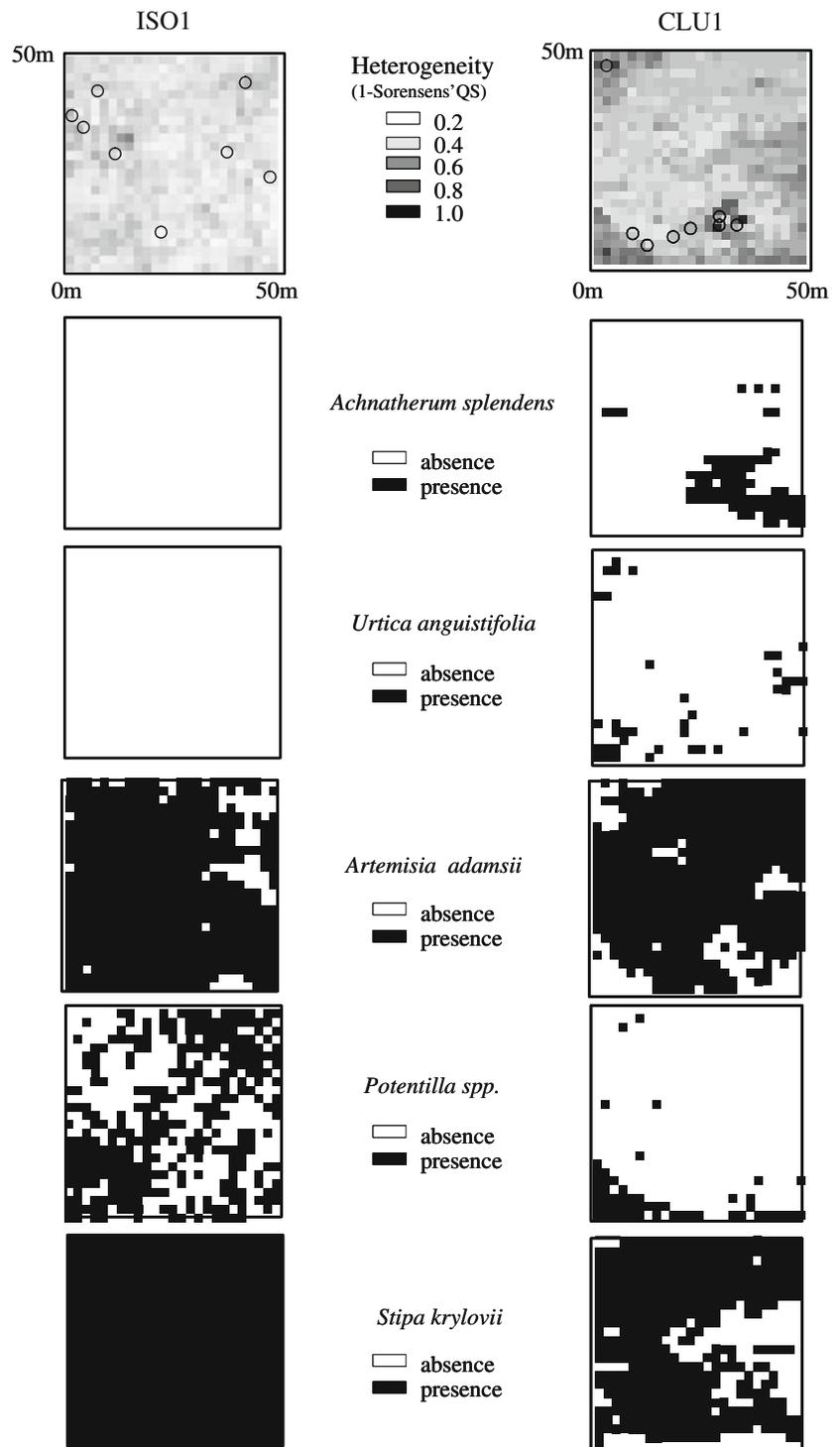
Fig. 3 Spatial heterogeneity of vegetation in each type. *OFF* off-colony plot; *ISO* isolated-burrows plots; *CLU* clustered-burrows plots. Heterogeneities were calculated over all possible pairs of quadrats within a plot and then averaged ($N = 195000$). We then presented the average for all three plots of the same type with the variation between plots. Bars show the standard error

clustered-burrows plots. *Achnatherum splendens* (Compositae) was found among the clustered burrows but not in the isolated-burrows plots (Figs. 4, 5, 6). *Artemisia adamsii* also showed the same tendency, although these plants were distributed more widely than *A. splendens* (Fig. 5). *Potentilla* spp. were found on isolated burrows or a little distance away from the clustered burrows (Figs. 4, 5, 6).

Spatial heterogeneity of soil properties

Total nitrogen ($F = 50.12$, $df = 1$, $P < 0.001$), $\text{NO}_3\text{-N}$ ($F = 3.93$, $df = 1$, $P < 0.001$), and K

Fig. 4 Spatial heterogeneity of vegetation and spatial distribution of five representative species differing in tolerance to disturbance in an isolated-burrows plot (ISO1) and a clustered-burrows plot (CLU1). Heterogeneity in each quadrat (grid) was calculated relative to that in other quadrats within each plot and is represented as mean values ($N = 624$). In the plot illustrations, *darker color* indicates a higher value of heterogeneity and *each circle* represents the position of a mound

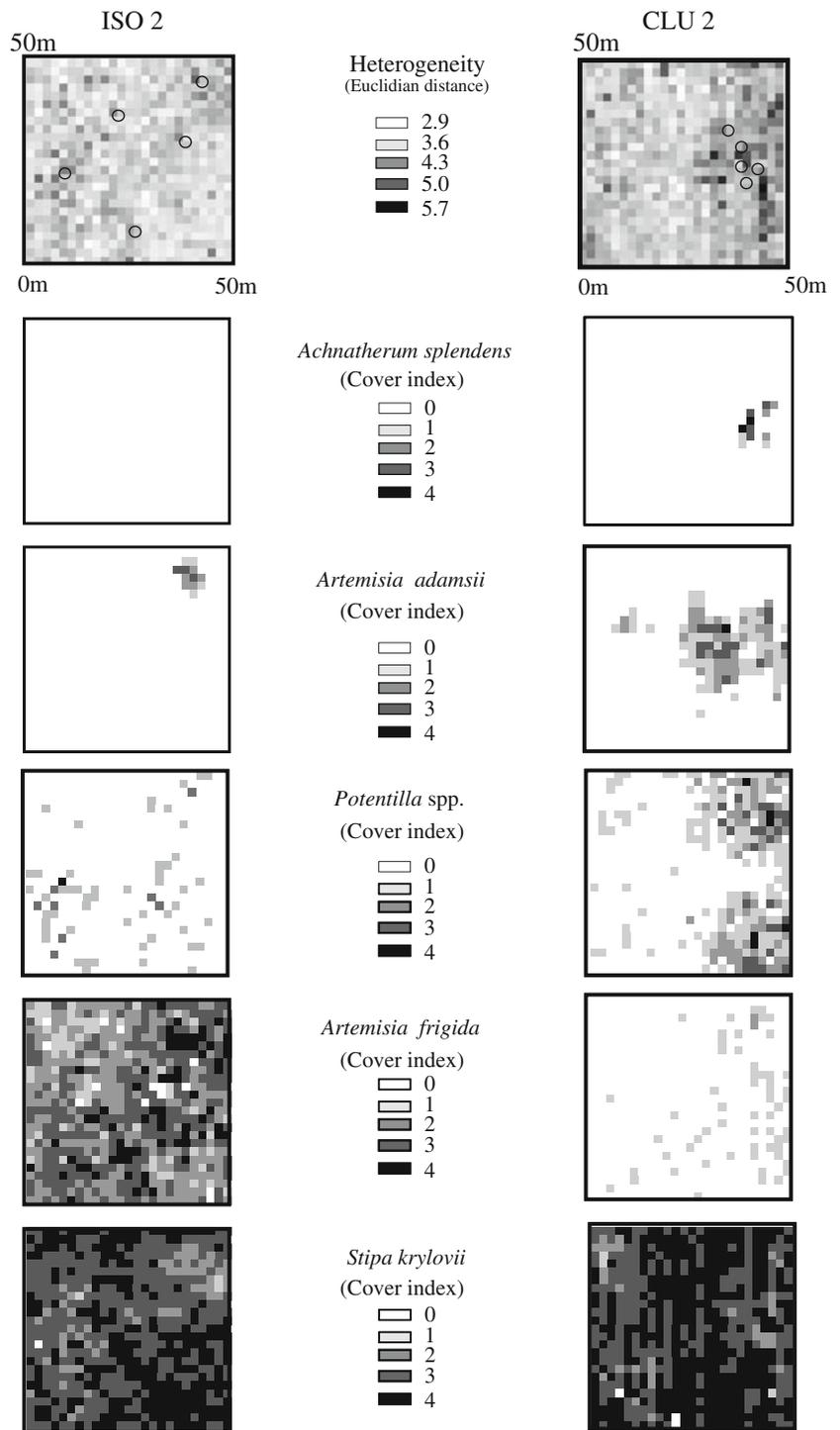


($F = 21.62$, $df = 1$, $P < 0.001$) exhibited significant differences between ISO2 and CLU2 (Table 1). The coefficients of variance showed a greater degree of variance for TN and $\text{NO}_3\text{-N}$ among plots. For all soil

nutrients, the mean and coefficients of variance were largest in CLU2.

Overall, semivariance at every lag size and sill values for semivariogram models were higher in

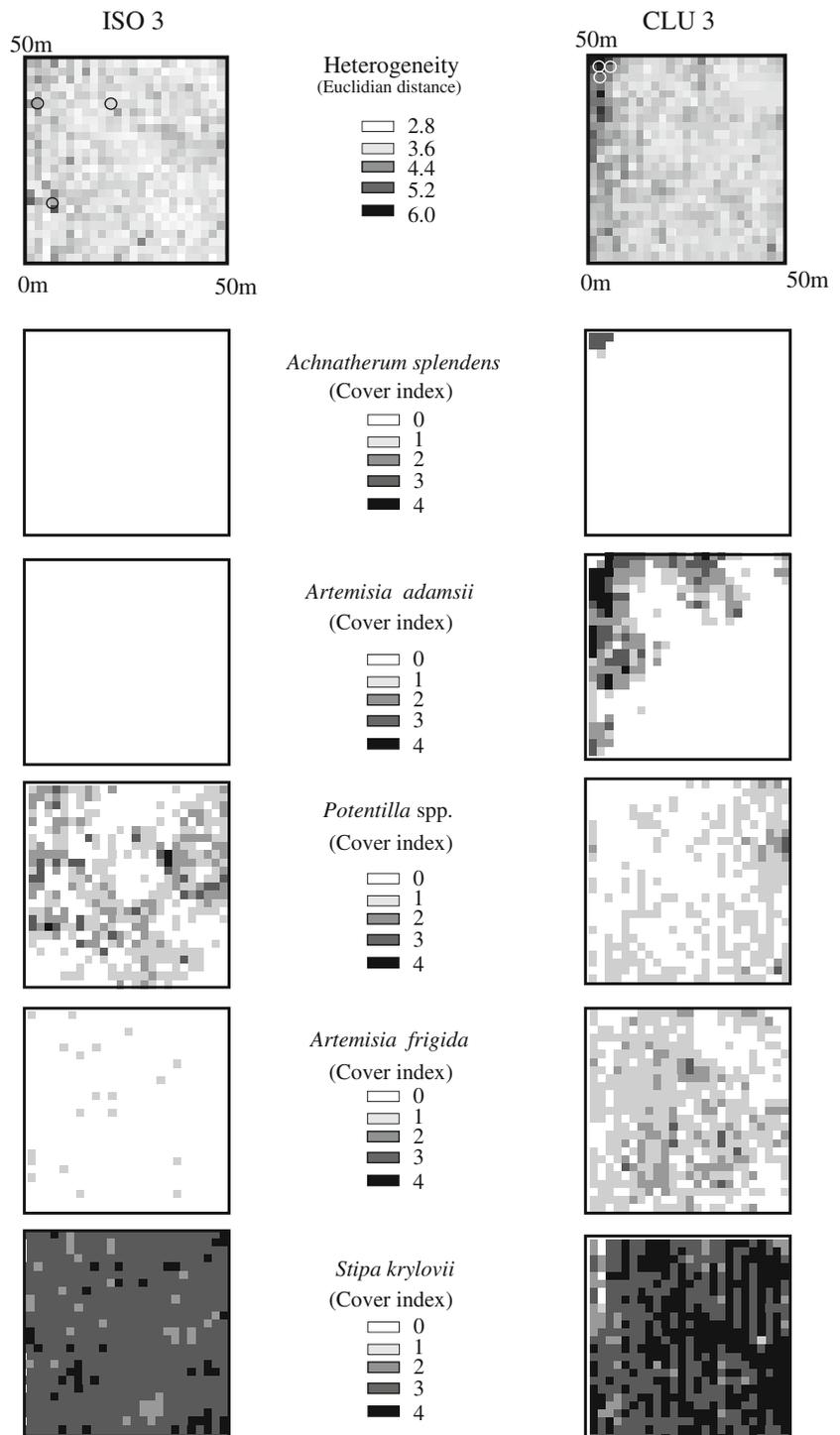
Fig. 5 Spatial heterogeneity of vegetation and spatial distribution and cover index value of five representative species differing in tolerance to disturbance in an isolated-burrows plot (ISO2) and clustered-burrows plot (CLU2). Heterogeneity in each quadrat was calculated relative to that in other quadrats within each plot and is represented as mean values ($N = 624$). In the plot illustrations, *darker color* indicates a higher value and *each circle* represents the position of a mound



CLU2 than in the off-colony or ISO2 (Fig. 7). The off-colony plot showed neither a spatial pattern nor patchiness. For all soil nutrients, the nugget values

were largest in CLU2 (Table 2). For soil TN, exponential models best fit the data in all plots (Table 2). For soil $\text{NO}_3\text{-N}$, ISO2 showed no spatial

Fig. 6 Spatial heterogeneity of vegetation and spatial distribution and cover index value of five representative species differing in tolerance to disturbance in an isolated-burrows plot (ISO3) and clustered-burrows plot (CLU3). Heterogeneity in each quadrat was calculated relative to that in other quadrats within each plot and is represented as mean values ($N = 624$). In the plot illustrations, *darker color* indicates a higher value and *each circle* represents the position of a mound



pattern, while CLU2 showed an oscillating spatial pattern (Fig. 7). In addition, the proportion of variance explained by small-scale patchiness was greater

and the range of autocorrelation was lower in CLU2 (Table 2), indicating that CLU2 had greatly increased fine-grain variability and that patches of $\text{NO}_3\text{-N}$

Table 1 Statistical characteristics of soil nutrition at each plot

Treatment	Total N (%)		NO ₃ (mg/g)		K (mg/g)	
	Mean	CV	Mean	CV	Mean	CV
Off-burrow (OFF)	0.20	0.13	0.62	0.58	12.52	0.15
Isolated burrows (ISO2)	0.16	0.19	0.62	0.61	21.38	0.43
Clustered burrows (CLU2)	0.22	0.33	0.87	1.17	31.78	0.52

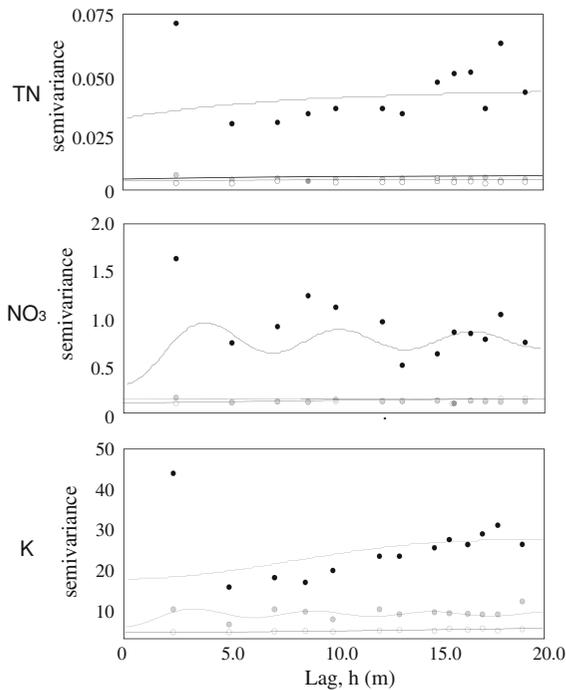


Fig. 7 Best-fit semivariograms for each soil nutrient property in the off-colony plot (*white circles*), isolated-burrows plot (ISO2, *gray circles*), and the clustered-burrows plot (CLU2, *black circles*)

show a repetitive pattern across the plot. For soil K, ISO2 showed oscillation in the spatial pattern, although the magnitude of semivariance was low (Fig. 7).

Based on the kriged map, each soil property exhibited highly heterogeneous patches in the CLU2, which corresponded to the positions of the clustered burrows (Fig. 8). In contrast, we could find no relationship between the heterogeneous patches and burrow positions in the ISO2.

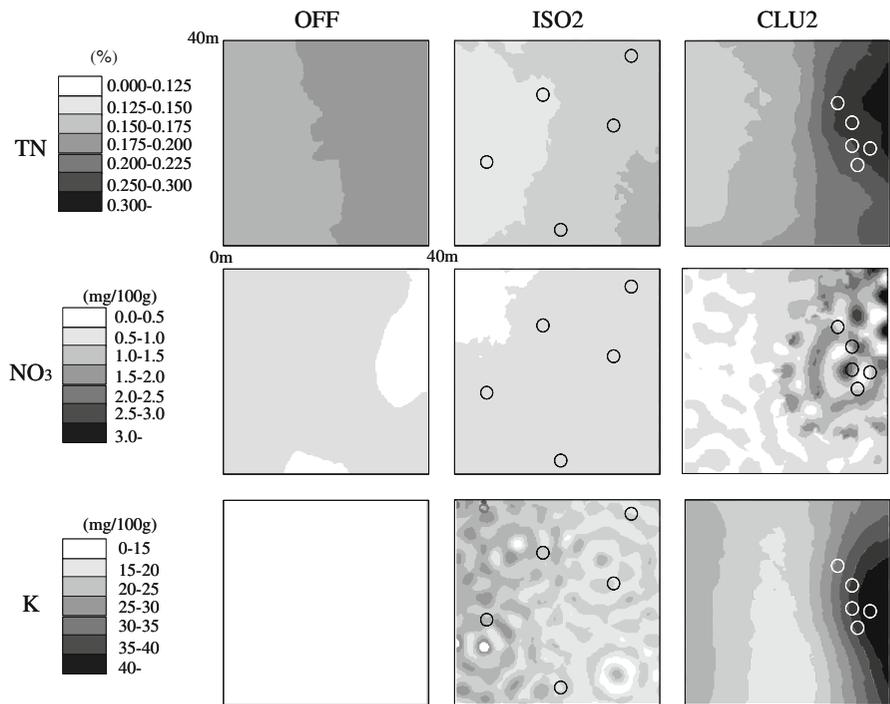
Discussion

Researchers have long debated whether the effects of disturbance on spatial heterogeneity depend on the size or intensity of the disturbance (Moloney and Levin 1996; Su et al. 2006). Our results demonstrated that the configuration of disturbance patches affected spatial heterogeneity by modifying the spatial pattern of disturbance frequency and had stronger effects on heterogeneity than the presence or absence of disturbance (Figs. 3, 8). The highly heterogeneous landscape in the clustered-burrows plots was attributed to the emergence of communities that do not

Table 2 Results of spatial structure of soil nutritional properties and root mean square error based on the best-fit model for semivariance at each plot

Soil properties	Treatment	Model	Nugget (C_0)	Sill ($C + C_0$)	Proportion $1 - (C_0/C + C_0)$	Range	RMSE
Total N	Off-burrow (OFF)	Exponential	0.006	0.007	0.15	19.63	0.03
	Isolated burrows (ISO2)	Exponential	0.007	0.008	0.13	25.38	0.03
	Clustered burrows (CLU2)	Exponential	0.03	0.04	0.28	24.54	0.05
NO ₃	Off-burrow	Spherical	0.09	0.15	0.38	19.59	0.36
	Isolated burrows	Gaussian	0.14	0.15	0.04	14.16	0.37
	Clustered burrows	J-Bessel	0.40	0.94	0.58	5.34	0.93
K	Off-burrows	Gaussian	2.13	4.37	0.51	38.39	0.52
	Isolated burrows	J-Bessel	3.91	7.97	0.51	5.13	8.45
	Clustered burrows	J-Bessel	15.81	25.58	0.38	27.07	9.55

Fig. 8 Spatial distribution of soil nutrient properties across the off-colony plot, the isolated-burrows plot, and the clustered-burrows plot based on interpolation with the best-fit semivariograms. Circles indicate the positions of mounds



occur until multiple disturbance patches overlap within the landscape (Figs. 4, 5, 6). In a simulated landscape, Moloney and Levin (1996) noted that the configuration of disturbance patches had a minor effect on the number of species present. This conclusion most likely arose because they ignored the emergent property when individual disturbance patches are overlapped; that is, they only considered the presence or absence of disturbance.

In accordance with our prediction, clustered burrows increased the spatial heterogeneity of vegetation by permitting the coexistence of several communities with various disturbance-tolerance levels. Various disturbance regimes divided areas into several floristic communities, corresponding with the disturbance magnitude (Figs. 4, 5, 6). For example, areas that experienced infrequent disturbance (A in Fig. 1) were dominated by *S. krylovii*, considered to be the Mongolian grassland species with the weakest tolerance of disturbance (Van Staalduijn and Werger 2007; Van Staalduijn et al. 2007). Those areas that experienced frequent disturbance (B in Fig. 1) were covered by *Potentilla acaulis* and *Potentilla bifurca* (Rosaceae). Previous studies indicated that *Potentilla* coverage increases with moderate grazing due to the plants' prostrate growth form in semiarid grasslands

of eastern Asia (Hilbig 1995; Liu et al. 2007). Finally, the most frequently disturbed areas (C in Fig. 1) were covered by *A. splendens* or *Urtica angustifolia*, which contributed to greater spatial heterogeneity in plots with clustered marmot burrows.

An *A. splendens* community was emergent among the clustered burrows but not on the isolated burrows, indicating that this species can adapt to frequent disturbance (Figs. 4, 5, 6). Unlike other species, *A. splendens* could adapt to fluctuating ground water levels under the clustered burrows. Clustered burrows can capture run-off from the upper mountain areas, resulting in temporal floods below the burrows, as tunnels connect the burrows underground. In arid environments, dense burrows dug by small mammals lead more water to deeper positions of the soil profile (Laundre 1993; Boeken et al. 1998). *Achnatherum splendens* tussocks grow on terraces in valleys and on the sides of banks and ridges along high-elevation streams and rivers, all of which experience such fluctuating ground water levels (Van Staalduijn 2005). Another reason that *A. splendens* was able to become established on the clustered burrows is due to the species' high resistance to grazing. Because of its hard leaves, *A. splendens* is unpalatable to grazers most of the year, except to horses, and thus would be

expected to increase in relative cover on heavily grazed sites (Fernandez-Gimenez and Allen-Diaz 2001). Further, this grass roots can reach depths of 1.6–2.0 m and can thus access deep water, including phreatic water. Hence, this might help *A. splendens* avoid the unfavorable condition of local salt accumulation derived from the sediments left after evaporation of urine in the topsoil (Pasturage and Veterinary Department of Agricultural Ministry of China 1996). *Urtica angustifolia* was also found only in the frequently disturbed area among the clustered burrows (Fig. 4). In a study of *Urtica dioica*, Teckelmann (1987) noted that its growth, development, and distribution are mainly dependent on high nutrient availability, such as is found in floodplains. This species also prefers elevated places on depressions where flooded conditions commonly prevail but no long-term flooding occurs (Srutek 1993, 1997).

Although there were no differences in soil nutrient properties between the off-colony and isolated-burrows plots, a marked difference was found between the isolated-burrows and clustered-burrows plots (Table 1, Fig. 8). Thus, isolated marmot burrows do not provide a degree of disturbance significant enough to affect soil properties, and the small amount of nutrients left in soils may have been absorbed by plants. In contrast, large patches of bare ground occurred near the clustered burrows due to frequent disturbance by marmots. Therefore, when marmots excrete dung or urine on these bare patches, high nutrient concentrations would remain in soils without significant absorption by plants. In other grassland systems, the spatial heterogeneity of soil nutrients is primarily associated with the presence or absence of bunchgrass (Gibson 1988; Canals et al. 2003). Figure 7 indicates that there is spatial dependence at smaller spatial scales than what can be detected with this sampling design and at larger spatial scales than what can be detected with the total plot size used.

In the clustered-burrows plot, the spatial patterns differed among the three soil nutrients measured in this study (Fig. 8), which can be attributed to differences in uptake rates by plants (Bachand and Horne 2000; Reilly et al. 2000) or diffusion rates in soil. Highly heterogeneous, large patches of TN and K likely reflect the places where these substances were excreted by marmots (Van Staaldin and Werger 2007). In contrast, the complex mosaic of $\text{NO}_3\text{-N}$ patches likely reflects the spatial distribution

of patches of bare ground and vegetation. Indeed, those patches with lower levels of $\text{NO}_3\text{-N}$ near the clustered burrows had relatively abundant plant coverage above them. Previous studies indicated that prairie dog colony sites exhibited greater net mineralization rates than sites away from the colony, leading to enhanced inorganic nitrogen (Holland and Detling 1990; Fahnestock and Detling 2002). However, the higher inorganic nitrogen concentration (e.g., $\text{NO}_3\text{-N}$) in soil is absorbed by plants, resulting in lower concentrations in soil. Alternatively, soluble $\text{NO}_3\text{-N}$ moves more rapidly than TN in soil (leaching) because it has no significant attachment to soil solids. The coarser particles and related large macropores in the mound soil as a result of burrowing may have accelerated vertical motion of $\text{NO}_3\text{-N}$ (Bundy et al. 1994; Sherrod and Seastedt 2001).

Overhunting has caused a sharp decline of Siberian marmot populations in Mongolia (Adiya 2000; Wingard and Zahler 2006), resulting in greater isolation of their burrows. Although it was unknown what process causes their burrows to be either clustered or isolated on the landscape, the clustered burrows were often observed in highly populated areas. In unprotected areas outside the HNP, the fraction of clustered burrows was lower than inside the park (38% inside, 17% outside). Numerous studies have shown that, in general, spatial heterogeneity is positively correlated with biodiversity (Huston 1994; Tews et al. 2004). Thus, through their direct and indirect effects on spatial heterogeneity of plant communities, marmot colonies are affecting biodiversity numerically (Yoshihara et al. 2009) or spatially (Fig. 3). Of the novel plant communities, *A. splendens* can make a strong contribution to biodiversity, especially due to its complex physical structure. Therefore, we caution that the isolation of marmot burrows that results from continued overhunting will deteriorate this animal's positive ecological roles in the grasslands of Mongolia.

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