Running title: Effect of disturbance on heterogeneity

Effects of disturbance by Siberian marmots (*Marmota sibirica*) on spatial heterogeneity of vegetation at multiple spatial scales

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Abstract

An understanding of the relationship between vegetation spatial heterogeneity and disturbance and its application to the management are important for maintaining biodiversity and functions of ecosystems. We examined the effects of disturbance by Siberian marmots on the spatial heterogeneity of vegetation at three spatial scales (fine, intermediate, coarse) in a Mongolian grassland. We established a 50 m × 50 m plot around 5 marmot mounds and another plot in an area with no mounds. Each plot was subdivided into 625 adjacent 4-m^2 square quadrats and the plants in them were surveyed. Spatial heterogeneity was calculated as the mean dissimilarity in species composition among sample quadrats in each plot. The off-colony plant community was dominated by graminoids, but a variety of plants, including graminoids, forbs and shrubs, were present in the on-colony plot. The slightly greater fine-scale heterogeneity in the on-colony plot compared to the off-colony plot reflected the presence of either disturbed or undisturbed patch within a single measurement unit, whereas the lower coarse-scale heterogeneity in the on-colony plot reflected the presence of both disturbed and undisturbed patches within a single measurement unit. Our results demonstrate the possibility of using the marmot as a conservation tool in our study site as far as a plant biodiversity is targeted.

Key-words: Ecosystem engineer; Mongolia; grasslands; on-colony; off-colony**.**

Introduction

Theoretical and empirical studies have shown that spatial heterogeneity is a major driver of species diversity in communities (Huston 1994; Tilman 1999; Moreno-Rueda and Pizarro 2007). Most papers have reported a positive relationship between habitat heterogeneity and biodiversity (Wright *et al.* 1993; Huston 1994; Williams *et al.* 2002; Tews *et al.* 2004); for example, because more heterogeneity is equivalent to more niches, it allows more species to coexist (Connell 1975; Rosenzweig 1995). Thus, from a management viewpoint, optimization of heterogeneity has been acknowledged as an effective approach to maintain high species richness, and consequent healthy ecological functioning (Lovett *et al.* 2005).

A primary driver of heterogeneity is disturbance (Levin 1992; White and Jensch 2001). Disturbance can be caused by natural disasters such as fire or hurricanes, or by organisms through ecosystem engineering (Jones *et al.* 1994). By their physical disturbances, ecosystem engineers act as key sources of heterogeneity in a variety of systems (Jones *et al.* 1997). However, despite the importance of animal-created spatial heterogeneity, the role of organisms in maintaining spatially heterogeneous landscapes has been less extensively studied (Turner 2005) than the role of natural disasters (Turner *et al.* 1997a; Turner *et al.* 1997b; Foster *et al.* 1998).

In grasslands throughout the world burrowing rodents play many important roles, such as creating shelter for other species of animals, acting as food resources for predators (Kotliar *et al.* 1999), facilitating nutrient cycling in the soil (Holland and Detling 1990; Sherrod and Seastedt 2001), and altering plant communities and biomass (Coppock *et al.* 1983; Guo 1996). Consequently, these animals have been used as conservation tools for maintaining sustainable grassland ecosystems (Smith and Foggin 1999; Hoogland 2006).

The Siberian marmot (*Marmota sibirica*) has been identified as a keystone species in Mongolia (Zahler *et al.* 2004); however, little is known about some of its ecological roles; in particular in creating spatial heterogeneity at the landscape scale. The types of vegetation that grow on the mounds created by Siberian marmots can differ greatly from that on the surrounding, comparatively homogeneous, grasslands, which are dominated by a few species of graminoids (Van Staalduinen and Werger 2007). This characteristic vegetation on mounds is in stable condition as far as the mounds have been used by them. Marmots modify the soil's physical and chemical properties through activities such as burrowing, grazing, and urinating, thereby affecting the distribution of plant species; this is an example of ecosystem engineering (Van Staalduinen and Werger 2007).

Our aim was to examine the effects of marmot disturbance (burrowing and grazing)

on spatial heterogeneity of vegetation. Generally, it is believed that the effect of grazing on the spatial distribution of vegetation is scale-dependent (Adler *et al.* 2001). Collins and Smith (2006) showed that bison consistently decreased spatial heterogeneity at three different spatial scales, but the prairie dog and vole increased spatial heterogeneity (Davidson and Lightfoot 2006; Questad and Foster 2007). These results also imply that the effect of grazing is dependent on the type of herbivore. The lack of information about the effect of various types of herbivores on spatial heterogeneity at multiple spatial scales has restricted our understanding of the mechanisms by which such heterogeneity occurs. We therefore examined the effects of the marmot disturbance on spatial heterogeneity at three spatial scales. We also explored the ecological roles of the marmot and its potential conservation.

Material and methods

Study areas

We selected study sites in Hustai National Park (HNP), 100 km west of Ulaanbaatar (47º50′N, 106º00′E, elevation 1100–1840 m). Hustai National Park receives an average annual precipitation of 232 mm and occupies approximately 600 km^2 of the forest steppe region of Mongolia. The average annual temperature is 0.2°C. Average monthly

temperatures vary greatly between –23 °C in January (coldest month) and +20 °C in July (hottest). 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 vegetation is dominated by *Stipa krylovii*, *Agropyron cristatum*, and *Artemisia frigida*. In 1998, the overall marmot density in HNP was 1.16 per ha (Takhi Reintroduction Center 1998). Marmots largely forage close to their burrows on alert for predators. Siberian marmots feed on 60 to 80 species of plants (Adiya 2000), but various young and juicy grasses predominate in their diet. They prefer to eat seeds, shoot and flower buds. Livestock have been excluded from HNP core areas for conservation purposes since 1992. Thus HNP seems to be a suitable site for detecting the effect of marmots disturbance (burrowing and grazing) on grasslands.

Sampling design

Our field surveys were conducted in July and August 2007. We established a 2500 m^2 (50 m × 50 m) plot without marmot burrows (off-colony), and a same-sized plot including five burrows (on-colony). We found marmots and their fresh scats within the on-colony, but neither of them within the off-colony. Each plot was subdivided into 625 adjacent 4 m^2 (2 m × 2 m) square quadrats (total investigated = 1250). The plots were separated by at least 500 m, but were within the same landscape and the same soil type.

In each 4 m^2 quadrat, we recorded the area of ground covered by each species by using a modified Daubenmire percent cover scale (Daubenmire 1959; Collins and Smith 2006).

Because marmots in our study sites largely foraged within 20m of their own burrows (Buuveibaatar *et al.*, unpublished data), our extent size (2500-m^2) was needed at least for reflecting the effects of grazing by them at colony scale. And also, because marmots constructed circular mounds with radius approximately 2m, our grain size (4-m^2) was needed at most for reflecting the effects of burrowing by them. In addition, to detect a spatial pattern and to improve the accuracy of analysis, we used adjacent quadrates. As the results, we could not obtain enough landscape replications for constraint of fieldwork.

Data analysis

To compare plant community composition between off-colony and on-colony plots, we calculated for each quadrat the frequency of each species, the mean cover scale values of each species, the coefficient of variation of the cover scale value of each species, and the number of species. The average number of total cover scale value per quadrat was obtained by adding the mean cover scale values of each species.

Spatial heterogeneity 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 Euclidian distance (ED) index for quantitative measurement of heterogeneity: a greater value of the index indicates higher spatial 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 different spatial scales: fine (4 m^2), intermediate (16 m^2), and coarse (100 m^2). For spatial heterogeneity at intermediate and coarse scales, we averaged species abundances among the 4 (2 × 2) and 25 (5 × 5) adjacent quadrats in each plot, respectively. We defined one quadrat at fine scale, the 4 adjacent quadrats at intermediate scale and the 25 adjacent quadrats at coarse scale as a unit, respectively. We calculated the average Euclidian value of all possible pairwise comparison of the units within each plot at fine scale (N=195000), intermediate scale (N=10296), and coarse scale (N=300). We further calculated the Euclidian value of a given unit in each plot as the average value of its pairwise comparisons with all the other units at a fine scale (N=624), at an intermediate scale (N=143), and at a coarse scale (N=24) within the plot. We compared the mean differences of ED between plots instead of statistical analysis.

Results

Plant community

Twenty-eight plant species were recorded in the off-colony plot and 40 in the on-colony plot (Table 1). The average number of plant species per quadrat was 7 in the off-colony plot and 9 in the on-colony plot. Among the 12 most abundant species, 4 (*Stipa krylovii*, *Kochia prostrata*, *Elymus chinensis* and *Cleistogenes squarrosa*) had greater average cover scale values in the off-colony plot than in the on-colony plot (Table 1). Three of these four species are graminoids. All the forbs and shrub species among the abundant species had greater average cover scale values in the on-colony plot than in the off-colony plot. All of the 14 species recorded in only the on-colony plot were forbs. The average number of total cover scale value per quadrat was 11.34 in the off-colony plot and 13.60 in the on-colony plot.

Spatial heterogeneity

The effect of marmots on spatial heterogeneity varied at different spatial scales (Figure 1). At a fine scale, the mean Euclidian distance of all possible pairwise comparison of units was 3.453 in the off-colony plot and 3.564 in the on-colony plot; at an intermediate scale, the mean Euclidian distance was 2.301 in the off-colony plot and 2.265 in the on-colony plot; and at a coarse scale, the mean Euclidian distance was 1.778 in the off-colony plot and 1.437 in the on-colony plot. At a fine scale the

Euclidian distance was high on the marmot burrows (mean Euclidian distance = 4.520, Figure 2). Large, clustered, heterogeneous patches were apparent in the off-colony plot at fine and intermediate scale. On the contrary, the highly heterogeneous patches were more scattered in the on-colony plot and were more numerous at a fine scale (mostly 1 to 4 quadrats) than at a coarse scale, where the highly heterogeneous patches disappeared.

Discussion

Mounds created by the Siberian marmot can be categorized according to the plant communities present on them, which represent vegetational succession in the following order: *Artemisia adamsii*, *E. chinensis*, and then *S. krylovii* communities (Van Staalduinen and Werger 2007). These three types of communities were recorded consistently in the on-colony plot, but the lack of *A. adamsii* in the off-colony plots (Table 1) indicates that the marmots maintained a mosaic of vegetational communities from various successional stages as a result of their disturbance of the grassland (Johnson and Cushman 2007). This phenomenon, i.e., higher diversity at the on-colony plot, could be explained by the intermediate disturbance hypothesis (Connell 1975; Begon *et al.* 1996). Because marmots in this park rarely construct new burrows (i.e.

continue to use same burrows for a long time) (Yoshihara *et al*., unpublished), the "disturbance" here means selective foraging and burrow maintenance.

Our results are not consistent with those of several studies that reported constant decrease in the spatial heterogeneity of vegetation as a result of grazing by herbivores at a fine scale (Glenn *et al.* 1992; Adler and Lauenroth 2000; Collins and Smith 2006). One possible reason for this difference in results is that the marmot's typical disturbance patch is smaller than those of livestock or bison. Cattle collect grass by using the tongue and have a mean bite area of up to 207 cm^2; the mean dung pat is about 30 cm in diameter, and the trampled ground within the hoof imprint is about 85 cm^2 (Ssemakula 1983; Dai 2000; Hongo and Akimoto 2003); our observations suggest that these disturbance patches created by cattle are likely to be bigger than the disturbance patches created by marmots. In the Chihuahuan Desert, the kangaroo rat and prairie dog have created a unique plant community because of the different sizes of their disturbance areas (Davidson and Lightfoot 2006). Therefore, the increase in spatial heterogeneity at a fine scale in our results may reflect the detecting their typical disturbance at this scale (4 m^2). Because of differences in the disturbance regime among species, when we judge the effect of disturbance on spatial heterogeneity, we should think not only in terms of the scale, but also in terms of the species of herbivore (i.e. size of herbivore).

The presence of the marmots decreased average value of spatial heterogeneity at a

coarse scale (Figure 1). Their disturbance may have reduced the contrast between quadrats or destroyed the inherent structural complexity among quadrats, resulting in homogenization. On the Mongolian steppe, as in other arid ecosystems, vegetation such as *Caragana microphylla* and *E. chinensis* is organized in patchy structures because of its rhizomatous life form. Each of these species grew as a large patch in the off-colony plot (corresponding to the highly heterogeneous patch shown in the lower part of Figure 2) which became smaller and more scattered in the on-colony plot. The homogeneity of the on-colony plot at the coarse scale would be explained by the inclusion of both disturbed and undisturbed patches in each measurement unit. Indeed, the fine mosaic structure of the various heterogeneous areas at a fine scale in the on-colony plot supports this hypothesis (Figure 2). Van Staalduinen *et al.* (2007) found that marmot grazing replaced large patches of bunch grass with smaller patches of them. And Seifan and Kadmon (2006) showed that intense cattle grazing reduced the clump of the dense vegetation and generated a more random pattern of shrub distribution.

Adler *et al.* (2001) hypothesized that the effect of grazing on vegetational heterogeneity depends on the interaction between the spatial distribution of grazing and the preexisting vegetational heterogeneity. If the spatial heterogeneity of grazing is stronger than the spatial heterogeneity of vegetation (referred to as "patch grazing"), then the spatial heterogeneity of the vegetation will increase following grazing. In

contrast, if the spatial heterogeneity of grazing is weak relative to the spatial heterogeneity of vegetation, then the spatial heterogeneity will decrease following grazing, which is then referred to as “homogeneous grazing”. Thus, at our site the patch-grazing scenario was played out at a fine scale, and the homogeneous grazing scenario was played out by the marmot at a coarse scale. This is because although the marmots could be selective in their choice of plant species at a fine scale (Adiya 2000), at a coarse scale the existence of predators regulated against selectivity of food choice in the grazing areas around their burrows (Holmes 1984). At our site, both the patchy and homogeneous grazing scenarios would have been occurring simultaneously at nested spatial scales.

Although our results of spatial heterogeneity have no landscape replications, the results demonstrate the possibility of using the marmot as a conservation tool of plant species in this site at this normal population density. Marmot disturbance allowed, without loss of plant abundance, the persistence of fugitive forb species that otherwise would have been excluded by late-successional dominant plants such as perennial grasses (Table 1). However, if marmots were locally overpopulated, rangeland productivities would decrease through increase of unpalatable species for livestock (e.g. *Saussurea salicifolia* in Table 1) or soil erosion. In our observations, not only plants, but also insects such as grasshoppers, bees, and beetles, were indirectly influenced by the

disturbance created by marmots on the Mongolian steppe; indeed, the biodiversity of pollinators was higher in plots that included marmot burrows and it may be attributable to the positive correlation with increase in the spatial heterogeneity of vegetation at fine scale (Yoshihara *et al*., unpublished). Therefore, protection of the Siberian marmot as a keystone species may enrich the local flora and fauna as far as the animal species are fond of higher spatial heterogeneous landscape at fine scale.

In Mongolia, the total population size of Siberian marmots has decreased sharply, from 40 million to 10 million in the last 60 years, because of overhunting (Adiya 2000; Wingard and Zahler 2006). Thus the decline would have been accompanied by a decline in the positive ecological roles of the marmot, which is problematic from a conservation perspective. We conclude that marmot disturbance affects the spatial heterogeneity of vegetation at coarse spatial scale by maintaining the mosaic structure of graminoids and forbs or by modifying patch structure. The generality of scale dependency of spatial heterogeneity by grazing can be explained by relative relationships between disturbance size and measurement scale.

Acknowledgments

We thank the project members for their kindness in helping with the field survey, and

especially J. Undarmaa, Mongolian State University of Agriculture and T. Okayasu, University of Tokyo. Thanks to the staff at Hustai National Park for all their help during the study, and to S. Takatsuki, Azabu College, and A. Campos Areceiz, University of Tokyo, for providing instructions in the fields and comments on our manuscript. This work was carried out under support from the Global Environmental Research Fund of Japan's Ministry of the Environment.

References

Adiya Y (2000) *Mongolian Marmots: Biology, Ecology, Conservation, and Use* (In Mongolian). Mammalian Ecology Laboratory, Institute of Biological Sciences, Mongolian Academy of Sciences, Mongolia.

Adler PB, Lauenroth WK (2000) Livestock exclusion increases the spatial heterogeneity of vegetation in the shortgrass steppe, Colorado. *Appl Veg Sci* 3: 213-222.

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479.

Begon M, Harper JL, Townsend CR (1996) *Ecology: Individuals, Populations and Communities*. Blackwell Science, London.

Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: *Ecology and Evolution of Communities.* (eds Cody ML, Diamond JM), Belknap, Cambridge, MA, 460–490.

Coppock DL, Detling JK, Ellis JE, Dyer MI (1983) Plant–herbivore interactions in a North-American mixed-grass prairie. 1. Effects of black-tailed prairie dogs on intraseasonal above-ground plant biomass and nutrient dynamics and plant-species diversity. *Oecologia* 56: 1–9.

Collins SL, Smith MD (2006) Scale-dependent interaction of fire and grazing on

community heterogeneity in tallgrass prairie. *Ecology* 87: 2058–2067.

Dai XB (2000) Impact of cattle dung deposition on the distribution pattern of plant species in an alvar limestone grassland. *J Veg Sci* 11, 715–724.

Daubenmire R (1959) A canopy-coverage method of vegetational analysis. *Northwest Sci* 33: 43-66.

Davidson AD, Lightfoot DC (2006) Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* 295: 755–765.

Foster DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1: 497–510.

Glenn SM, Collins SL, Gibson DJ (1992) Disturbances in tallgrass prairie: local and regional effects on community heterogeneity. *Landscape Ecol* 7: 243-251.

Guo QF (1996) Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia* 1062, 247–256.

Holland EA, Detling JK (1990) Plant-response to herbivory and belowground nitrogen cycling. *Ecology* 713: 1040–1049.

Holmes WG. (1984) Predation risk and foraging behavior of the Hoary Marmot in Alaska. *Behav Ecol Soci* 15: 293–301.

Hongo A, Akimoto M (2003) The role of incisors in selective grazing by cattle and

horses. *J Agr Sci* 140: 469–477.

Hoogland JL (2006) *Conservation of the Black-tailed Prairie Dog: Saving North America's Western Grasslands*. Island Press, USA.

Huston MA (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, UK.

Johnson BE, Cushman JH (2007) Influence of a large herbivore reintroduction on plant invasions and community composition in a California grassland. *Conserv Biol*. 21: 515–526.

Jones CG., Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69: 373–386.

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957.

Kotliar NB, Baker BW, Whicker AD, Plumb G (1999) A critical review of assumptions about the prairie dog as a keystone species. *Environ Manage* 24: 177–192.

Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.

Lovett GM, Jones CG., Turner MG., Weathers KC (2005) *Ecosystem Function in Heterogeneous Landscapes*. Springer, USA.

Moreno-Rueda G., Pizarro M (2007) The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain. ***Acta Oecol*** 32: 50-58.

Questad EJ, Foster BL (2007) Vole disturbances and plant diversity in a grassland metacommunity. *Oecologia* 153: 341–345.

Rosenzweig ML (1995) Species Diversity in Space and Time. Cambridge University, UK.

Seifan M, Kadmon R (2006) Indirect effects of grazing on shrub spatial pattern in a mediterranean scrub community. *Basic Appl Ecol* 7: 496-506.

Sherrod SK, Seastedt TR (2001) Effects of the northern pocket gopher *Thomomys talpoides* on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry* 552: 195–218.

Smith AT, Foggin JM (1999) The plateau pika *Ochotona curzoniae* is a keystone species for biodiversity on the Tibetan plateau. *Anim Conserv* 2: 235–240.

Ssemakula J (1983) A comparative study of hoof pressures of wild and domestic ungulates. *Afr J Ecol* 21: 325–328.

Takhi Reintroduction Centre (1998) *Inventories and monitoring at Hustain Nuruu National Park.* Mongolian Association for Conservation of Nature and the Environment, Internal report.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31: 79– 92.

Tilman D (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80: 1455–1474.

Turner MG., Dale VH, Everham EH (1997a) Fires, hurricanes, and volcanoes: Comparing large disturbances. *Bioscience* 47: 758-768.

Turner MG, Romme WH, Gardner RH, Hargrove WW (1997b) Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* 67: 411-433.

Turner MG. (2005) Landscape ecology: what is the state of the science? *Ann Rev Ecol Sys* 36: 319–344.

Van Staalduinen MA, Werger MJA (2007) Marmot disturbances in a Mongolian steppe vegetation. *J Arid Environ* 69: 344–355.

Van Staalduinen MA, During H, Werger MJA (2007) Impact of grazing regime on a Mongolian forest steppe. *Appl Veg Sci* 10: 299–306.

Wallis de Vries MF, Manibazar N, Dügerlham S (1996). The vegetation of the forest-steppe region of Hustain Nuruu, Mongolia. *Vegetatio* 122: 111–127.

White PS, Jensch A (2001) The search for generality in studies of disturbance and

ecosystem dynamics. *Progr Bot* 62: 399–449.

Williams SE, Marsh H, Winter J (2002) Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rainforest. *Ecology* 83: 1317–1329.

Wingard JR, Zahler P (2006) *Silent steppe: the illegal wildlife trade crisis in Mongolia: Mongolia discussion papers*, East Asia and Pacific environment and social development department. World Bank, USA.

Wright DH, Currie DH, Maurer DJ (1993) Energy supply and patterns of species richness on local and regional scales. In: *Species Diversity in Ecological Communities: Historical And Geographical Perspectives*. (eds Ricklefs RE, Schluter D), University of Chicago Press, Chicago, USA, 66–74.

Zahler P, Lhagvasuren B, Reading RP, Wingard JR (2004) Illegal and unsustainable wildlife hunting and trade in Mongolia. *Mongol J Biol Sci* 21: 23–31.

Figure legends

Figure 1 Spatial heterogeneity of plant species in each plot at three spatial scales. Left bar: off-colony plot; right bar: on-colony plot. Heterogeneity was calculated all possible pairwise comparisons of the units within one plot and then averaged. Bars show the standard error.

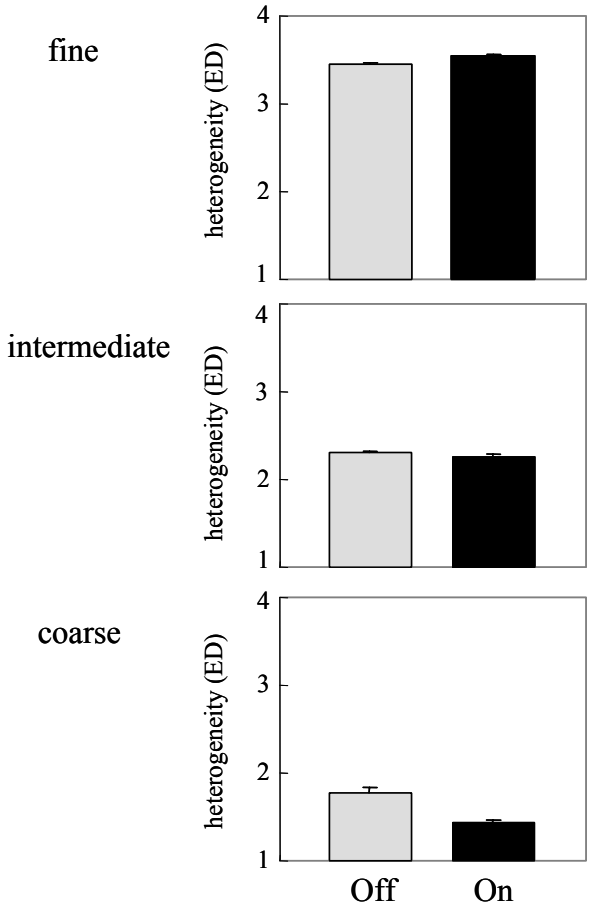
Figure 2 Spatial heterogeneity of plant species and marmot mounds (○) in the off-colony plot, left column, and on-colony plot, right column, at three spatial scales. The Euclidian value of a given unit (grid) in each plot was calculated as the average value of its pairwise comparisons with all the other units within the plot. Darker color indicates higher heterogeneity. Smaller plot size at the intermediate scale, 48 m × 48 m, results from exclusion of the outermost lines of quadrats from the calculation.

Table 1 Frequency of occurrence, mean percent cover scale value, and coefficient of variation (CV) of percent cover scale value of species associated with off-colony and on-colony plots

Species		Off-colony			On-colony		
		Freq-uency	Cover value	CV	Freq-uency	Cover value	CV
Stipa krylovii Roshev.	G	625	3.42	0.21	625	3.29	0.20
Allium bidentatum Fisch. ex Prokh.	F	400	0.84	0.89	552	1.20	0.55
Caragana pygmaea (L.) DC.	S	396	0.73	0.89	513	0.89	0.55
Kochia prostrata (L.) Schrad.	F	371	0.93	0.99	60	0.11	3.31
Elymus chinensis (Trin.) Keng	G	363	0.87	1.07	167	0.35	1.84
Carex korshinskyi Kom.	G	360	0.60	0.90	437	0.81	0.89
Artemisia frigida Willd.	F	347	1.15	1.04	614	2.47	0.36
Agropyron cristatum (L.) P.B.	G	340	0.67	1.04	445	0.92	0.78
Cymbaria dahurica L.	F	267	0.46	1.22	286	0.50	1.16
Poa attenuata Trin.	G	254	0.42	1.24	244	0.46	1.36
Caragana microphylla (Pall.) Lam.	S	230	0.49	1.50	291	0.62	1.22
Cleistogenes squarrosa (Trin.) Keng.	G	214	0.41	1.51	35	0.06	4.17
Astragalus sp.	F	56	0.09	3.19	150	0.24	1.80
Iris tigridia Bge.	F	44	0.07	3.64	143	0.23	1.85
Bupleurum bicaule Helm.	F	39	0.06	3.93	65	0.11	3.05
Goniolimon speciosum (L.) Boiis.	F	13	0.02	6.87	12	0.02	7.16
Koeleria macrantha (Ldb.) Schult.	F	10	0.02	7.85	20	0.03	5.63
Potentilla bifurca L.	F	8	0.01	9.17	33	0.06	4.50
Polygonum angustifolium Pall.	F	8	0.01	8.79	8	0.01	8.80
Haplophyllum dauricum (L.) G. Don.	F	7	0.01	9.40	120	0.20	2.09
Saussurea salicifolia (L.) DC.	F	5	0.01	11.14	121	0.23	2.18
Potentilla conferta Bge.	F	4	0.01	12.47	23	0.04	5.42
Amblynotus rupestris Pall.	F	3	0.00	14.41	3	0.00	14.42
Silene repens Patr.	F	3	0.00	14.41	3	0.00	14.42
Chenopodium album L.	F	2	0.00	17.66	16	0.03	6.51
Sibbaldianthe adpressa (Bge.) Juz.	F	1	0.00	25.00	28	0.05	4.70
Stellaria dichotoma L.	F	1	0.00	25.00	28	0.04	4.63
Serratula centauroides L.	F	1	0.00	25.00			
Convolvulus ammanii Desr.	F	1	0.00	25.00			
Pulsatilla ambigua (Turcz. ex Hayek) Juz.	F				190	0.34	1.62

Pedicularis flava Pall.	F	77	0.13	2.76
Ptilotrichum canescens C.A. Mey.	F	42	0.07	3.78
Artemisia adamsii Bess.	F	12	0.04	7.71
Potentilla acaulis L.	F	6	0.01	10.17
Thermopsis dahurica Czefr.	F	4	0.01	12.48
Artemisia glauca Pall.	F	4	0.01	13.21
Lepidium densiflorum Schrad.	F	3	0.00	14.42
Thalictrum squarrosum Steph. ex Willd.	F	3	0.00	14.42
Ephedra monosperma G.G. Gmel. ex C.A.	F	2	0.00	17.68
Heteropappus biennis (Ldb.) Tamamsch.	F	1	0.00	25.02
Artemisia dracunculus L.	F	1	0.00	25.02
Medicago lupulina L.	F	1	0.00	25.02
Scutellaria scordifolia Fisch. ex Schrank.	F	1	0.00	25.02

The area of ground covered by each species was recorded by using a percent cover scale: 0, absent; 1, <1%; 2, 2–5%; 3, 6–25%; 4, 26–50%; 5, 51–75%; 6, 76–95%; 7, >95%. Letters following each species name signify graminoid (G), forb (F) or shrub (S).



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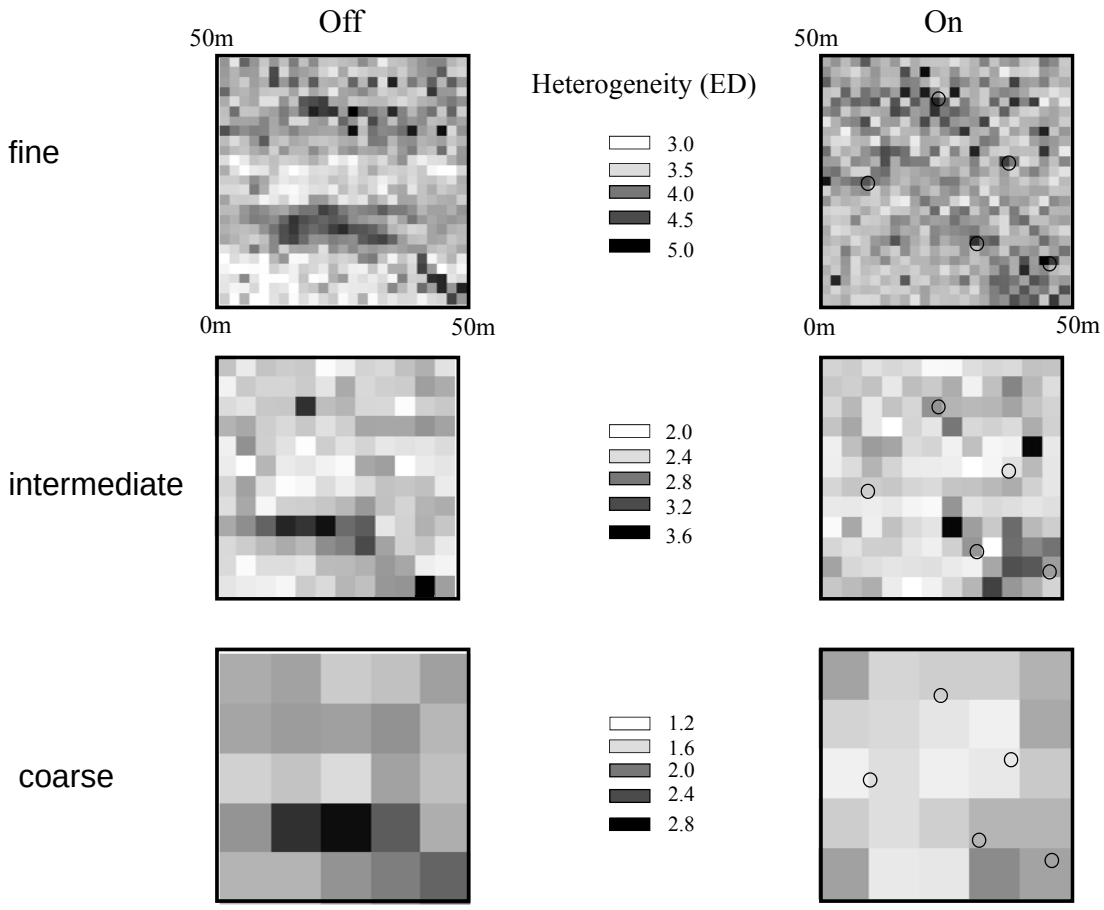

Yoshihara et al. Figure 2