Agriculture, Ecosystems and Environment 135 (2010) 155–159

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Short communication

Complementary effects of disturbance by livestock and marmots on the spatial heterogeneity of vegetation and soil in a Mongolian steppe ecosystem

Yu Yoshihara [a,*], Toshiya Okuro [a], Bayarbaatar Buuveibaatar [b], Jamsran Undarmaa [c], Kazuhiko Takeuchi [a]

[a] School of Agriculture and Life Sciences, The University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo 113-8023, Japan
[b] Institute of Biology, Mongolian Academy of Sciences, Ulaanbaatar 51, Mongolia
[c] Center for Ecosystem Study, Mongolian State University of Agriculture, Ulaanbaatar 210153, Mongolia

ARTICLE INFO

Article history:
Received 20 April 2009
Received in revised form 11 September 2009
Accepted 15 September 2009
Available online 3 October 2009

Keywords:
Grazing
Mongolian steppe
Multiple spatial scales
Degradation-indicator species
Ecosystem engineers

ABSTRACT

In the Mongolian steppes, livestock and burrowing rodents are the main animal modifiers of the habitat. Although grazing lands and rodent habitats overlap, the combined effects of livestock and rodent disturbance on spatial heterogeneity of plants and soil have rarely been evaluated. We established study plots at each of four sites: sites heavily grazed by livestock, with and without marmots, and ungrazed sites, with and without marmots. We subdivided each plot into quadrats to survey the plant species composition and soil nutrient properties, and calculated the spatial heterogeneity of vegetation at three spatial scales using non-metric multidimensional scaling analysis. We also calculated the coefficient of variance among the soil samples. The vegetation's spatial heterogeneity did not differ significantly between grazed and ungrazed plots; however, it was higher under marmot disturbance than in the absence of marmots at a fine scale, but lower under marmot disturbance at a coarse scale, irrespective of livestock grazing. At a fine scale, unique habitats were formed by each combination of livestock grazing (presence/absence) and marmots (presence/absence). In addition, the plant species composition in the grazed plots was distinct from that in the ungrazed plots at the coarser scale. The occurrence of degradation-indicator plant species depended on the presence of grazing rather than on the additive effect of grazing and marmots. Marmots increased the abundance of degradation-indicator species only in the ungrazed plots. Each herbivore group increased the spatial heterogeneity of soil nutrients at coarser scales, but these influences were lost when both herbivore groups coexisted. These results show that the ecological roles of livestock and marmots are complementary, not functionally equivalent. That is, livestock modified the overall vegetation composition, and thereby modified spatial heterogeneity at the landscape scale, whereas marmots modified spatial heterogeneity at the local scale. Proper manipulation of the livestock grazing regime can maintain species-rich communities without serious land degradation in the Mongolian steppe.

1. Introduction

In many countries, intensive agriculture designed to provide high productivity has only temporarily succeeded. Two processes may account for this phenomenon. First, homogenization of the spatial distribution of biological resources caused by agricultural activities can lead to an alarming degradation of biodiversity (Duelli, 1997), particularly where native species are vulnerable to pesticides (Bullock et al., 2001) or vulnerable to weed invasion (Tracy and Sanderson, 2004). Second, there is a time lag in the response of biodiversity to agricultural production (Bullock et al., 2001). Therefore, maintaining biodiversity in agroecosystems is more likely to permit sustainable land use for agricultural activity and sustainable agricultural production.

In Mongolia, almost 75% of grasslands are subjected to livestock grazing (National Scientific Office of Mongolia, 2007). The Mongolian steppe has been used sustainably for grazing for centuries. However, recent increases in livestock populations have been remarkable; for example, the goat population increased from 10.65 million in 2003 to 15.45 million in 2006 (National Scientific Office of Mongolia, 2007). The increasingly heavy grazing of the Mongolian steppes has caused vegetation changes (Sasaki et al., 2008), has weakened the ecosystem's ecological functions by impoverishing the diversity of flowers and pollinators, and consequently their mutual network structure (Yoshihara et al., 2008a), and has elevated the concentrations of soil K and P (Fernandez-Gimenez and Allen-Diaz, 2001). These vegetation changes have constrained the feeding behavior of Mongolian livestock (Yoshihara et al., 2009a), adversely impacted the body condition of sheep (Retzer, 2007), and created the

* Corresponding author. Tel.: +81 03 5841 5052; fax: +81 03 5841 5052.
E-mail address: marmota.sibirica@gmail.com (Y. Yoshihara).

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doi:10.1016/j.agee.2009.09.009

possibility of livestock competing with wildlife for food resources (Campos-Arceiz et al., 2004; Yoshihara et al., 2008b).

Rodents cause significant damage to a range of agricultural crops (Brown et al., 2007), and may have a transformative effect not far behind that of livestock in Mongolia. Burrowing rodents live in colonies in underground galleries and form mounds of about 1 m in diameter and 0.1 m in height at burrow entrances. The animals emerge from burrows to graze on foliage and defecate. Disturbance by rodents increased the abundance of rhizomatous species and fugitive forbs, species richness at a colony scale, nitrogen concentrations in the on-mound vegetation, soil nitrate-nitrogen and soil phosphorus. However, their disturbance has also decreased plant biomass, species richness at the mound scale, standing dead vegetation, the standing crop of vegetation, and the live:dead plant ratio (Retzer, 2007; Van Staalduinen et al., 2007; Van Staalduinen and Werger, 2007; Wesche et al., 2007; Yoshihara et al., 2009b).

Differences in foliage preferences and foraging habits (e.g., radius of activity) between large and small mammals lead to different vegetation structures, vegetation compositions, and soil nutrient properties in vegetation communities inhabited by these animals (Olff and Ritchie, 1998; Rook et al., 2004). In arid grasslands, the coexistence of multiple herbivores often creates unique habitats that differ greatly from those created by a single herbivore (Davidson and Lightfoot, 2006, 2008). This is particularly true in Mongolia because the lands used for grazing livestock and as habitat for rodents such as the Siberian marmot (*Marmota sibirica*) have overlapped in many parts of the country. However, no studies have evaluated the combined effects of livestock and rodent disturbance on spatial heterogeneity of plants and soil in the Mongolian steppe ecosystem.

It is necessary to understand the effects of disturbance on spatial heterogeneity, because spatial heterogeneity is an important characteristic of biodiversity (Huston, 1994) and of grassland degradation, and the role of grazing animals has already been elucidated (Wang et al., 2002; Parsons and Dumont, 2003). Marmots also create spatially heterogeneous grasslands at a fine scale by enhancing the contrast between disturbed and undisturbed patches (Yoshihara et al., 2009b). We thus predicted that the degree to which marmots increase the spatial heterogeneity would be diminished under the influence of simultaneous livestock grazing. In contrast, Retzer (2007) observed that the combined effects of livestock grazing and rodents on phytobiomass or plant height reduction in Mongolian grasslands were greater than where either herbivore group existed alone. Thus, we also predicted that the degree to which the coexistence of livestock and marmots causes habitat degradation would be substantially greater than at sites where either herbivore group exists alone. To test these two predictions, we empirically compared the spatial heterogeneity of plant composition and soil nutrient properties under the influence of livestock and marmots, both individually and together. Based on our results, we discuss how to match the two herbivore groups with the desired Mongolian steppe with regard to increased biodiversity and reduced land degradation.

2. Materials and methods

Our study site was located within Mongolia's Hustai National Park (HNP; 47°50′N, 106°00′E). The annual average temperature is 0.2 °C. The mean annual precipitation in HNP is 232 mm.

2.1. Sampling design

Our field surveys were conducted in July 2008. We established 2500 m^2 (50 m × 50 m) plots that represented the four possible combinations of livestock and marmot pressure: ungrazed by livestock and without marmot burrows (the control), ungrazed and with marmots (the marmot plot), grazed by livestock and without marmots (the livestock plot), and grazed by livestock and with marmots (the livestock and marmot plot). Each plot was subdivided into 625 adjacent 4-m^2 (2 m × 2 m) square quadrats, for a total of 2500 quadrats. The four plots were separated by at least 500 m, but were within the same general landscape (a valley foot slope) and had the same soil type (a Haplic Kastanozem) based on soil profile morphology and physico-chemical properties (FAO/ISRIC/ISSS, 1998). In each 4-m^2 quadrat, we recorded the area of ground covered by each species by using a modified Daubenmire percentage cover scale (Collins and Smith, 2006).

To investigate the soil properties, we extracted 36 core samples (10-cm diameter × 15-cm depth) from 30 m × 30 m areas situated at the centers of each plot, with 5-m spacing between points. At each point, we extracted three core samples (a three-point replication method) and homogenized the samples. In the laboratory, 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 concentration of salicylic acid was used to determine nitrate-nitrogen (NO_3-N), and the Bray and Kurtz method was used to measure potassium (K) (Sparks et al., 1996).

2.2. Data analysis

To quantify the spatial heterogeneity of the vegetation within a plot and compare species composition among the four plots, we performed a non-metric multidimensional scaling ordination (NMDS), which is a robust nonparametric ordination method (Minchin, 1987), using the coverage by each species as the input data. We used the score distribution for the samples and the gradient length in the ordination space for qualitative measurement of heterogeneity: a greater distribution and a longer gradient length indicate higher spatial heterogeneity. We used the PC-ORD software for this analysis (version 4.0; McCune and Mefford, 1999). 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 the spatial heterogeneity at the intermediate and coarse scales, we averaged species abundances among 4 (2 × 2) and 25 (5 × 5) adjacent quadrats, respectively, in each plot.

To compare the plant community composition among the four plots, we used the frequency of each species (i.e., the number of quadrat) in each plot to calculate Shannon's index of diversity ($H = -\sum P_i \ln P_i$, where P_i is the relative abundance of species i), and we observed the frequencies and ranks of plant species that indicate habitat degradation in each plot (i.e., degradation indicators). Whether a species was a degradation indicator was determined according to the criteria of Jigjidsuren and Johnson (2003). The criterion for whether a species is a degradation indicator is whether it is unpalatable for livestock and is observed with increased frequency in places degraded by unsuitable management.

To evaluate the contribution of disturbance by marmots to biodiversity at the broad scale, we used a landscape richness enhancement (LRE) parameter that reflects the degree to which ecosystem engineering has introduced new species into a community (Badano and Cavieres, 2006). This parameter is defined as follows:

$$\mathrm{LRE} = N_s/N_u$$

where N_s represents the number of habitat specialists (i.e., species found only in the engineered patches) and N_u represents the number of species that inhabit unmodified habitats. Thus, LRE will increase as more species become dependent on the environmental changes caused by the ecosystem engineer.

Similar to the vegetation analysis, we evaluated the spatial heterogeneity of the soil at three spatial scales: 25, 100, and 225 m^2. For spatial heterogeneity at the 100 and 225-m^2 scales, we averaged the soil values among four (2 × 2) and nine (3 × 3) adjacent soil samples in each plot, respectively. We defined the one sample at the 25-m^2 scale, the four adjacent samples at the 100-m^2 scale, and the nine adjacent samples at the 225-m^2 scale as a unit in this analysis. We calculated the mean of all samples (N = 36) and coefficient of variation within each plot at the 25-m^2 scale (N = 36 units), the 100-m^2 scale (N = 9), and the 225-m^2 scale (N = 4).

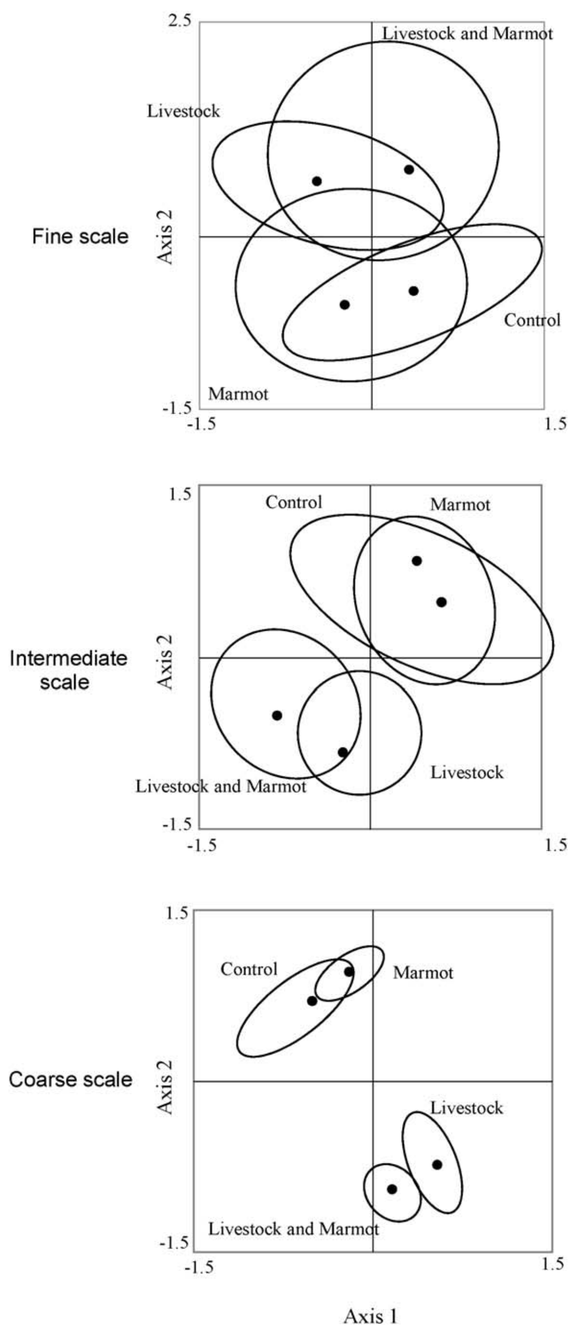

Fig. 1. Results of the NMDS ordination for the four plots at the three spatial scales. The figure visually depicts the responses of plant composition to the different herbivore pressures. Data points represent the mean scores for each plot, and ellipses encompass all samples in the plot.

3. Results

3.1. Spatial heterogeneity of the plants

At the fine scale, the area of the ellipses was larger in the marmot plot and the marmot and livestock plot than in the control plot and the livestock plot (Fig. 1). The mean NMDS scores between the different plots showed relatively clear separation within the ordination space. At the intermediate scale, the areas of the ellipses were comparable among plots. The ellipses for the control plot and the marmot plot overlapped considerably, as did those for the livestock plot and the livestock and marmot plot, but the two groups did not overlap. At the coarse scale, the areas of the ellipses for the marmot plot and the livestock and marmot plot were slightly smaller than those of the control plot and the livestock plot. The relative allocation relationship of the four ellipses at the coarse scale showed similar trends to the ordination results at the intermediate scale; the plant compositions of the control plot and

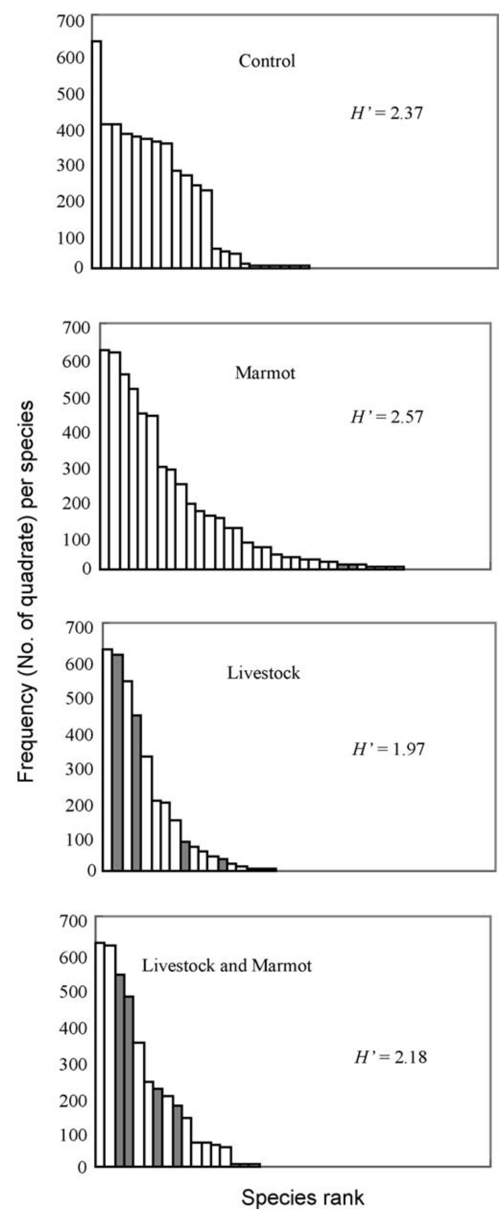

Fig. 2. Rank-frequency distributions for the total community of plants in the four plots. The grey bars represent degradation-indicator species. H' represents Shannon's diversity index.

Table 1
Mean values of the soil nutrient parameters in each plot. TN, total nitrogen; NO_3, nitrate-nitrogen; K, potassium.

Plot	TN (%)	NO_3 (mg/g)	K (mg/g)
Control	0.16	0.62	21.38
Marmot	0.20	0.62	12.52
Livestock	0.20	0.47	133.26
Livestock + marmot	0.21	0.44	99.19

Table 2
Coefficients of variance of the soil nutrient parameters in each plot at three spatial scales. TN, total nitrogen; NO_3, nitrate-nitrogen; K, potassium.

Scale	Plot	TN (%)	NO_3 (mg/g)	K (mg/g)
25 m^2	Control	0.19	0.61	0.43
	Marmot	0.13	0.58	0.15
	Livestock	0.17	0.51	0.45
	Livestock + marmot	0.18	0.36	0.41
100 m^2	Control	0.06	0.32	0.11
	Marmot	0.10	0.37	0.25
	Livestock	0.12	0.36	0.34
	Livestock + marmot	0.08	0.23	0.22
225 m^2	Control	0.08	0.15	0.10
	Marmot	0.11	0.33	0.20
	Livestock	0.11	0.13	0.31
	Livestock + marmot	0.05	0.15	0.07

the marmot plot were strikingly distinct from those of the livestock plot and the livestock and marmot plot. This resulted from the replacement of tall perennial grasses (e.g., *Elymus chinensis* and *Agropyron cristatum*) by degradation-indicator ruderal forbs (e.g., *Artemisia adamsii* and *Chenopodium* spp.) in response to livestock grazing.

Species richness and Shannon's index were highest in the marmot plot due to the variety of species observed in the plot (Fig. 2). However, both parameters were lower under livestock grazing because of a reduction in the number of rare species. Degradation-indicator species were highly placed on the plants list in the livestock plot and the livestock and marmot plot. LRE was 0.48 in the absence of livestock grazing and decreased to 0.00 under livestock grazing, indicating that marmot disturbance did not enhance the number of newly established species under livestock grazing.

3.2. Spatial heterogeneity of the soil

Total soil nitrogen (TN) tended to differ among the four plots (Table 1). For soil NO_3, there was a tendency of higher mean value in the plots with no livestock grazing (the control plot and the marmot plot) than in the plots with livestock grazing. In contrast, soil K tended to have lower mean value in the plots with no livestock grazing. The coefficient of variation exhibited complex patterns (Table 2). At the 100 and 225-m^2 scales, the coefficient of variation with both herbivores groups present was still larger than that in the control, but the combination of the herbivores had a lower coefficient of variation than in the plots with only one herbivore group.

4. Discussion

The influence of herbivore disturbance on spatial heterogeneity and species composition was scale-dependent. Spatial heterogeneity of the vegetation was higher under marmot disturbance at the fine scale, but lower at the coarse scale, irrespective of whether livestock were present (Fig. 1). The spatial heterogeneity of the vegetation subject to livestock grazing did not differ from that in the control at multiple spatial scales. At the fine scale, unique habitats were formed by each combination of livestock (presence/absence) and marmot (presence/absence). However, the species composition changed noticeably in the presence of livestock at the coarse spatial scale. The occurrence of degradation-indicator plant species depended on the presence of livestock grazing rather than on the coexistence of livestock grazing and marmots (Fig. 2).

Livestock grazing had less impact than marmot disturbance on the spatial heterogeneity of vegetation at the fine spatial scale (Fig. 1), but livestock remarkably changed the plant community, independent of disturbance by marmots, particularly because the livestock increased the number of degradation-indicator species (Fig. 2). Livestock grazing distributed the pressure more evenly throughout the plot, whereas marmot disturbance tended to be more concentrated. This might explain why livestock did not increase the spatial heterogeneity of vegetation as much as marmots did at a fine scale, as was reported by Collins and Smith (2006).

The presence of marmots increased spatial heterogeneity of the vegetation at a fine scale, but decreased heterogeneity at a coarse scale, even in the presence of livestock grazing (Fig. 1). This scale dependency may reflect relationships between disturbance size and measurement scale: that is, at a fine scale, each quadrat is more likely to contain only a disturbed patch or an undisturbed patch, whereas at a coarse scale, the larger quadrats are more likely to contain both disturbed and undisturbed patches. Fahnestock and Detling (2002) observed a large impact of colony construction by prairie dogs on plant species composition regardless of whether other herbivores (in their study, bison) grazed within the prairie dog colonies. This indicates that (1) grazing and burrowing (physically modifying the site) appear to impose independent forms of disturbance on plants; (2) burrowing has a stronger effect on vegetation than grazing; and (3) soil disturbance by burrowing rodents is mainly responsible for the species composition change at a fine scale. The different types of disturbance—livestock remove the aboveground parts of plants, whereas marmots disturb the soil and roots—create different levels of damage for different species, thereby contributing to a differentiation of vegetation communities with distance from the marmot burrows, even in the presence of livestock grazing. For example, McNaughton (1983) reported that different species exhibited different degrees of compensatory growth in response to herbivory, and Nemoto and Lu (1992) reported variation in root plasticity in response to soil disturbance.

Livestock and marmots, acting alone, tended to increase the spatial heterogeneity of soil nutrient properties at coarser scales, but heterogeneity decreased when the two herbivores groups were both present within the same plot (Table 2). Herbivores with different foraging habits distribute their dung deposits in different ways (patchily or locally), but mainly around good feeding patches (Bakker et al., 2004; Retzer, 2007). When livestock and marmots were both present, a scarcity of food resources may have forced the marmots to search for edible plant patches that were left behind by the livestock, and this may have resulted in a more homogeneous spatial distribution of dung. This hypothesis must be confirmed by surveying the actual distribution of their dung in a future study.

5. Implications for sustainable livestock grazing

Our results demonstrated that livestock and marmots create complementary disturbances, leading to the creation of landscape heterogeneity at multiple spatial scales (Fig. 1). Livestock modified the overall vegetation composition at broader scales, thereby affecting spatial heterogeneity at the landscape scale, whereas marmots modified spatial heterogeneity more at finer scales. Davidson and Lightfoot (2006, 2008) reached the same conclusion for sites under the coexistence of two different rodent species. Based on these results, the maintenance of sites in Mongolia under either herbivore group and under both groups simultaneously will lead to diverse vegetation communities at multiple spatial scales in these arid grasslands, and this may have beneficial effects on biodiversity. This increased biodiversity may ensure more sustainable forage production through the fertilizing effect of legumes and the presence of a greater range of life forms (Thompson et al., 2005; Bullock et al., 2007). However, livestock grazing must be carefully monitored, because the large numbers of livestock that are currently grazed on this land have increased the abundance of degradation-indicator species (Fig. 2), and this may over time lead to a net loss in forage production.

As the LRE results suggest, the presence of marmots at sites subjected to livestock grazing did not positively influence steppe plant biodiversity. This is partially linked to the concentrated grazing by livestock near the marmot mounds, as large herbivores have shown a strong preference for forage on mounds created by rodents due to their higher nutrient contents (Coppock et al., 1983). However, marmots increased species diversity compared to the control, without leading to significant damage to the agricultural crops, whereas in the presence of both marmots and livestock, species diversity decreased and the number of degradation-indicator species increased. This suggests that protecting the areas around marmot burrows may improve biodiversity, at least at finer spatial scales. Therefore, proper manipulation of the livestock grazing regime (i.e., lower livestock grazing intensity around marmot colonies) can maintain species-rich communities without serious land degradation in the Mongolian steppe.

Acknowledgements

We thank the project members, especially T. Okayasu of the University of Tokyo, for their kind help with the field survey. We also thank the staff of the Hustai National Park for their help during our study. This work was carried out with support from the Global Environmental Research Fund (G-071) of Japan's Ministry of the Environment.

References

Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128, 465–479.

Badano, E.I., Cavieres, L.A., 2006. Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. Divers. Distrib. 12, 388–396.

Bakker, E.S., Olff, H., Boekhoff, M., Gleichman, J.M., Berendse, F., 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. Oecologia 138, 91–101.

Bullock, J.M., Pywell, R.F., Burke, M.J.W., Walker, K.J., 2001. Restoration of biodiversity enhances agricultural production. Ecol. Lett. 4, 185–189.

Brown, P.R., Huth, N.I., Banks, P.B., Singleton, G.R., 2007. Relationship between abundance of pest rodents and damage to agricultural crops. Agric. Ecosyst. Environ. 120, 405–415.

Bullock, J.M., Pywell, R.F., Walker, K.J., 2007. Long-term enhancement of agricultural production by restoration of biodiversity. J. Appl. Ecol. 44, 6–12.

Campos-Arceiz, A., Takatsuki, S., Lhagvasuren, B., 2004. Food overlap between Mongolian gazelles and livestock in Omnogobi, southern Mongolia. Ecol. Res. 19, 455–460.

Collins, S.L., Smith, M.D., 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology 87, 2058–2067.

Coppock, D.L., Ellis, J.E., Detling, J.K., Dyer, M.I., 1983. Plant-herbivore interactions in a North-American mixed-grass prairie. 2. Responses of bison to modification of vegetation by prairie dogs. Oecologia 56, 10–15.

Davidson, A.D., Lightfoot, D.C., 2006. Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. Ecography 29, 755–765.

Davidson, A.D., Lightfoot, D.C., 2008. Burrowing rodents increase landscape heterogeneity in a desert grassland. J. Arid Environ. 72, 1133–1145.

Duelli, P., 1997. Biodiversity evaluation in agricultural landscapes: an approach at two different scales. Agric. Ecosyst. Environ. 62, 81–91.

Fahnestock, J.T., Detling, J.K., 2002. Bison-prairie dog-plant interactions in a North American mixed-grass prairie. Oecologia 132, 86–95.

FAO/ISRIC/ISSS, 1998. World reference base for soil resources. World Soil References Reports 84, FAO, Rome.

Fernandez-Gimenez, M., Allen-Diaz, B., 2001. Vegetation change along gradients from water sources in three grazed Mongolian ecosystems. Plant Ecol. 157, 101–118.

Huston, M.A., 1994. Biological Diversity: the Coexistence of Species on Changing Landscapes. Cambridge University Press, UK.

Jigjidsuren, S., Johnson, D.A., 2003. Forage Plants of Mongolia. Admon Publishing, Ulaanbaatar, Mongolia.

McCune, B., Mefford, M.J., 1999. PC-ORD for Windows: Multivariate analysis for Ecological Data, Version 4.0. MjM Software, Gleneden Beach, Oregon.

McNaughton, S.J., 1983. Compensatory plant-growth as a response to herbivory. Oikos 40, 329–336.

Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69, 89–107.

National Scientific Office of Mongolia, 2007. Mongolian Statistical Yearbook 2006. National Scientific Office of Mongolia, Ulaanbaatar.

Nemoto, M., Lu, X., 1992. Ecological characteristics of *Agriophyllum squarrosum*, a pioneer annual on sand dunes in eastern inner Mongolia. China Ecol. Res. 7, 183–186.

Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grassland plant diversity. Trends Ecol. Evol. 13, 261–265.

Parsons, A.J., Dumont, B., 2003. Spatial heterogeneity and grazing processes. Anim. Res. 52, 161–179.

Retzer, V., 2007. Forage competition between livestock and Mongolian pika (*Ochotona pallasi*) in Southern Mongolian mountain steppes. Basic Appl. Ecol. 8, 147–157.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., Wallis De Vries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures—a review. Biol. Conserv. 119, 137–150.

Sasaki, T., Okayasu, T., Jamsran, U., Takeuchi, K., 2008. Threshold changes in vegetation along a grazing gradient in Mongolian rangelands. J. Ecol. 96, 145–154.

Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E., 1996. Methods of Soil Analysis. Part 3. Chemical Methods. Soil Science Society of America, Madison, WI, USA.

Thompson, K., Askew, A.P., Grime, J.P., Dunnett, N.P., Willis, A.J., 2005. Biodiversity, ecosystem function and plant traits in mature and immature plant. Funct. Ecol. 19, 355–358.

Tracy, B.F., Sanderson, M.A., 2004. Forage productivity, species evenness and weed invasion in pasture communities. Agric. Ecosyst. Environ. 102, 175–183.

Van Staalduinen, M.A., During, H., Werger, M.J.A., 2007. Impact of grazing regime on a Mongolian forest steppe. Appl. Veg. Sci. 10, 299–306.

Van Staalduinen, M.A., Werger, M.J.A., 2007. Marmot disturbances in a Mongolian steppe vegetation. J. Arid Environ. 69, 344–351.

Wang, Y.S., Shiyomi, M., Tsuiki, M., Tsutsumi, M., Yu, X.R., Yi, R.H., 2002. Spatial heterogeneity of vegetation under different grazing intensities in the Northwest Heilongjiang Steppe of China. Agric. Ecosyst. Environ. 90, 217–229.

Wesche, K., Nadrowski, K., Retzer, V., 2007. Habitat engineering under dry conditions: the impact of pikas (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. J. Veg. Sci. 18, 665–674.

Yoshihara, Y., Chimeddorj, B., Buuveibaatar, B., Lhaquasuren, B., Takatsuki, S., 2008a. Effects of livestock grazing on pollination on a steppe in eastern Mongolia. Biol. Conserv. 141, 2376–2386.

Yoshihara, Y., Ito, T.Y., Lhagvasuren, B., Takatsuki, S., 2008b. A comparison of food resources used by Mongolian gazelles and sympatric livestock in three areas in Mongolia. J. Arid Environ. 72, 48–55.

Yoshihara, Y., Chimeddorj, B., Buuveibaatar, B., 2009a. Heavy grazing constraints on foraging behavior of Mongolian livestock. Grassland Sci. 55, 29–35.

Yoshihara, Y., Ohkuro, T., Buuveibaatar, B., Takeuchi, K., 2009b. Effects of disturbance by Siberian marmots (*Marmota sibirica*) on spatial heterogeneity of vegetation at multiple spatial scales. Grassland Sci. 55, 89–95.