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Effects of livestock grazing on the spatial heterogeneity of net soil nitrogen mineralization in three types of Mongolian grasslands

Muneto Hirobe · Junji Kondo · Altangerel Enkhbaatar · Narantsetseg Amartuvshin · Noboru Fujita · Keiji Sakamoto · Ken Yoshikawa · Knut Kielland

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Abstract

Purpose Small-scale soil heterogeneity relates to productivity and biodiversity and is crucial to understand. Soil heterogeneity could be affected by vegetation structure, and large mammal grazers could modify it through herbivory and excretion. The objective is to clarify the effects of livestock grazing on the small-scale (~3 m) soil heterogeneity in three types of Mongolian grasslands.

Materials and methods We sampled soils from inside (ungrazed) and outside (grazed) exclosures in three vegetation types: forest-steppe, shrub-steppe, and desert-steppe. We measured laboratory rates of soil net nitrogen (N) mineralization and net nitrification and geostatistically analyzed heterogeneity.

Results and discussion Average rates of net N mineralization and net nitrification were lower at shrub-steppe and desert-steppe and were decreased by grazing. Semivariograms showed vegetation-induced heterogeneity in ungrazed plots, except for net nitrification at forest-steppe. We found linear change with distance under dense and uniform vegetation at forest-steppe, 1.3 m patch under patchy vegetation at shrub-steppe, and linear change, but with much smaller semivariance, under sparse and poor vegetation at desert-steppe. At forest-steppe, grazing randomized the spatial patterns of net N mineralization and net nitrification. At shrub-steppe and desert-steppe, grazing greatly decreased the semivariances of net N mineralization and net nitrification as well as their averages, and the soil heterogeneity was virtually disappeared.

Conclusions Grazing in Mongolian grasslands homogenized the spatial patterns of net N mineralization and net nitrification, irrespective of their original spatial patterns determined by the differences in vegetation structure.

Keywords Livestock grazing · Mongolian grasslands · Semivariogram · Soil heterogeneity · Soil nitrogen mineralization · Vegetation structure

1 Introduction

On a small spatial scale, the distributions of soil nutrients in grassland ecosystems play a crucial role in determining the coexistence of plant species (Bonanomi et al. 2008), species

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M. Hirobe (✉) · J. Kondo · K. Sakamoto · K. Yoshikawa
Laboratory of Forest Ecology, Department of Environmental Ecology, Division of Environmental Science, Graduate School of Environmental and Life Science, Okayama University, Okayama 700-8530, Japan
e-mail: mhirobe@cc.okayama-u.ac.jp

A. Enkhbaatar
Institute of Geoecology, Mongolian Academy of Sciences, Ulan Bator, Mongolia

N. Amartuvshin
Institute of Botany, Mongolian Academy of Sciences, Ulan Bator, Mongolia

N. Fujita
Research Institute for Humanity and Nature, Kyoto, Japan

K. Kielland
Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK, USA

diversity (Aguiar and Sala 1999; Gutiérrez et al. 1993), plant productivity (Augustine et al. 2003), and plant composition and population dynamics (Gross et al. 1995; Robertson et al. 1988). Therefore, the spatial heterogeneity of soil nutrients, especially limiting nutrients such as N, is of great interest (e.g., Augustine and Frank 2001; Hirobe et al. 2001; Schlesinger et al. 1996), and researchers have identified various factors affecting the spatial heterogeneity of soil nutrients (e.g., Hirobe et al. 2001; Kondo et al. 2012; Schlesinger et al. 1996).

For example, the differences in vegetation types can affect the spatial heterogeneity of soil nutrients (Schlesinger et al. 1996). Since the main source of soil nutrients in natural ecosystems is litter input, the spatial heterogeneity of soil nutrients may be random in the dense, uniform vegetation of relatively humid regions (Schlesinger et al. 1996). On the other hand, in the patchy vegetation of more arid regions, concentrated distributions of nutrients beneath vegetation patches are often observed and referred to as "islands of fertility" (e.g., Garner and Steinberger 1989; Hirobe et al. 2001; Kondo et al. 2012).

Grazing by large mammals also directly and indirectly affects the spatial heterogeneity of soil nutrients through herbivory, excretion, trampling, and their interactions (Augustine and Frank 2001; Day and Detling 1990; Rietkerk et al. 2000). Defecation and urination by grazers have direct effects on the spatial distribution of soil nutrients (Augustine and Frank 2001; Day and Detling 1990; Orwin et al. 2009; Rietkerk et al. 2000). Grazers redistribute a large fraction of consumed elements, such as carbon (C), N, phosphorus (P), and exchangeable cations, into the soil by their excretions (Jewell et al. 2007; Shand and Coutts 2006). However, deposition patterns differ by livestock species. Sheep create mosaics of excretion areas by avoiding forage contaminated by their excreta (Hutchings et al. 2001a), whereas cattle deposit their excreta at random on a landscape scale (White et al. 2001). In addition, the effects on local soil at a small spatial scale are thought to be more prominent for cattle than for sheep or goats (Norman and Green 1958), as the frequency of excretion by cattle is lower, but the amount is larger (Haynes and Williams 1993). Therefore, livestock excretion may alter the spatial distributions of soil nutrients and affect nutrient availability for plants (Hirata et al. 2011).

Grazing-induced changes in the spatial structure of vegetation have an indirect effect on the spatial distribution of soil nutrients (Adler et al. 2001; Rietkerk et al. 2000). Grazers often feed selectively on the most palatable vegetation and avoid vegetation contaminated by dung (Hutchings et al. 2001b). Repeated grazing of specific vegetation is called "patch grazing" and may occur when the target vegetation can compensate by regrowing new shoots with higher nutrients and tenderness (Adler et al. 2001). Therefore, these effects of grazing on the spatial heterogeneity of soil nutrients may be different depending on the original vegetation type.

The Mongolian grasslands span arid and semi-arid climates with a latitudinal aridity gradient. The mean annual precipitation exceeds 500 mm in the northern part of the grasslands but is less than 50 mm in the southern part (National Climate Data 2008). Within this precipitation gradient, the vegetation changes from north to south, from taiga forest on the northern edge to forest-steppe, steppe, desert-steppe, and then to the Gobi-desert on southern edge. The grassland vegetation is densely and uniformly distributed in the forest-steppe and steppe regions; it then becomes patchy or discontinuous in the transition region of steppe and desert-steppe (hereafter shrub-steppe), and sparse and poor in the desert-steppe region. In addition, these grasslands have been long grazed by the livestock of the nomads who have historically inhabited the region (Batjargal 1997).

This study aimed to clarify the effects of livestock grazing on the spatial heterogeneity of soil net N mineralization at a small spatial scale (~3 m) in these Mongolian grassland ecosystems with different vegetation types. Soil net N mineralization was selected since it is one of the most dynamic soil processes and is highly susceptible to the biological modifications (Chen and Stark 2000; Hirobe et al. 2003). The examined spatial scale (~3 m) was expected to reflect the modification of spatial heterogeneity by vegetation and grazing in grassland.

2 Materials and methods

2.1 Study sites

The study sites were established in three vegetation types (forest-steppe, shrub-steppe, and desert-steppe) along a precipitation gradient from north to south in the Mongolian grasslands. The forest-steppe site was located near Gachuurt, Bayanzürkh (48°05′N, 107°14′E, ~1,745 m in elevation). The shrub-steppe site was near Mandalgobi, Dundgobi (45°43′N, 106°16′E, ~1,370 m in elevation), and the desert-steppe site was near Dalanzadgad, Omnogobi (43°34′N, 104°25–26′E, ~1,455 m in elevation).

The northern slope and ridge of the forest-steppe site were dominated by larch (*Larix sibirica* Ledeb.) or birch (*Betula platyphylla* Suk.), whereas the southern slope was dominated by grasses described later. The climate is characterized by dry and extremely cold winters and relatively humid and cool summers. The mean annual precipitation is 299 mm from 1998 to 2007, with about 80 % of precipitation falling as rain during July and August (National Climate Data 2008). The mean annual air temperature is −0.6 °C, ranging from −22.3 °C in January to 16.9 °C in July (National

Climate Data 2008). The soil is Mollisol (Soil Survey Staff 2006), with a clay loam texture.

At the shrub-steppe site, the dominant vegetation was patchily distributed grass or shrubs. The climate is characterized by intense aridity and strong winds, with a mean annual maximum wind velocity of 14.3 m s^{-1}. The mean annual precipitation is 156 mm from 1998 to 2007, with about 80 % of precipitation falling as rain during July and August (National Climate Data 2008). The mean annual air temperature is 3.0 °C, ranging from −17.3 °C in January to 21.1 °C in July (National Climate Data 2008). The soil is Aridisol (Soil Survey Staff 2006), with a sandy loam texture and abundant gravels.

At the desert-steppe site, the dominant vegetation was sparsely distributed grasses. The climate is characterized by extremely intense aridity and strong winds, with a mean annual maximum wind velocity of 14.6 m s^{-1}. The mean annual precipitation is 142 mm from 1998 to 2007, and about 80 % of precipitation falling as rain during July and September (National Climate Data 2008). The mean annual air temperature is 6.0 °C, ranging from −19.0 °C in January to 28.0 °C in July (National Climate Data 2008). The soil is Aridisol (Soil Survey Staff 2006) having a sandy loam texture with abundant gravels.

The main livestock species in each region were cattle, sheep, and goats in Bayanzürkh (forest-steppe site); sheep, goats, and horses in Mandalgobi (shrub-steppe site); and sheep, horses, and camels in Dalanzadgad (desert-steppe site). In units of sheep equivalents (Hoshino et al. 2009), livestock densities at these sites were 1.0 (sheep-heads ha^{-1}), 0.8 (sheep-heads ha^{-1}), and 1.14 (sheep-heads ha^{-1}), respectively (Kondo et al. 2011). However, these densities are calculated from the total number of livestock animals at a level of Soum (which is a second level administrative subdivision of Mongolia). Therefore, more livestock likely concentrated in our study sites because each site was close to the urban area and grazing pressure is severer near settlements (Batjargal 1997).

We established a total of six study plots in 2008, one inside (ungrazed) and one outside (grazed) of an exclosure fence at each of the three study sites. The minimum size of the exclosure fence was approximately 50×50 m. The livestock exclosure fences were established in 1994 at the forest-steppe site, in 1981 at the shrub-steppe site, and in the 1960s at the desert-steppe site; the fences have been maintained since establishment. There was only one pair of unglazed and grazed plots at each of the three study sites, and there were differences in grazing livestock animals and in the time since the installment of exclosure fence among study sites. However, highly different climatic conditions are the prominent factor determining differences in vegetation structure and soil among study site (Fujita and Amartuvshin 2013; Tamura et al. 2013), and these plots gave a unique opportunity to compare grazing with ungrazed conditions under different vegetation types in Mongolian grasslands.

The mean grass heights in ungrazed and grazed plots were 26.0 and 8.20 cm, 17.0 and 3.88 cm, and 15.0 and 3.40 cm at the forest-steppe, shrub-steppe, and desert-steppe sites, respectively (N. Fujita unpublished data; N. Amartuvshin, unpublished data). The dominant plant species at the forest-steppe site were *Carex duriuscula* C. A. Mey., *Poa pratensis* L., and *Potentilla mongolica* Krasch. in the ungrazed plot, and *Calamagrostis mecilentha* (Griseb.) Litv., *Astragalus mongholicus* Bge, and *Artemisia laciniata* Willd. in the grazed plot; at the shrub-steppe site, those were *Allium pollyrhizum* Turcz. et. Rgl., *Stipa glareosa* P. Smirn., and *Caragana leucophloea* Pojark. in the ungrazed plot, and *A. pollyrhizum* and *S. glareosa* in the grazed plot; at the desert-steppe site, those were *A. pollyrhizum*, *S. glareosa*, and *Convolvulus ammanji* Desr. in the ungrazed plot, and *A. pollyrhizum*, *S. glareosa*, and *Ajania fructicosa* (Ledeb.) Pojark. in the grazed plot. *A. pollyrhizum*, *C. duriuscula*, and *S. glareosa* were palatable for all livestock species, and *P. pratensis* and *C. ammanji* were palatable for particular species. The other plant species were either unpalatable or of unknown palatability (Grubov 2008; Jigjidsuren and Johnson 2003). In addition, at the shrub-steppe site, especially shrub vegetation patches were accompanied by soil mound in the ungrazed plot, whereas substantial gravel was exposed by erosion in the grazed plot.

Soil pH (H_2O) values of the surface mineral soil in ungrazed and grazed plots were 6.2 and 6.2, 7.7 and 8.1, and 8.6 and 8.8, at the forest-steppe, shrub-steppe, and desert-steppe sites, respectively (Kondo et al. 2011).

2.2 Soil sampling

Soil samples were collected in late June 2008. We employed and modified the sampling design of Gross et al. (1995). In each plot, we established a 14×14 m sampling plot and set 16 base points in a 4×4 matrix in the sampling plot, offset 2 m from the edge. Base points were spaced 2 m in both N–S and W–E directions. At each base point, we placed a 2-m transect, with the center (100 cm) at the base point of a randomly assigned cardinal direction (e.g., N, NE, E, SE) and located four additional sampling points at 0, 40, 60, 80, and 200 cm or 0, 20, 60, 80, and 200 cm on the transect. Consequently, 96 sampling points were established at each plot, and overall total was 576 soil samples. At each sampling point, mineral soil was taken from a depth of 0–5 cm, using a 100-ml soil core (5 cm in diameter and 5.1 cm in height).

2.3 Laboratory analyses

Samples taken at the forest-steppe site were relatively moist (water content: 27% *w*/*w* on average), whereas those from the shrub-steppe and desert-steppe sites were nearly air-dried at the time of sampling. All of the soil samples were air-dried and passed through a 2-mm sieve to remove debris and gravel. These samples were used for analyses of laboratory rates of net N mineralization and net nitrification by aerobic incubation. Use of field-moist soil samples is recommended to avoid the enhanced N mineralization of rewetted soils, especially for the first 7 days, due to a flush of microbial activity (Beauchamp et al. 1986; Bundy and Meisinger 1994; Nordmeyer and Richter 1985). However, for <30 days incubation, the difference between fresh and rewetted soils is rather stable (Nordmeyer and Richter 1985), and use of air-dried samples may produce satisfactory results where a relative comparison of soil N availability is desired (Bundy and Meisinger 1994). In addition, soils were nearly air-dried at the time of sampling at two drier sites, and the moisture condition of surface mineral soil could sometimes be very dry even at the forest-steppe site. In this study, we employed the incubation of rewetted soil to make the incubation condition be constant for all soil samples and to process many soil samples at the same time.

We extracted exchangeable NH_4^+–N and NO_3^-–N before incubation using 2 M KCl (soil/extractant=1:10). A 3.5-g soil sample was aerobically incubated in the dark at 25 °C for 28 days with moisture initially adjusted at 60 % of the water-holding capacity and held constant during incubation. After incubation, we extracted exchangeable NH_4^+–N and NO_3^-–N, using the methods described above. The net N mineralization rate was calculated as the difference in the total inorganic N (NH_4^+–N+NO_3^-–N) pool before and after incubation, and the net nitrification rate was calculated as the difference in the NO_3^-–N pool before and after incubation. The concentrations of NH_4^+–N and NO_3^-–N in the extracts were determined colorimetrically, using the indo-phenol blue method and diazotization after reduction to NO_2^-–N using a copperized cadmium column, respectively (Keeney and Nelson 1982).

2.4 Statistical analysis

The spatial patterns of net N mineralization and net nitrification were analyzed geostatistically using semivariograms. The calculation of semivariances from the field data and the fitting of models to semivariograms were performed using GS^+ (Robertson 1998). The data were not normally distributed except for net N mineralization rates in unglazed and grazed plots at forest-steppe site, and for net nitrification rate in grazed plot at forest-steppe site. However, for semivariogram analysis, data were not transformed to allow for unbiased comparisons among sites of semivariance (extent of dissimilarity) and of scales of spatial dependence (Gross et al. 1995; Isaaks and Srivastava 1989), and because there were negative values of net N mineralization and net nitrification rates in most plots that did not show normal distributions.

The semivariance, $\gamma(h)$, for each specific lag distance h was calculated as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_i + h) \right]^2 \tag{1}$$

where N(h) is the number of data pairs of positions separated by distance h, $z(x_i)$ is the measured sample value at position x_i, and $z(x_i+h)$ is the value of the variable at position x_i+h. The semivariance data of net N mineralization and net nitrification rates in each plot were fitted to a spherical or a linear function (Hirobe et al. 2003; Schlesinger et al. 1996), based on the smaller reduced sum of square (Robertson 1998). If the selected function showed very low r^2 value ($r^2<0.2$), the other function was checked, but there was no case that the other function showed higher r^2 value. The spatial pattern of net N mineralization or net nitrification rate was interpreted as random when neither a spherical nor linear function fitted well ($r^2<0.2$). Since we focused on the soil heterogeneity that could be modified by vegetation and grazing in grassland, we employed a 0.2 m lag interval, which was the minimum distance between sample positions, and a 3.0 m lag distance. The minimum and maximum numbers of pairs per lag interval were 16 at 1.2 and 1.4 m, and 98 at 3.0 m, respectively. Model parameters were used to evaluate the magnitude of spatial dependence and the scale of spatial autocorrelation for net N mineralization and net nitrification rates (Robertson et al. 1988). The nugget (C_0) variance is either a random error or represents a spatial dependence at a scale smaller than the minimum distance examined (Isaaks and Srivastava 1989). The scale of spatial autocorrelation is indicated by the estimated spatial autocorrelation “range.” The proportion of structural variance (C) to the estimated total sample variation (sill; $C+C_0$) is used to evaluate the magnitude of spatial dependence.

3 Results

3.1 Means and CVs

Net N mineralization and net nitrification rates differed by more than one order of magnitude among sites, being highest at the forest-steppe and lowest at the desert-steppe (Table 1). Both net N mineralization and net nitrification

Table 1 Rates of net N mineralization and net nitrification in ungrazed and grazed plots in three types of Mongolian grasslands

Property	Grassland type	Plot	Mean (min.–max.)	CV[a]
Net N mineralization rate (mg-N kg soil^{-1} day^{-1})	Forest-steppe	Ungrazed	16.70 (6.24–25.14)	23
		Grazed	14.90 (7.80–21.33)	18
	Shrub-steppe	Ungrazed	1.75 (−2.06–10.37)	119
		Grazed	0.59 (−0.59–1.39)	41
	Desert-steppe	Ungrazed	0.98 (−1.03–4.15)	101
		Grazed	0.56 (0.09–2.46)	74
Net nitrification rate (mg-N kg soil^{-1} day^{-1})	Forest-steppe	Ungrazed	10.17 (6.24–26.89)	54
		Grazed	7.11 (7.80–10.51)	64
	Shrub-steppe	Ungrazed	2.22 (−2.06–4.46)	107
		Grazed	0.75 (−0.59–18.32)	49
	Desert-steppe	Ungrazed	1.12 (−1.03–2.72)	90
		Grazed	0.66 (0.09–2.64)	66

[a] Coefficients of variation [(SD/mean) × 100 %]

rates were reduced by grazing (see Table 1). Coefficient of variation (CV) was larger at the drier sites than at the forest-steppe within ungrazed or grazed plots for net N mineralization rate, but it was larger at the drier sites only within ungrazed plots for net nitrification rate. At the same time, CV was smaller in grazed plots than in ungrazed plots, especially at the drier sites.

3.2 Geostatistics

At the forest-steppe site, net N mineralization in the ungrazed plot fitted a linear function with a moderate spatial dependence ($C/(C_0+C)=0.56$) within the spatial scale examined (~3 m) (Fig. 1a, Table 2), while neither a spherical nor a linear function fitted well in the grazed plot ($r^2<0.2$) (see Fig. 1b, Table 2). At the shrub-steppe site, net N mineralization in the ungrazed plot fitted a spherical function with strong spatial dependences ($C/(C_0+C)=0.73$) and with a mean spatial autocorrelation range of 1.32 m (see Fig. 1c, Table 2). In the grazed plot, a spherical function fitted with a strong spatial dependence ($C/(C_0+C)=0.93$) and with a mean spatial autocorrelation range of 0.44 m (see Fig. 1d, Table 2); however, the semivariance was greatly reduced relative to that in the ungrazed plot. At the desert-steppe site, net N mineralization in the ungrazed plot fitted a linear function with weak spatial dependences ($C/(C_0+C)=0.36$) (see Fig. 1e, Table 2), and the semivariance was much lower than those at the forest-steppe and shrub-steppe sites. In the grazed plot, the semivariance was greatly reduced relative to that in the ungrazed plot and neither a spherical nor a linear function fitted well in the grazed plot ($r^2<0.2$) (see Fig. 1f, Table 2)

Net nitrification at the forest-steppe site fitted a spherical function with a strong spatial dependence ($C/(C_0+C)=1.00$) and with a mean spatial autocorrelation range of 0.65 m in the ungrazed plot (Fig. 2a, Table 2). In the grazed plot, however, neither a spherical nor a linear function fitted well ($r^2<0.2$) (see Fig. 2b, Table 2). At the shrub-steppe site, net nitrification in the ungrazed plot fitted a spherical function with strong spatial dependences ($C/(C_0+C)=0.80$) and with a mean spatial autocorrelation range of 1.34 m (see Fig. 2c, Table 2). In the grazed plot, however, the semivariance was greatly reduced relative to that in the ungrazed plot and neither a spherical nor a linear function fitted well ($r^2<0.2$) (see Fig. 2d, Table 2). At the desert-steppe site, net nitrification in the ungrazed plot fitted a linear function with weak spatial dependences ($C/(C_0+C)=0.33$) (see Fig. 2e, Table 2), and the semivariance was much lower than those at the forest-steppe and shrub-steppe sites. In the grazed plot, the semivariance was greatly reduced relative to that in the ungrazed plot and neither a spherical nor a linear function fitted well in the grazed plot ($r^2<0.2$) (see Fig. 2f, Table 2).

4 Discussion

This study demonstrated that rates of net N mineralization and net nitrification were decreased by aridity and grazing for surface mineral soils (0–5 cm) in Mongolian grasslands (see Table 1). The effects of grazing were probably caused by the changes of litter quality at the forest-steppe site, by decreased input of organic materials due to degraded vegetations, and by depressed microbial activity due to increased alkalinity at the drier sites (Kondo et al. 2011).

The spatial heterogeneity of soil nutrients varies across vegetation types (Schlesinger et al. 1996). Under dense and uniform grass cover, the scales of spatial autocorrelation of limiting nutrients are generally greater than that under

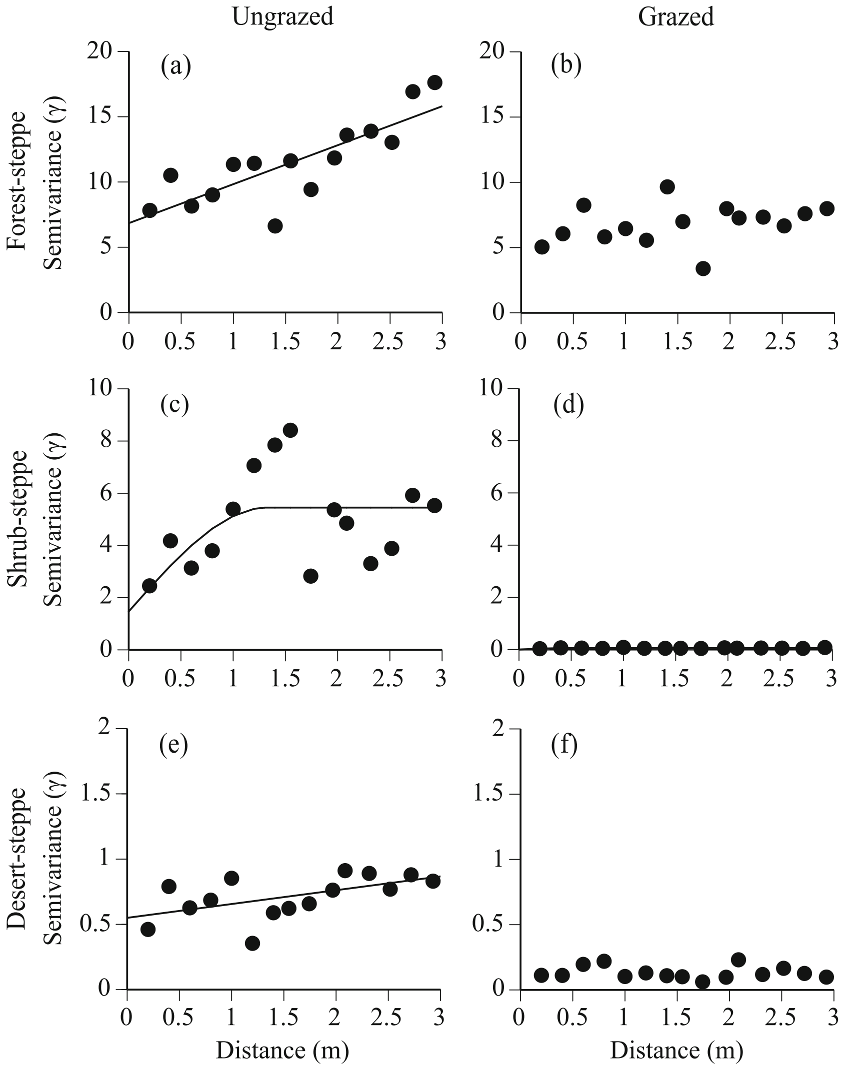

Fig. 1 Semivariograms for net N mineralization rate at the forest-steppe (**a**, **b**), shrub-steppe (**c**, **d**), and desert-steppe (**e**, **f**) sites in ungrazed and grazed plots in Mongolian grasslands

patchy woody shrubs (Gross et al. 1995; Schlesinger et al. 1996). To create these patterns, biotic processes, such as nutrient uptake and litter input by plants, are the most important (Garner and Steinberger 1989; Schlesinger et al. 1996). In the present study, we found similar differences in the spatial heterogeneity of net N mineralization and net nitrification rates in ungrazed plots that were induced by changes of vegetation structure along the aridity gradient, except for net nitrification at the forest-steppe site (see Figs. 1 and 2, Table 2). At the forest-steppe site, the linear relationship with moderate spatial dependence for net N mineralization within the spatial scale examined (see Fig. 1a) appeared to reflect the dense and uniform vegetation cover (Schlesinger et al. 1996). In contrast, at the shrub-steppe site, we found spatial autocorrelation ranges of 1.3 m with strong spatial dependences for both net N mineralization (see Fig. 1c) and net nitrification (see Fig. 2c, Table 2). These spatial patterns likely could result from the patchy vegetation cover and are known as "islands of fertility" (e.g., Hirobe et al. 2001; Kondo et al. 2012; Schlesinger et al. 1996). At the desert-steppe site, we observed linear relationships with weak spatial dependences, and much lower semivariance than at the other two sites (see Figs. 1e and 2e, Table 2). These relatively homogeneous patterns could result from the poor and sparse vegetation cover under the extremely dry climate. In the case of net nitrification at the forest-steppe site, however, the mean spatial autocorrelation range of 0.65 m with a strong spatial dependence would not be induced by the dense and uniform vegetation cover. Since autotrophic nitrifiers are known to be sensitive to local environmental factors (Clein and Schimel 1995; Hirobe et al. 1998), the spatial pattern found in net nitrification at the forest-steppe site might be due to the variations in unknown local environmental factors.

In many grassland ecosystems, grazing can alter the spatial distribution of soil nutrients directly by excretion and/or indirectly by herbivory (Afzal and Adams 1992; Augustine and Frank 2001; Rietkerk et al. 2000) and might facilitate or impede the development of small-scale heterogeneity (Augustine and Frank 2001; Lin et al. 2010; Wiesmeier et al. 2009). For example, Augustine and Frank

Table 2 Summary of semivariogram model parameters for net N mineralization and net nitrification rates in ungrazed and grazed plots in three types of Mongolian grasslands

Property	Grassland type	Plot	Model	RSS	r^2	Nugget (C_0)	Sill (C_0+C)	Range (m)	$C/(C_0+C)$
Net N mineralization	Forest-steppe	Ungrazed	Linear	46.9	0.664	6.85	15.6	≥3.0	(0.56)
		Grazed	Spherical[a]	28.8	0.103	–	–	–	–
			Linear	28.9	0.098	–	–	–	–
	Shrub-steppe	Ungrazed	Spherical[a]	34.3	0.261	1.47	5.45	1.32	0.73
		Grazed	Spherical[a]	0.0021	0.204	0.0010	0.056	0.44	0.93
	Desert-steppe	Ungrazed	Linear	0.26	0.308	0.55	0.86	≥3.0	(0.36)
		Grazed	Spherical[a]	0.033	0.013	–	–	–	–
			Linear	0.033	0.000	–	–	–	–
Net nitrification	Forest-steppe	Ungrazed	Spherical[a]	425	0.353	0.010	29.07	0.65	1.00
		Grazed	Spherical[a]	525	0.184	–	–	–	–
			Linear	656	0.053	–	–	–	–
	Shrub-steppe	Ungrazed	Spherical[a]	34.9	0.423	1.42	7.07	1.34	0.80
		Grazed	Spherical[a]	0.040	0.030	–	–	–	–
			Linear	0.041	0.000	–	–	–	–
	Desert-steppe	Ungrazed	Linear	0.32	0.226	0.61	0.89	≥3.0	(0.33)
		Grazed	Spherical[a]	0.043	0.009	–	–	–	–
			Linear	0.043	0.000	–	–	–	–

All semivariograms were constructed using 0.2-m lag intervals to a maximum lag of 3.0 m

RSS reduced sum of square

[a] For $h\leq$range, $\gamma(h)=C_0+C$h/range)−0.5 (h/range)3}; $h>$range, $\gamma(h)=C_0+C$

(2001) reported that grazers in the northern winter range of Yellowstone National Park developed spatial heterogeneity of soil mineral N in 4×4-m plots by urine input. On the other hand, in China, severe grazing was suggested to spatially homogenize the organic C and/or total N pools in approximately 2-m plots (Lin et al. 2010; Wiesmeier et al. 2009).

Our comparison of ungrazed and grazed plots showed that grazing homogenized spatial heterogeneity of net N mineralization and net nitrification in Mongolian grasslands, irrespective of their original spatial patterns determined by the differences in vegetation structure (see Figs. 1 and 2, Table 2). At the forest-steppe site, grazing did not greatly change the semivariances of net N mineralization and net nitrification but randomized their original spatial patterns (see Figs. 1b and 2b, Table 2). Because the vegetation appeared to be grazed almost uniformly at the spatial scale examined in the grazed plot at the forest-steppe site (J. Kondo, personal observation), the indirect effects of grazing, i.e., changes in spatial vegetation structure due to selective grazing and/or patch grazing (Adler et al. 2001; Rietkerk et al. 2000), seemed to be not strong. Therefore, we suggested that the direct effects of grazing contribute the changes in the spatial heterogeneity of net N mineralization and net nitrification rates. The livestock we observed during field study was cattle which may deposit excreta largely at random except in resting areas (Hirata et al. 2011), and the size of the dung patch might not be detectable at our minimum lag interval (20 cm; Afzal and Adams 1992). The urine patch scale of cattle is reported between 0.40 and 0.71 m (Haynes and Williams 1993; Pleasants et al. 2007). However, this scale could be modified by soil conditions such as soil moisture and/or clay content, which affects diffusion (Day and Detling 1990; Haynes and Williams 1993; Orwin et al. 2009). Therefore, random redistribution processes might be more effective than localization by excreta for the spatial patterns examined in this study.

At the shrub-steppe site, grazing greatly decreased the semivariances of net N mineralization and net nitrification and changed their spatial patterns (see Figs. 1d and 2d, Table 2). Although a reduced size of patch was detected for net N mineralization under grazing, the lower net N mineralization as well as its much lower semivariance than those in the ungrazed plot suggests a rather homogeneous pattern of net N mineralization. For net nitrification, grazing randomized the originally patchy spatial pattern. The much smaller (<20 cm) and sparser vegetation patches in the grazed plot at the shrub-steppe site (J. Kondo, personal observation) suggest that the homogenization of the soil heterogeneity was mainly caused by an indirect effect of grazing (Adler et al. 2001; Lin et al. 2010; Wiesmeier et al. 2009), i.e., the loss of "islands of fertility," In the windy region such as two drier sites in our study, the degraded

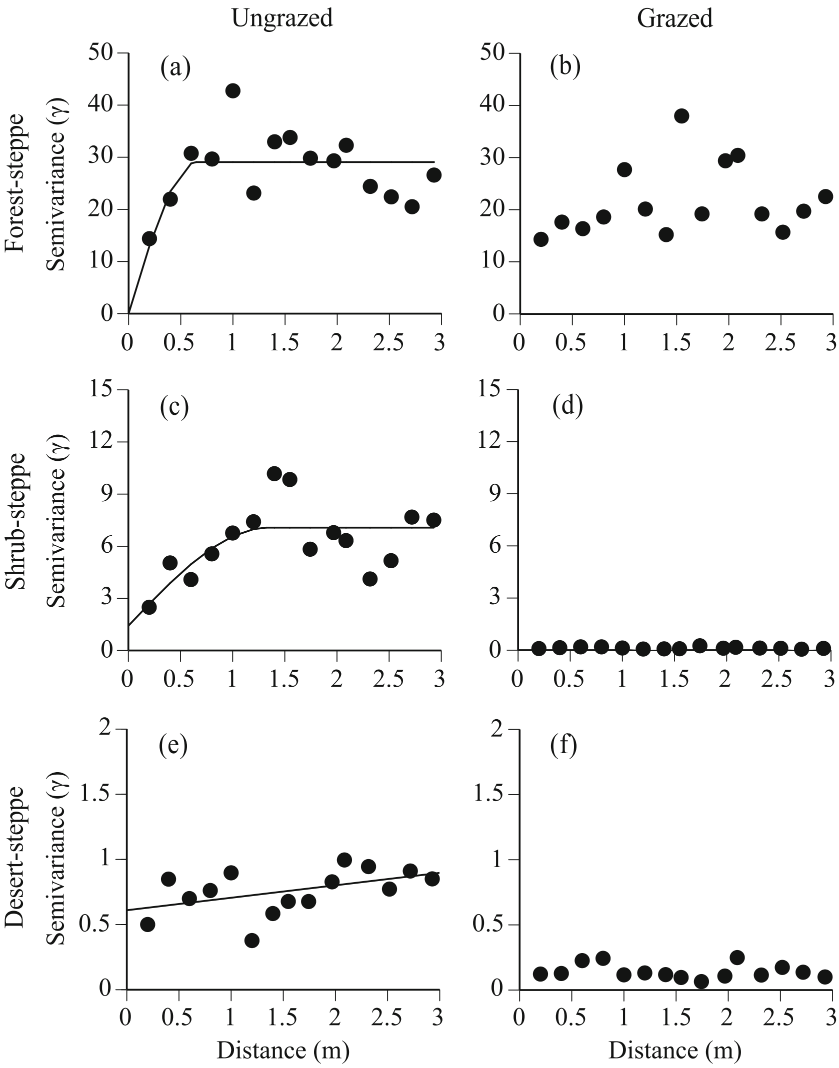

Fig. 2 Semivariograms for net nitrification rate at the forest-steppe (**a**, **b**), shrub-steppe (**c**, **d**), and desert-steppe (**e**, **f**) sites in ungrazed and grazed plots in Mongolian grasslands

vegetation could not only enhance the erosion of the surface soil in bare land but could also induce the erosion of the trapped and accumulated materials under vegetation (Burke et al. 1999; Hirobe et al. 2001; Kondo et al. 2012). In addition, the degraded vegetation would reduce the visiting frequency and shorten the residence time of grazers, and it in turn could result in reduced excreta input (Auerswald et al. 2010; du Toit et al. 2008; White et al. 2001). Hence, the reduced direct effects might partly contribute to reducing soil spatial heterogeneity (Lin et al. 2010; Wiesmeier et al. 2009).

At the desert-steppe site, grazing greatly decreased the semivariances of net N mineralization and net nitrification and randomized the originally linear spatial patterns (see Figs. 1f and 2f, Table 2). This was likely because grazing greatly diminished the originally poor, sparse vegetation. As at the shrub-steppe site, such degraded vegetation would not be attractive for livestock animals and would reduce the direct effects of grazing that may facilitate soil heterogeneity.

5 Conclusions

In this study, we found that grazing in Mongolian grasslands homogenized the spatial patterns of net N mineralization and net nitrification, irrespective of their original spatial patterns determined by the differences in vegetation structure. At the forest-steppe site, grazing randomized the spatial patterns of net N mineralization and net nitrification, but it had relatively small effects on the semivariances of net N mineralization and net nitrification as well as on their averages (see Figs. 1 and 2, Tables 1 and 2). By contrast, at two drier sites, grazing not only reduced the average rates of net N mineralization and net nitrification for more than 40 % from ungrazed conditions but also greatly reduced their semivariances, suggesting the virtual disappearance of heterogeneity under extremely low soil N availability. This change by grazing was the most prominent at the shrub-steppe site which is characterized by patchy vegetation. Soil heterogeneity could play an important role in grassland ecosystems including plant productivity and biodiversity

(Aguiar and Sala 1999; Augustine et al. 2003; Gutiérrez et al. 1993). In the shrub-dominated ecosystems, the clumped plant distribution represents nutrient-rich patches for herbaceous species (Burke et al. 1999; Kondo et al. 2012; Perroni-Ventura et al. 2009) and contributes to maintain species richness and seedling establishment (Collins et al. 1998; El-Bana et al. 2002). Therefore, the virtual disappearance of heterogeneity under extremely low soil N availability, which was induced by the loss of large vegetation patches and associated "island of fertility", would have large effects on the entire grassland ecosystem at the shrub-steppe site.

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