論 文 の 内 容 の 要 旨

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論文題目　The effects of disturbance by Siberian marmots on spatial heterogeneity of vegetation and soil in a steppe in Mongolia, and its applicability to conservation managements
（シベリアマーモットによる撹乱が植生と土壌の空間的異質性に与える影響と、
モンゴル草原の保全管理への適用性）

Chapter 1 Introduction

Grasslands have long been utilized for cultivation and grazing. Recently, their value in maintaining biodiversity (wide array of taxa) has been recognized as well. Spatial heterogeneity is a major driver of species diversity. Most papers have reported a positive relationship between habitat heterogeneity and species diversity; for example, because more heterogeneity is equivalent to more niches, it allows more species to coexist. Thus, from a management viewpoint, optimization of heterogeneity has been acknowledged as an effective approach to maintaining high species richness, and consequent healthy ecological functioning.

Disturbance is the main factor generating spatial heterogeneity. The disturbance regime includes characteristics such as spatial distribution of the disturbance; disturbance frequency, return interval, and rotation period; and disturbance size, intensity, and severity. In the context of communities at the landscape scale, because the disturbance regime controls the proportion of the landscape at each succession stage, it is essential to consider the disturbance regime when examining the dynamics of spatial heterogeneity. According to the previous findings, biodiversity is maximized where multiple kinds, frequencies, severities, periodicities, sizes, shapes, and/or durations of disturbance occur concomitantly in a spatially and temporally distributed fashion. Seeking for a appropriate disturbance regime to maintain spatial heterogeneity is an effective conservation manner.

In Mongolian grasslands, Marmots modify the soil’s physical properties and chemical properties through activities such as burrowing, grazing, and urinating, thereby affecting the distribution of plant species. Because marmots disturb grasslands heterogeneously in space, they can be a potentially important tool for conservation management. However because ground-dwelling rodents damage a range of agricultural crops and cause soil erosion around the world, managing rodents in arid or semi-arid grasslands should consider their negative influence as well. Because the effects of keystone species or ecosystem engineers on ecosystems at broad scale are context-dependent, *a priori* evaluation of the impact of marmots on communities at landscape scale is needed.

My final goal is therefore to evaluate the impact of marmot on Mongolian steppe at the landscape and local scales based on the theory of landscape ecology, thus providing an appropriate tool for the sustainable management of healthy Mongolian steppe. Specifically, by clarifying the effects of disturbance by marmots on species diversity (vegetation)

and soil among landscape divisions (Chapter 2) and between land use divisions (Chapter 3), the broad-scale management options of land can be elucidated. Clarifying the effects of disturbance by marmots on spatial heterogeneity of vegetation and soil among the disturbance regimes at the colony scale (Chapter 4) will reveal management options using marmots at the local scale.

Chapter 2. The effects of disturbance by marmot on vegetation among landscapes

Can an *a priori* evaluation of the impact of keystone species (ecosystem engineers) reveal the general susceptibility of ecosystems to disturbance at a broad scale, thereby revealing vulnerable areas and allowing managers to optimize the performance of the keystone species? To answer the question, I surveyed plants growing on and off the mounds created by marmots (*Marmota sibirica*) among 14 landscape positions and within a single mountain slope in Hustai National Park (HNP) in a forested steppe region of Mongolia. Significant interactions between landscape position and soil disturbance by marmots were seen in forb volume. The impact of soil disturbance was low in mountain areas and high on depositional plains. Soil disturbance may have changed microenvironments from xeric to more humid or from moist to more xeric, depending on the other site characteristics. Marmots enhanced newly established species in the landscape positions close to the forested mountain or river. Collectively, my results indicate that sedimentation, preexisting water conditions, slope angle, all modify the relationships between soil disturbance and landscape position. My *a priori* evaluation of the influence of keystone engineer on ecosystems at a broad scale could provide insights into how to optimize the performance of ecosystem engineering in a way that is beneficial to ecosystem management.

Chapter 3. Effects of disturbance by marmots on vegetation and soil by land use

In the Mongolian steppes, livestock and rodents are the main habitat modifiers. Although grazing lands and rodent habitats overlap, the combined effects of disturbance by livestock and rodents on spatial heterogeneity have rarely been evaluated. I established a 50-m × 50-m plot in each of four sites: heavily grazed by livestock with and without marmot burrows, and ungrazed with and without marmot burrows. I subdivided each plot into 4-m^2 quadrats and surveyed the plant composition and soil nutrient properties in each quadrat. The spatial heterogeneity of vegetation and soil nutrient properties were calculated by using non-metric multidimensional scaling analysis and the coefficient of variance among soil samples at three spatial scales. The spatial heterogeneity of the vegetation did not differ between grazed by livestock and ungrazed plots; it was higher under marmot disturbance than in the absence of marmots at a fine scale, but lower under marmot disturbance than in the absence of marmots at a coarse scale irrespective of livestock grazing. At a fine scale, unique habitats were formed in each combination of grazing presence/absence and marmot presence/absence. In addition, the species composition in the grazed plots was distinct from that in the ungrazed plots at the coarser scale. The occurrence of degraded plant species depended on the presence of grazing rather than on the additive effect of both habitat modifiers. Marmots enhanced newly established species only in the ungrazed plots. These results show that the ecological roles of livestock and marmots are not functionally substitutable, but are complementary. That is, livestock modified the whole vegetation composition, and thereby spatial heterogeneity at the landscape scale, while marmots modified spatial heterogeneity at the local scale.

Chapter 4 The effects of disturbance by marmots on spatial heterogeneity at local scale

4-1 The effects of marmot density on spatial heterogeneity

I 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. I established three 50 m × 50 m plots according to burrow density and another plot in an area with no burrows. Each plot was subdivided into 625 adjacent 4-m^2 square quadrats and the plants and soil nutrient properties in them were surveyed. Spatial heterogeneity was calculated for vegetation using the mean dissimilarity of species composition among sample quadrats and geostatistical analysis was used to calculate soil properties. 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 plots. The greater fine-scale heterogeneity in the high-density burrows 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 plots reflected the presence of both disturbed and undisturbed patches within a single measurement unit. My results demonstrate the possibility of using the marmot as a conservation tool in my study site as far as a plant biodiversity is targeted.

4-2 The effects of spatial configuration of burrows on spatial heterogeneity

Disturbance frequency is key factor responsible for changes in spatial heterogeneity. My objective was to examine how the configuration of disturbance by burrowing rodents affected the spatial heterogeneity of vegetation and soil nutrient properties through the spatial pattern of disturbance frequency. I established three 2500-m^2 (50 m × 50 m) isolated-burrows plots and three 2500-m^2 clustered-burrows plots in a Mongolian grassland. Each plot was subdivided into 4-m^2 quadrats, and the plant species richness, percent coverage and soil nutrient properties in the quadrats were surveyed. Spatial heterogeneity was calculated for vegetation using the mean dissimilarity of species composition among sample quadrats and geostatistical analysis was used to calculate soil properties. Heterogeneous patches of plants such as *Achnatherum splendens* and higher nutrient concentrations were found only near the clustered burrows. As a result, spatial heterogeneities of vegetation and soil nutrient properties were higher in the clustered colony than those in the isolated colony. I considered that *Achnatherum splendens* may have grown near the clustered burrows because such structures captured a great amount of temporal water flows. Patches of higher soil nutrient concentrations can be attributed to locally concentrated excretions by the rodents and a reduction of uptake by plants in highly disturbed areas. I concluded that the configuration of disturbance patches affected the spatial heterogeneity at the local scale through the spatial pattern of disturbance frequency.

4-3. The effects of spatial grazing pattern of marmot on spatial heterogeneity

Disturbance size and intensity are key factors responsible for changes in spatial heterogeneity. If I consider that herbivore behavior will affect their disturbance regime (size and intensity), then it will also change the associated spatial heterogeneity. In this study, I examined whether the pattern of spatial disturbance created by a herbivore, the Siberian marmot (*Marmota sibirica*), affects the spatial heterogeneity of vegetation and soils at a colony scale in the Mongolian steppes. I estimated the pattern of spatial disturbance based on the spatial allocation of marmot burrows and feces and by direct observation of their grazing behavior in protected and unprotected areas. I then surveyed plant communities and soil nutrients in these areas to assess the spatial heterogeneity. I found that disturbance was more concentrated near marmot burrows in the unprotected area, where the degrees of spatial heterogeneity of vegetation and soil nitrate-nitrogen were greater than in the protected area, where disturbance was more widely distributed. These results indicate that the spatial pattern of disturbance by herbivores affects the spatial heterogeneity of vegetation and soils through changes in the disturbance regime. This finding also supports the hypothesis that the intensity of disturbance is more important than its size in determining community structure in the Mongolian steppes, thereby providing empirical support for the importance of considering the behavior (spatial grazing pattern) of herbivores in

future grazing studies.

Chapter 5. Synthesis and application

The combined results supported the following generalizations on the effects of disturbance by marmots on the Mongolian steppe.

At the landscape scale, the impact of disturbance by marmots on plant community structure differs more among landscape divisions than between land use divisions. Marmots enhanced plant species diversity at sites close to seed sources (e.g., forested mountains and rivers) or under low livestock grazing intensities, but not at sites far from seed sources or under heavy grazing intensities. Depositional plains showed some evidence of degradation by disturbance.

Marmot disturbance allowed, without loss of plant abundance, the persistence of fugitive forb species, resulted in increase of species richness and spatial heterogeneity of vegetation at fine grain size. However, the effect of disturbance by marmots on spatial heterogeneity of vegetation was scale-dependent; decreased at coarse grain size. Marmot also created the high soil nutrient concentration near their burrows by a combination of high deposition of dung and urine and modification of soil physical structures, resulted in increase of spatial heterogeneity of soil NO_3-N at local scale.

At the local scale, spatial heterogeneity was increased when the plot included many burrows, clustered burrows, or marmots with a small activity range. Clustered marmot burrows especially yielded higher spatial heterogeneity, but high population densities caused marked land deterioration.

The density of herbivore, the configuration of their disturbance patches and spatial grazing pattern of herbivores affected the spatial heterogeneity through change in the disturbance regime. The frequency of disturbance is important in determining the spatial heterogeneity at the local scale.

On the basis of these generalizations, I consider that the following goals would be useful for managing ecosystems sustainably through the use of marmots in Mongolian steppes: (1) When the conservation target is ecosystem engineers, *a priori* evaluation of the influence of the ecosystem engineers on the ecosystems at broad scale could provide insights into how to optimize the performance of ecosystem engineering in a way that is beneficial to ecosystem management. (2) Because the landscapes and land use divisions can be classified clearly into those that received only positive influences and those that received only negative influence from the marmot disturbance, zoning becomes more meaningful. (3) When the aim is enhancement of plant species diversity by marmots, landscape positions located close to seed sources or areas under low livestock grazing may become priority marmot conservation areas. (4) Because landscape positions located far from seed sources or landscape positions under heavy livestock grazing exhibited low enhancement of species diversity by marmots, and actually depositional plains showed some evidence of degradation, these landscape positions cab be used for sustainable use of marmots. (5) When the aim is to maintain spatial heterogeneity at the local scale, clustered marmot burrows can be conserved, but density must be limited. (6) When the aim is to maintain biodiversity at the local scale, a higher level of spatial heterogeneity in plots with frequently disturbed but patchily distributed small disturbances (i.e., heterogeneous disturbance regime) is appropriate.

Further experimental research is needed to determine guidelines for managing marmots in the Mongolian steppes.