Integrating Ecosystem Engineering and Spatial Heterogeneity Concepts: Toward a Biologically Diverse Mongolian Steppe

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Abstract

I report on my attempt to integrate ecosystem engineering and spatial heterogeneity concepts and examine how consideration of these concepts can be used in the restoration of the Mongolian steppe, aiming for a biologically diverse steppe. Lots of studies have showed spatial heterogeneity and biodiversity to be positively correlated, and the actions of ecosystem engineers (i.e., organisms that create or modify habitats) have increased spatial heterogeneity, indicating them to be a potential tool for maintaining biodiversity. Potential ecosystem engineers in Mongolia include large herbivores (such as livestock), burrowing rodents and shrubs. Judging from their contributions to spatial heterogeneity, the latter two are more promising engineers. However, we must evaluate the influence of ecosystem engineers on the spatial heterogeneity of the targeted landscape at the targeted spatial scale in the advance of their introduction; otherwise we might obtain opposite results. More studies are needed in order to better understand biodiversity, spatial heterogeneity and ecosystem engineering, as well as the interactions among them, in the Mongolian steppe for successful introduction of ecosystem engineers.

Key words: burrowing rodents, grazing, landscape dependency, shrubs, soil heterogeneity, spatial scale, vegetational heterogeneity

1. Introduction

In the face of current degradation of rangeland ecosystems in developing countries, there is an increasing need for the development of cost-effective techniques for restoration of biodiversity and consequent ecosystem functions and services. With regard to restoration projects in ecosystems, special attention has recently been given to controlling the availability of resources to some organisms by causing physical state changes in biotic or abiotic materials with the aim of aiding other organisms (ecosystem engineers) instead of using nonbiological approaches such as constructing fences to prevent livestock grazing (Jones et al., 1994; Zhang et al., 2004; Boogert et al., 2006; Byers et al., 2006; Crain & Bertness, 2006). At the same time, spatial heterogeneity — the point-to-point dissimilarity in environmental conditions, species composition or process rates in space (e.g., Inouye et al., 1987) — is a major driver of species diversity (Huston, 1994; Tilman, 1999). These two concepts are related each other, because ‘physical state changes caused by ecosystem engineers’ potentially affect spatial heterogeneity.

Here, I tried to integrate ecosystem engineering and spatial heterogeneity concepts and examine how consideration of these concepts can be used in restoring the Mongolian steppe, aiming for a biologically diverse steppe. For this purpose, I (1) introduce the relationships between biodiversity and spatial heterogeneity and the mechanism lying under the relationship, (2) seek potential effective ecosystem engineers in Mongolia and then (3) show the type of key ecological considerations necessary for successful application of these ecosystem engineers.

2. Biodiversity and Spatial Heterogeneity

2.1 Theoretical background

Species diversity is strongly associated with ecosystem function and resiliency (Naem et al., 1999). Thus, species diversity is a good barometer of healthy ecosystems. Nowadays, conservation of biodiversity is acknowledged as a management goal even in production-oriented agricultural grasslands (Isselstein et al., 2005). The main environmental factors affecting species diversity at a local scale are productivity, disturbance and spatial heterogeneity (Huston, 1994). Productivity and disturbance have a unimodal relationship with plant species diversity (Huston, 1994). Thus, it appears that from the perspective of management it would be difficult to...
find and maintain an “intermediate” level for maximizing species diversity. In contrast, spatial heterogeneity has positive associations with species diversity (Huston, 1994; Tilman, 1999). Therefore, from a management viewpoint, optimization of heterogeneity has been acknowledged as an effective approach to maintaining high species richness and consequent healthy ecological functioning. According to the species coexistence theory, greater heterogeneity of resources or other fitness-constraining environmental factors promotes species diversity (Hutchinson, 1959; Tilman & Pacala, 1993; Huston, 1994). This “habitat heterogeneous hypothesis” assumes that structurally complex habitats provide more niches and diverse ways of exploiting environmental resources and thus increase species diversity (Bazzaz, 1975; Rosenzweig, 1995). However, in cases where key biological processes such as dispersal and resource acquisition are disrupted through the creation of heterogeneity, negative correlation may occur (Saunders et al., 1991; Tews, 2004).

2.2 Spatial heterogeneity of vegetation and animal species diversity

Probably the most well studied relationship between biodiversity and spatial heterogeneity is that of animal species diversity and the spatial heterogeneity of vegetation. Tews (2004) found that 85 percent of published studies reported a positive correlation between spatial heterogeneity and animal species diversity. With regard to grasslands, variation in the vertical structure had clear effects on the number of species and total abundance of small arthropods compared to variation in the horizontal structure (Dennis et al., 1998). The abundance of insects is enhanced by vegetation heterogeneity (Kruess & Tscharntke, 2002). The structural complexity of the habitat had a positive influence on the diversity of web-building and plant-wandering spiders in a savanna (Whitmore et al., 2002). More bird and mammal species were found in heterogeneous environments formed by evenly spaced Acacia trees in a savanna (Dean et al., 1999). Horizontal heterogeneity of the local-scale habitat promoted local-scale species richness and diversity of small mammals (Williams et al., 2002). Thus, numerous studies have found that the relationship between species diversity and spatial heterogeneity in grasslands is positive for a wide array of taxa. Spatial heterogeneity of vegetation may allow animals to persist by providing habitat refuges (Hanski, 1998) or diverse habitat types to support different behavioral activities like feeding, nesting, and brood-rearing (Fuhlendorf & Engle, 2001).

2.3 Spatial heterogeneity of soil and vegetational species diversity

Plant growth is affected by the sum of soil nutrients, but their spatial pattern also strongly affects the performance of individual plants and thereby the community structure. Soil nutrient heterogeneity is ubiquitous within natural habitats at a variety of scales in time and space (Cain et al., 1999; Richard et al., 2000), especially in arid lands (Titus et al., 2002). Plants can assess soil environmental quality and invest root biomass appropriately for efficient resource acquisition, as proven by the selective placement of roots in nutrient-rich soil patches (Day et al., 2003a; Wijesinghe et al., 2005). Thus, populations growing in nutritionally heterogeneous environments produce significantly more root biomass and suffer lower mortality, presumably because competitive areas are confined to a smaller proportion of the entire habitat (Day et al., 2003a, 2003b). At the community level, if plants become established on homogeneous soil environments, they acquire nutrients in proportion to their biomass, regardless of species (Weiner et al., 1997; Berntson & Wayne, 2000). However, the degree of nutrient acquisition in response to nutrient heterogeneity is species specific (Casper & Jackson, 1997; Farley & Fitter, 1999; Wijesinghe et al., 2001), probably due to differences in root physiological plasticity (Fransen et al., 1999) or the rate of root proliferation (Robinson et al., 1999). It has been suggested, however, that the areas of low resource availability in patchy environments thus may provide refuges from strong competition (Day et al., 2003b). Therefore, heterogeneous soil environments could permit the survival of both competitively inferior and superior species, resulting in more species of plants and higher biomass (Steineur & Collins, 1995; Collins & Wein, 1998b; Lundholm & Larson, 2003).

3. Potential Ecosystem Engineers in Mongolia

3.1 Using grazing by large herbivores to increase spatial heterogeneity

Grazing by large herbivores itself seems to have a weak or negative impact on spatial heterogeneity over a small range size (Fig. 1, Collins & Smith, 2006; Yoshihara et al., 2010a). This is because they mainly remove parts of plants above ground and have a low impact underground. However, human intervention could enhance their potential as ecosystem engineers.

In prairie ecosystems, many managers believe that specialized grazing systems in which livestock are rapidly rotated among pastures to achieve a uniform distribution of grazing would improve the rangeland condition and livestock production better than a system of continuous grazing (Fuhlendorf & Engle, 2001). In recent decades, however, it has been recognized that such spatially uniform disturbance regimes (e.g., controlled fire or grazing) are not conducive to the maintenance of biodiversity (Collins, 2000; Fuhlendorf et al., 2006). Instead, Fuhlendorf and Engle (2001) proposed a heterogeneous approach (patch treatment) that imposes spatially and temporally variable disturbance patches at random across a landscape with the aim of creating a structurally heterogeneous landscape (Fig. 2). For land managers attempting to retain plant diversity on grazed landscapes, it would be desirable to provide all levels of grazing pressure across the landscape, including areas protected from livestock grazing (McIntyre et al., 2003). Moreover, increasing the heterogeneity of the plant
functional-group composition and structure does not reduce livestock production (Fuhlendorf & Engle, 2001, 2004). Other researchers have also suggested that this approach should be the basis for an alternative paradigm in ecosystem management and conservation (Pickett & Rogers, 1997; Fuhlendorf & Engle, 2001; McIntyre et al., 2003; Fuhlendorf et al., 2006).

3.2 Using burrowing rodents

Major habitats for burrowing rodents range from typical grasslands to deserts throughout the world. Burrowing semi-fossorial animals such as pocket gophers and prairie dogs have been shown to modify chemical and physical soil properties by depositing of dung or

Fig. 1 Results of NMDS ordination for four plots at 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. See details in Yoshihara et al., (2010a).

Fig. 2 (a) Landscape plan for rotational grazing. A cross-fencing scheme for a traditional grazing management plan to implement a rapid rotational grazing system. (b) Landscape plan for patch treatment. Chronology of patch burning within the bison enclosure on the Tallgrass Prairie Preserve, Oklahoma, 1993-1995. Numbers refer to the order in which burns were conducted. Bison within this area were allowed unrestricted selection of patches within the landscape. Figure from Coppedge and Shaw (1998). (c) Structural heterogeneity of vegetation within units in response to different grazing systems across several spatial scales (i.e., feeding station, patch, landscape) of herbivore site selection.
urine and creating micro-highlands as a result of gradual accretion of excavated soil, thereby affecting grassland plant communities (Coppock et al., 1983; Holland & Detling, 1990; Kinlaw, 1999; Sherrod & Seastedt, 2001). Their burrows serve as focal points for their activities (Behrends et al., 1985; Branch 1993), e.g. to minimize their predation risk (Holmes, 1984), and thus inter-burrow areas are less affected, resulting in spatially heterogeneous grasslands (Davidson & Lightfoot, 2006; Questad & Foster, 2007).

On the Mongolian steppe, Siberian marmots (*Marmota sibirica*) increase spatial heterogeneity of vegetation and soil nutrients at the landscape scale (Fig. 3), especially when (1) their population density is high (Figs. 4, 5), (2) their burrows are clustered (Fig. 6, Fig. 3 Siberian marmot in Hustai National Park (Mongolia).

![Fig. 3 Siberian marmot in Hustai National Park (Mongolia).](image)

![Fig. 4 Spatial heterogeneity of plant species and density of marmot burrows in a plot at three spatial scales using the three metrics. Heterogeneity was calculated through pairwise comparison of units within 50 × 50 m plots and then averaged. See details in Yoshihara et al. (2009a).](image)

![Fig. 5 Spatial distribution of soil nutrient properties (total nitrogen, nitrate nitrogen and potassium) across the off-burrow plot, medium-density-burrows plot and high-density-burrows plot based on interpolation with best-fit semivariograms. Circles indicate the positions of burrows. See details in Yoshihara (2009a).](image)
Yoshihara et al., 2010b), or (3) their activity range is limited to close to their burrows (Yoshihara et al., 2010c) through various magnitudes of disturbance frequency or intensity coexisting in the same space.

3.3 Using shrubs

In sandy grasslands, shrub canopies intercept wind-blow dust, slowly forming uncrusted soil mounds that function as hydrological sinks, creating physically heterogeneous lands together with small islands of fertility (Fig. 7). This soil amelioration results in greater diversity and biomass of herbaceous species (Su & Zhao, 2006; Zhang et al., 2004; Zhao et al., 2007), thus has received considerable attention as a tool for accelerating vegetation restoration processes (Flores & Jurado, 2003; Brooker et al., 2008). The shrub species most likely to play this role in Mongolia is Caragana spp. (Fabaceae). For more information, see “Yoshikawa” in this special issue, pp 37-46.

4. Key Ecological Considerations Necessary for Application of Ecosystem Engineers

4.1 Spatial scale

The spatial scale consists of several main components, such as the grain, or elementary sampling unit; and extent, or total length of the area (Legendre & Legendre, 1998; Fortin & Dale, 2005). Scale and heterogeneity are two key concepts which are inherently related. Heterogeneity makes no sense without the explicit consideration of scale, and scale matters little without heterogeneity (Wu, 2007).

Although the grazing impact of large herbivores on the spatial heterogeneity of vegetation and soil are independent at spatial scales (Collins & Smith, 2006; Yoshihara et al., 2010a), the impact of burrowing strongly depended at the spatial scale (Fig. 1, Questad & Foster 2007; Yoshihara et al., 2009b; Yoshihara et al., 2010a), particularly because grazing livestock distribute their pressure more evenly throughout the study plot, whereas the disturbance by burrowing rodents tends to be more concentrated. Indeed, the effects of marmots on vegetation heterogeneity were clearly expressed (increased) at a fine spatial scale (2 × 2 m), but not at a coarse spatial scale (Fig. 1, 10 × 10 m), which may reflect the detection of their typical disturbance at this scale (Yoshihara et al., 2009a).

This scale dependency was also observed in the effect of shrubs. According to Wright et al. (2006), the facilitative effect of shrubs and the mounds they create on plant species richness was dependent on the spatial scale, and the effect was most pronounced at the largest scale. A similar pattern has recently been found in a semi-desert area in Mongolia (Yoshihara et al., unpublished data). Both researchers shared the common perception that this scale dependency may have reflected the degree to which spatial heterogeneity of habitats within the plots increased as plot size increased.

4.2 Environmental context dependency

Empirical studies have shown that the effects of ecosystem engineers at a broad scale are context-dependent (Badano & Cavieres, 2006; Crain & Bertness, 2006; Wright et al., 2006). In general, organisms tend to have positive ecosystem effects in harsher environments through the amelioration of physical stress, and negative interactions in more benign physical environments (Crain & Bertness, 2006, Yoshihara et al., 2009b).

In the Mongolian steppe, a topography- or landscape-dependent grazing effect was apparent. The effects of livestock grazing on plant community composition varied along a slope gradient (Fujita et al., 2009) and among landforms (Sasaki et al., 2008). The impact of soil disturbance by Siberian marmots on species composition was low in mountain areas and high on depositional plains, the microenvironments of which may have changed from xeric to more humid or from moist to more xeric, depending on other site characteristics. (Fig. 8, Yoshihara et al., 2010d).
5. Applicability of Ecosystem Engineers to the Mongolian Steppes and Future Challenges

Sufficient evidence has proven that biodiversity increases with spatial heterogeneity, and ecosystem engineers create heterogeneous habitats through the modification of physical states. I thus recommend the use of ecosystem engineers as a potential conservation program. Because of clear results of spatial heterogeneity effects in Mongolia, burrowing rodents and shrubs are potential ecosystem engineers. However, we must determine the target landscape and spatial scale before we introduce the ecosystem engineers (Yoshihara et al., 2010d), then examine whether the ecosystem engineers have really increased the spatial heterogeneity in the targeted landscape at that spatial scale. If they have increased it, we can more confidently consider their introduction as ecosystem engineers without significant damages to the landscape. Planting of shrubs in sandy land at high-density (461 trees / 2,500m²) could increase plant biodiversity, and thus potentially control desertification and ensure sustainable use of resources. (Yoshihara et al., unpublished data).

In parallel with the introduction of ecosystem engineers, we also must address the questions of whether spatial heterogeneity increases biodiversity in the Mongolian steppe, whether a different grazing regime would modify the effect of livestock grazing on spatial heterogeneity of vegetation and soil in Mongolia, and whether the effect of shrubs depends on the environmental context in the Mongolian steppe, because few studies to have elucidated the biodiversity, spatial heterogeneity and ecosystem engineering in the Mongolian steppe and the interactions among these factors. We should answer the questions posed here in future efforts to ensure the successful introduction of ecosystem engineers.

References


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(Received 9 March 2010, Accepted 7 June 2010)