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ORIGINAL ARTICLE

Responses of vegetation to soil disturbance by Sibelian marmots within a landscape and between landscape positions in Hustai National Park, Mongolia

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Ecosystem engineer; keystone species; landscape richness enhancement; susceptibility to disturbance; zoning.

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Abstract

Can an examination of the interactive effects of soil disturbance by rodents and landscape positions on vegetation response evaluate the ecological role of the keystone species (ecosystem engineers) at a broad scale, thereby providing good approaches to the management of the key engineers for healthy Mongolian steppes? To answer this question, we surveyed plants growing on and off the mounds created by Siberian marmots (*Marmota sibirica*) among 14 landscape positions and within a single mountain slope 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 on species composition 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. Collectively, our results suggest that sedimentation and pre-existing water conditions modify the relationships between soil disturbance and landscape position. Because the landscapes can be divided clearly into those that received only positive influences and those that received only negative influence from the marmot disturbance, zoning becomes more meaningful. Our *a priori* evaluation of the influence of keystone engineers 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.

Introduction

Until recently, ground-dwelling rodents had been considered to be pests that damage a range of agricultural crops (Poche *et al.* 1982; Singleton *et al.* 1999) and cause soil erosion (Sherrod and Seastedt 2001; Reichman and Seabloom 2002) around the world. Their ecological roles in biodiversity maintenance are now being reconsidered, as has been done for North American prairie dogs (Ceballos *et al.* 1999; Kotliar *et al.* 1999; Miller and Cully 2001). In Mongolia, the impacts of rodents on ecosystems deserve further attention, particularly since herders consistently identify them as one of the major causes of pasture degradation (Fernandez-Gimenez and Allen-Diaz 2001). However, Siberian marmots (*Marmota sibirica*, called *tarbagan* in Mongolian) are the most common rodent in Mongolia, and play many important roles, such as increasing species diversity of vegetation and modifying the soil's physical properties through burrowing, grazing, urinating and defecating; this is an example of a keystone species acting as an ecosystem engineer (Adiya 2000; Yoshihara *et al.* 2009a; Yoshihara *et al.* 2010a,b).

Empirical studies have shown that the effects of ecosystem engineers at a broad scale are context-dependent (Lawton and Jones 1995; Badano and Cavieres 2006; Crain and

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Bertness 2006). Landscapes contain specific soil structures dependent on the parent materials and pedogenic processes. Thus, it is reasonable to expect that the effects of soil disturbance by marmots on vegetation will differ among landscapes. Because marmots mix surface soil with subsoil during excavation of their burrows, we predicted that the impact of their soil disturbance would reflect the degree of environmental heterogeneity between soil structures. Thus, for instance, if they dig in poorly drained soil, the impact would be low, because the water content of the surface soil would not be greatly affected. In contrast, if they dig in well-drained surface soil with a saturated subsoil layer, the impact would be high, because the content of the surface soil would be greatly affected. However, to date there have been few attempts to examine the susceptibility of an ecosystem to soil disturbance by organisms, or the severity of the impact, at the landscape scale. To our knowledge, only Carlson and Cristo (1999) and Kerley *et al.* (2004) have reported using prairie dogs and gophers, but no study has examined the impact by marmots at the landscape scale.

The goal of the present study was thus to assess the influence of soil disturbance by marmots in Mongolian ecosystems at the landscape scale by examining the interactive effects of soil disturbance and landscape position on the vegetation response. We also evaluate these positive and negative influences in terms of biodiversity and degradation in each landscape. On the basis of these evaluations, we hope to provide good approaches to the management of marmots for maintaining biodiversity of Mongolian steppes without significant degradation.

Materials and methods

Study site

Our study site is located 100 km west of Ulaanbaatar (47°50′N, 106°00′E), Mongolia, in the 600-km^2 Hustai

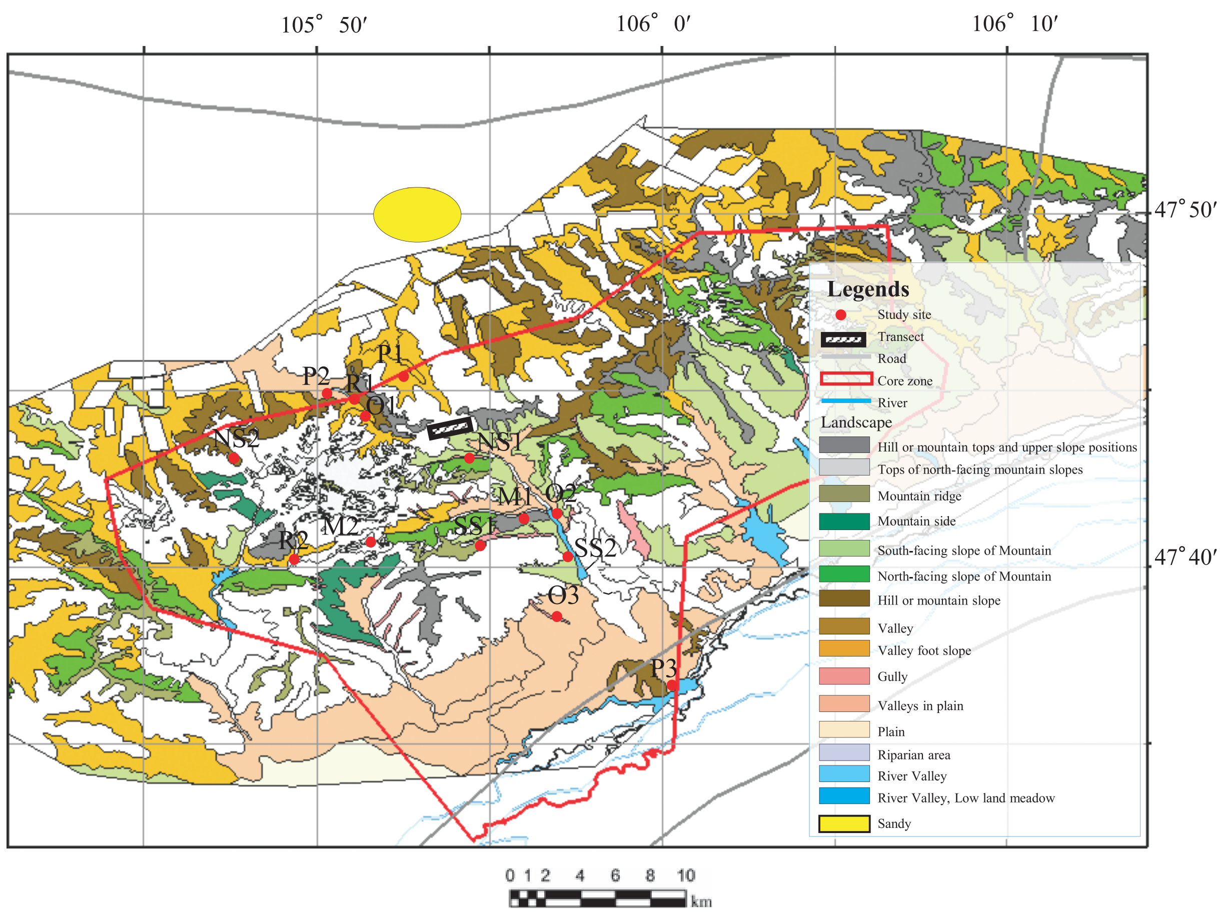

Figure 1 Map of the main landscape positions in Hustai National Park, and the locations of the study sites. See Table 1 for description of sites. This map was provided by the Takhi Reintroduction Team (Ulaanbaatar, Mongolia).

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National Park (HNP) in Mongolia's forest steppe region. HNP received 232 mm of annual precipitation, averaged over the past decade. The annual average temperature is 0.2°C, and average monthly temperatures vary greatly, between −20.6°C in January and +19.0°C in July.

HNP ranges in elevation from 1100 to 1840 m above sea level (asl) (Hustai Mountain). The landscape is dominated by a central mountain range composed primarily of granitic rocks. The land is mostly a rolling plain that slopes downhill from the north toward the south, where it borders on the broad valley of the Tuul river (Wallis de Vries *et al.* 1996). The zonal soils are identified as Haplic Kastanozems by the World reference base for soil resoruces (FAO/ISRIC/ISSS 1998) based on soil profile morphology and physico-chemical properties.

HNP contains representative types of all the main Mongolian landscapes: grasslands, shrubland steppes, birch-dominated forests, hills and mountains, rivers, sand dunes, and abandoned croplands. For the past 15 years, livestock have been excluded from core areas of HNP for conservation purposes. The overall marmot density in HNP was 1.16 per ha in 1998 (Takhi Reintroduction Centre 1998).

Sampling design

We compared the effects of soil disturbance by marmots among landscape positions and within a single landscape position (along a transect from a mountain slope). We selected examples of all typical landscape positions from the HNP landscape map, except for landscape positions that had no marmot mounds (Figure 1); namely (i) hill or mountain tops and upper slope positions; (ii) tops of north-facing mountain slopes; (iii) mountain ridges; (iv) south-facing slopes of a mountain; (v) north-facing slopes of a mountain; (vi) hill or mountain slopes; (vii) valleys at the foot of a mountain slope; (viii) valleys in a plain; (ix) river valleys; (x) riparian areas; and (xi) gullies (Table 1). Although these landscape positions had distinctive soil types, we added two sites to include two additional soil types that are commonly found in the park: a shallow chestnut soil and an alpine meadow soil (valleys in a plain 2 (12) and valleys at the foot of a mountain slope 2 (13) in Table 1). In addition, we established a site at the border between landscape positions where marmot mounds were constructed on a steep cliff (14) because of the uniqueness of this site.

Our field surveys were conducted in late July 2007. In each landscape position, we selected five separated marmot mounds that were still in use, and that were neither old (abandoned) nor new (still showing evidence of ongoing construction, such as the presence of fresh sand deposited outside the mound) to remove the effects of usage history on the vegetation. At each mound, we established a 1 × 1-m quadrat (mound size) on the mound and a second one off

Table 1 Characteristics of each study site. The sampling sites in this table are presented in sequence from mountain to dry riverbed positions

Landscape unit	Altitude (m asl)	Soil texture	Sampling site (landscape position)
M (mountain 1)	1360	G	Hill or mountain tops and upper slope positions
M2	1700	G	Tops of north-facing mountain slopes
SS (south-facing slope 1)	1420	G/F	Mountain ridges
SS2	1260	G	South-facing slopes of a mountain
NS (north-facing slope 1)	1420	F	North-facing slopes of a mountain
NS2	1460	F	Hill or mountain slopes
P (plain1)	1360	G/S/F	Valleys at the foot of a mountain slope
P2	1360	G/F/S	Valleys in a plain
P3	1180	G/F	Valleys in a plain 2
R (dry riverbed 1)	1360	F/G	River valleys
R2	1440	G/F	Riparian areas
O (other 1)	1420	G/F	Valleys at the foot of a mountain slope 2
O2	1300	F/G	Steep cliff
O3	1260	G/F	Gullies

Soil textures: G, gravel; S, sand; F, fine-textured material (e.g., silt and clay).

the mound at a location that received the least influence from animals around the mound (Van Staalduinen and Werger 2007). We estimated cover and average height for each species found in the quadrat. Sampling size is small (10 quadrats in each landscape position = total 140 quadrats) because we had a low possibility of finding new species in each landscape position.

For our within-landscape position study, we selected a single focal landscape position and established a 700 m × 10 m transect along a mountain slope that ran uphill from the toe slope to the summit of the mountain (Figure 1). We established pairs of 1 × 1-m quadrats (on the mounds and off the mounds) along the transect at every ~ 40 m (total investigated = 34 quadrats), using the same approach that we used for the between-landscape comparison, and recorded the ground cover and height data for each plant species. Infact, one of the plots was always on-mound and the second one was off-mound.

Data analysis

We used the Arcmap 9.1 software (ESRI) to calculate the topographic characteristics of the study sites. On the basis of the observed combinations of landscape positions, soil types and the landform classification according to contour maps,

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we grouped the 14 landscape positions into six main landscape units (Table 1): mountain (M), south-facing slope (SS), north-facing slope (NS), plain (P), dry riverbed (R), and other (O). To evaluate the contribution of disturbance by marmots to plant biodiversity at the landscape scale, we used the parameter "landscape richness enhancement" (LRE), which 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 total number of habitat specialists (i.e., species found only in the engineered mound quadrats) per landscape position and N_u represents the total number of species that colonize unmodified habitats (i.e., off-mound quadrats) per landscape position. Thus, LRE will increase as more species become dependent on the environmental changes caused by the ecosystem engineer.

For the between-landscape position study, we pooled the vegetation data from the five replicated quadrats (five mounds) per position (on-mound or off-mound) in each landscape position into a single averaged value. Then, we used detrended correspondence analysis ordination (DCA; Hill 1979a) to examine all changes in plant species composition between the on- and off-mound positions between sites, using the PC-ORD software (version 4.0; McCune and Mefford 1999). Prior to the analysis, vegetation data were log-transformed to meet the assumptions of normality.

For our statistical analysis, we used two-way analysis of variance (ANOVA) to test for differences among the five main landscape units in total plant volume (plant height × cover) and in species richness by species and life form, differences between the two quadrat positions (on and off the mounds), and landscape–disturbance interactions. We separated the plant data into life forms (grasses, forbs or shrubs) because a community's response to disturbance depends on the life-history characteristics of the component species. When necessary, plant data were log-transformed to meet the assumptions of normality. These statistical analyses were performed using the STATISTICA 6.0J software for Windows (StatSoft Inc., Tulsa, OK, USA).

To classify the vegetation samples in the within-landscape position study (along the mountain slope), we analyzed data from the individual quadrats by two-way indicator-species ordination analysis (TWINSPAN; Hill 1979b) under compositional similarity using the PC-ORD software (version 4.0; McCune and Mefford 1999). Maximum level of division was set to 6. From the results, we classified individual quadrats into four community types at each topographical position. Then, we used the DCA analysis to examine all changes in plant species composition between topographical positions within a landscape position.

Results

Plant community in each landscape

Across all landscapes, we recorded a total of 55 plant species, with an average of 4.1 per quadrat. Plant species richness varied significantly as a function of landscape and soil disturbance by marmots (Table 2). The total species richness was higher off mounds than on mounds (Figure 2), especially at sites NS1 (8 *vs* 3 species, respectively), NS2 (24/15), and R1 (12/6). LRE varied greatly among the landscape positions, ranging from 0 at site R2 to 0.83 at site P3 (Figure 2).

Total plant volume was significantly affected only by disturbance (Table 2). In addition, volumes of all three plant life forms showed no significant landscape effect, but only grasses showed a significant disturbance effect, and only the forbs showed a significant landscape × disturbance interaction. All landscape positions except sites M1 and P3 showed higher total vegetation coverage off the mounds (Figure 2). Although the cover of grasses was greater off the mounds in all landscape units, the magnitude of the difference varied greatly among landscape positions (Figure 2). For instance, although the cover of grasses off the mounds was seven times the value on the mounds at P1, it was only slightly higher off the mounds at M1 and NS2. The mean coverage by forbs was notably greater off the mounds at NS2 than at the other sites, attributable to the presence of *Pedicularis flava* Pall., but was higher on the mounds at P1 (Figure 2). The differences in mean cover by shrubs can be explained by landscape differences, since shrubs were not found at every site (Table 2). The mean coverage by shrubs was greater on the mounds at M2, SS1, NS2, P3 and O3 (Figure 2).

Ordinations for each landscape

The Eigenvalues were 0.634 and 0.365 for DCA axes 1 and 2, respectively, and the lengths of the corresponding

Table 2 Summary of the two-way ANOVA results. Explanatory variables are landscape units (L, df = 4), disturbance (D, df = 1) and their interaction ($L \times D$, df = 4)

Criterion variable	L	D	$L \times D$
Plant volume			
Total	NS	***	NS
Grasses	NS	***	NS
Forbs	NS	NS	*
Shrubs	NS	NS	NS
Plant species richness			
Total	**	**	NS

*, **, and *** indicate significant effects at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. NS indicates no significant effect.

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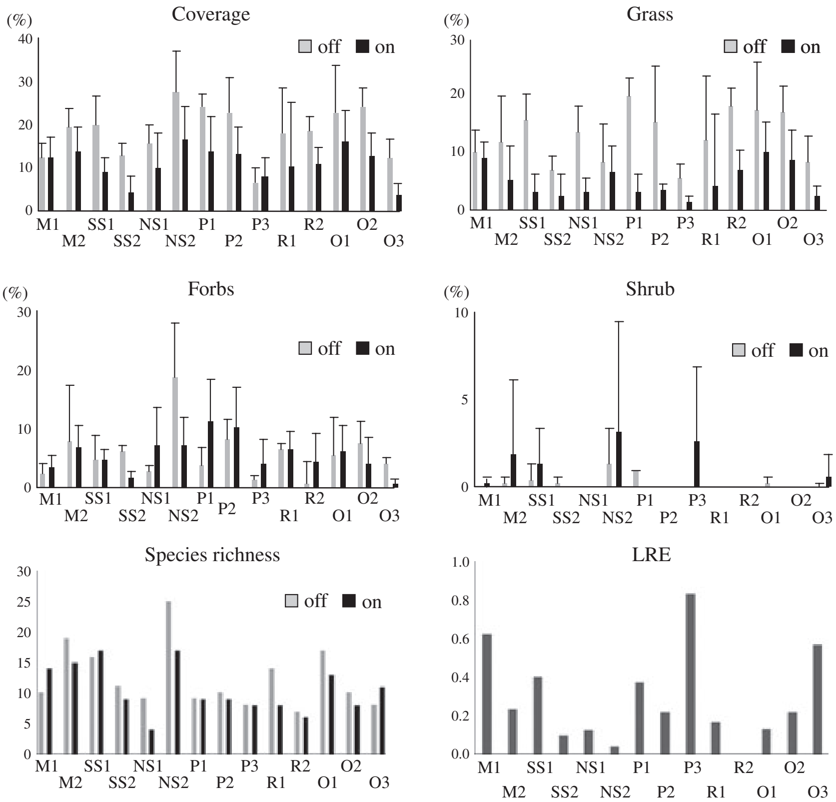

Figure 2 Mean coverage (%) of each life form per quadrat (+SD) and total number of species in the off-mound quadrats and in the on-mound quadrats, and landscape richness enhancement (LRE) values in each landscape position.

gradients were 3.144 and 3.477. P1, SS1 and SS2 showed large distance in their site scores between the on- and off-mound quadrats, whereas M1, M2 and O1 showed relatively little movement (Figure 3a). Landscape positions with a lower score along axis 1 (less than approximately 150) for the off-mound quadrats tended to move towards a higher score along axis 1 for the on-mound quadrats. In contrast, two landscape positions (NS1 and R1) had higher scores along axis 1 (greater than approximately 150) for the off-mound quadrats than for the on-mound quadrats; that is, the landscape positions with both extreme sides of axis 1 for the off-mound clustered around the middle of axis 1 by marmot disturbances (Figure 3a).

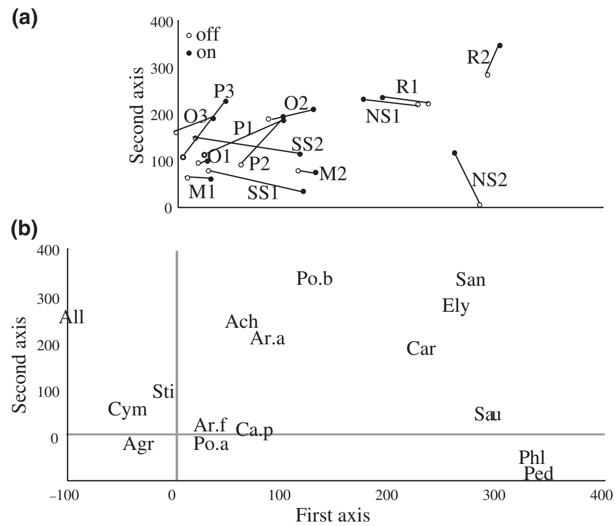

Figure 3 (a) Results of the detrended correspondence analysis (DCA) ordination of the site scores for the 14 landscape positions. Lines connect the off-mound and on-mound values for each landscape. Table 1 defines the landscape characteristics for each abbreviation. (b) Plots of the DCA scores for 16 representative species: Ach, *Achnatherum splendens*; Agr, *Agropyron cristatum*; All, *Allium bidentatum*; Ar.a, *Artemisia adamsii*; Ar.f, *Artemisia frigida*; Ca.p, *Caragana pygmaea*; Car, *Carex korshinskii*; Cym, *Cymbaria dahurica*; Ely, *Elymus chinensis*; Ped, *Pedicularis flava*; Phl, *Phlomis tuberosa*; Po.a, *Potentilla acaulis*; Po.b, *Potentilla bifurca*; Sau, *Saussurea salicifolia*; San, *Sanguisorba officinalis*; Sti, *Stipa krylovii*.

Species composition and TWINSPAN ordination along the mountain slope transect

At the first level of division, the plots were divided into two groups (Figure 4a), which corresponded to toe-slope sites and other sites (midslope positions and summits, Figure 5), respectively. Thus, topographic-derived sedimentation and water availability seem to be the important factors in this division. At the second level of division, the first group was divided into groups 1 and 2 based on the presence or absence of mounds, respectively, and the second group was divided into groups 3 and 4 based on topography (summits

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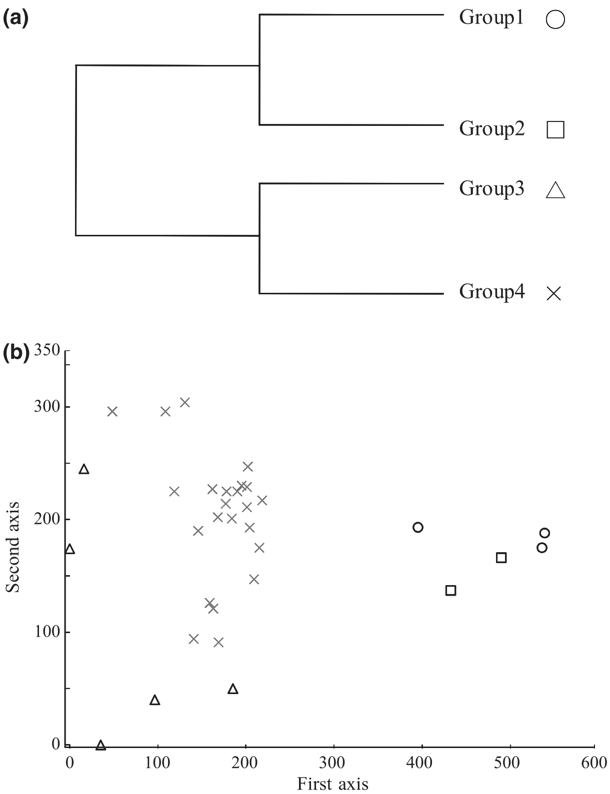

Figure 4 Classification results produced by the TWINSPAN ordination (a) and results of the detrended correspondence analysis ordination for the on- and off-mound plots along the mountain slope transect within a landscape position (b). Symbols represent the classification of each plot in TWINSPAN.

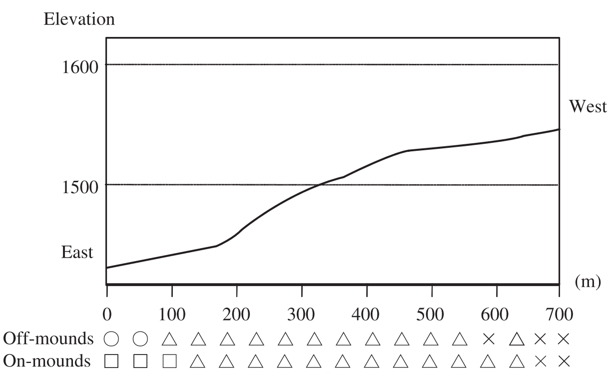

Figure 5 Distribution of elevations along the east to west transect, and classification results based on species composition along the transect. Symbols below the *x*-axis indicate the results of TWINSPAN. ○:Group 1; □:Group 2; △:Group 3; ×:Group 4.

and midslope positions, respectively; Figures 4a,5). Disturbance by marmots and soil texture may thus have affected this division.

Group 1 included plots off the mound on toe-slopes (Figure 5), and was characterized by marsh vegetation such as *C. korshinskii* and *Artemisia dracunculus* L.. At these sites, the soil surface was covered by clayey sediments with high water-holding capacity. Group 2 included plots on mounds in toe-slope positions (Figure 5), and was characterized mainly by the perennial grass *Elymus chinensis* (Trin.) Keng. Their soil was drier and soil texture was coarser than in group 1.

At the midslope positions, we found no obvious difference in species composition between the off- and on-mound positions, and thus both belonged to the same group 3 in the analysis (Figures 4a,5). The dominant species in this group (*S. krylovii*, *Potentilla acaulis L.*, and *Artemisia frigida* Willd.) are typical steppe species that were found at most sites. In addition, perennial forbs such as *Geranium pseudosibiricum* J. Mayer., *Rheum undulatum* L., and *Saussurea salicifolia* (L.) DC. appeared only occasionally on the mounds. Soil texture was intermediate between that on toe-slopes and at the summits, and was mainly a mixture of sand and gravel.

Group 4 included summit quadrats (Figure 5), in which the species composition varied dramatically. The dominant grass changed from *S. krylovii* at the midslope positions to *Festuca sibirica* Hack. Ex Boiiss. and *Agropyron cristatum* (L.) P.B.. *Allium bidentatum* Fisch. ex Prokh. and plants that grow in rocky soils such as *Orostachys spinosa* (L.) C.A. and *Arenaria capillaris* Poir. appeared, and increased the species richness. The on-mound and off-mound positions had similar species at these mountain sites. The soils were rocky, which meant soil water was low.

DCA showed that five plots on toe slopes (group 1, 2) and other slope positions (groups 3 and 4) were separated in the ordination space (Figure 4b). The Eigenvalues were 0.837 and 0.460 for DCA axes 1 and 2, respectively. The plots at the midslope and summit positions were sparse along axis 2 and in the ordination space, respectively. Along axis 1, we found a gradient in the landscape position in the order group 3, 4, 2 and 1, which coincides with the topographic gradient from the highest summit to the lowest toe-slope. Thus, axis 1 is associated with topographic-derived soil particle size or water availability.

Discussion

Susceptibility against disturbance

In mountain areas, the DCA ordination showed short gradient length between on- and off-mound positions, indicating a lower sensitivity to marmot disturbance (Figure 3a). This observation was supported by the results along the mountain slope transect, which showed similar vegetation types on the summits regardless of the presence or absence of disturbance (Figure 5). On the tops of mountains and at upper

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slope positions, loss of vegetation cover is caused predominantly by landslides, which produce rocky outcrops even in deeper soils. Thus, when marmots excavate their burrows, they mostly pile rocks to create their mounds. The result is a similarity of soil environments off and on the mounds, which may have caused the similarity of plant species compositions at these two positions. A similar result was obtained in the Chihuahuan desert, where some differences in soil properties and plant coverage between gopher mounds and undisturbed soil were observed at lower slope positions, whereas the differences on ridges were not significant (Kerley *et al.* 2004).

Cingolani *et al.* (2003) showed that the magnitude of changes in floristic composition produced by grazing decreased with increasing soil moisture. Similarly, Wright *et al.* (2006) demonstrated that the magnitude of the effects of ecosystem engineering (shrub mounds) on plants communities was smaller in years with higher precipitation. Our results show the opposite trend, with less floristic changes in dry mountain ridge areas, perhaps because burrowing modified soil moisture levels more directly than did grazing and shrub mounds.

Differential responses to disturbance

We found significant landscape × disturbance interactions for forbs (Table 2). Plains areas and site NS1 both showed increased forb cover with marmot disturbance, attributable to the increase of *Artemisia adamsii*. In contrast, NS2, O2 and O3 showed decreased forb cover, contradicting the results of previous studies (Coppock *et al.* 1983; Archer *et al.* 1987; Van Staalduinen *et al.* 2007). One possible explanation is that marmots created mounds on steep slopes in these landscapes, causing the scooped-out soils to fall down the slope. Such excavation-induced soil movements on mounds may have interrupted the establishment of plants.

The high score on axis 1 at humid sites such as R1 and R2 and the low score at drier sites such as M1 indicate that axis 1 is associated with water conditions: the higher the score on this axis, the more water is present (Figure 3a). This interpretation is supported by the presence of plants that require moist conditions, such as *Carex korshinskii* Kom., *Phlomis tuberose* L., and *Sanguisorba officinalis* L., towards the right side of axis 1 (Figure 3b, Wallis de Vries *et al.* 1996). Dissected upper-mountain landscapes such as M1, M2, and SS1 had a lower score along axis 2, whereas fluvial and sedimentary landscapes such as R1 and R2 had a higher score (Figure 3a), which suggests that axis 2 is associated with geological processes. We thus hypothesized that landscapes respond differently to marmot disturbance according to the pre-existing abundance of water. Our results support this hypothesis by the fact that surface soils that may become relatively more humid as a result of soil disturbance were located on the south-facing slopes of mountains (Figure 3a). In general, such slopes have drier surface soils than the north-facing slopes because of the higher intensity of sunlight and greater snowmelt (Isard 1986). Therefore, frequent excavation of humid soil from deeper down, or offer of shade may have favored the survival of plants that are adapted to humid soils such as *Carex* spp. Soil surface moisture was positively correlated with burrow density in an area with ground squirrels (Laundre 1993).

On the other hand, mounds on sites NS1 and R1 may have changed to relatively drier environments as a result of soil disturbance, and were located in relatively humid environments (Table 1). Marmots must dig vertically into the soil in flat areas (6° in NS1 and 4° in R1), so mounds rise higher above the surrounding terrain than in other areas. Therefore, the soil of the mounds may becomes drier because it is far above the watertable, and runoff water from mountain slopes bypasses them, resulting in relatively drier soils in the mounds than off the mounds. Furthermore, small particles (organic-rich sediments) that have been carried down from higher positions in the mountains are deposited in these landscapes (Burke *et al.* 1995). Thus, if marmots excavate the soils vertically at these sites, soils with a high proportion of sand or gravel that are poor in organic matter and that derive from deeper soil layers are transported above the finer materials that have been deposited at the surface. These mounds thus have poor water-retention ability. This was evident along the mountain slope transect (groups 1 and 2 in the TWINSPAN ordination). A similar effect was reported in a previous study, in which the finer soil fractions were progressively lost from gopher mounds (Sherrod and Seastedt 2001).

Taken together, these results suggest that creation of the mounds may have changed not only the soil water status, but also the soil organic matter content and soil texture, leading to the creation of heterogeneous patches. However, there are limitations to the current study regarding sample size and lack of information on soil properties. More work needs to be done to elucidate the mechanisms underlying these patterns.

Despite belonging to the same landscape units, LRE values were notable at sites SS1 among the main landscape units (south-facing slope) and P3 among the main landscape units (plain) (Figure 2). SS1 is located close to forested zones and P3 is located close to the river. Previous research showed that soil pits (which are also created next to each mound by the marmots' digging) were effective as traps for seeds (Reichman 1984), and were consequently colonized at higher densities by species with dispersed seeds (Boeken *et al.* 1995). In this light, site SS1 is likely to receive seed rains from forest species, whereas site P3 will receive more seed rains from species that become established near flowing rivers, and these seeds can successfully colonize the

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bare ground of the mounds created by marmots. Indeed, newly established species such as *Amygdalus pedunculata* and *Dasiphora fruticosa* were unique to forested zones, whereas *Caragana microphylla* and *Convolvulus ammanii* are characteristically observed near the Tuul River. Therefore, the numbers of species that colonize the marmot mounds may depend not only on landscape units, but also on surrounding sources of seed. Regional-scale control of species richness may thus play an important role at our study sites.

Disturbance by marmots is a double-edged sword. As the LRE results show, disturbance had greater positive effects in landscape positions surrounded by key seed sources, such as M1, M2, SS1 and P3 (Figure 2). However, plant volume, which is one of the important criteria for increasing site productivity and decreasing soil erosion (Trimble and Mendel 1995; Pimentel and Kounang 1998), decreased on mounds at most sites, with the exceptions of M1 and P3 (Figure 2). Therefore, the landscapes can be divided clearly into those that received only positive influences and those that received only negative influence from marmot disturbance.

Management implication

Marmots have been used sustainably as an important traditional food source and as a source of foreign income through the sale of skins (Adiya 2000). However, because of a recent sharp decline in marmot populations, the Mongolian government prohibited hunting of these animals throughout Mongolia from 2005. Yet despite the ban, more than 26 000 marmot skins had been confiscated by the end of August 2005 (Wingard and Zahler 2006). This shows the difficulty of moderating the strong demand for marmots and of controlling illegal hunting in a thinly populated developing country.

To combat this problem, we call for alternative measures such as zoning, in which government managers would designate a strictly controlled conservation area in which no hunting is allowed and other areas in which hunting is permitted (Walther 1986; Newing 2001). Because the landscapes can be divided clearly into those that received only positive influences and those that received only negative influence from the marmot disturbance, keystone modifiers (*sensu* Mills *et al.* 1993) may be targeted for conservation in certain contexts; the areas in which they have positive effects could be established as conservation (non-hunting) areas, and areas in which they have a negative effect could be designated as hunting zones, thereby meeting both conservation objectives and local demands to utilize this resource.

Thus far, traditional conservation efforts have focused on attractive species or on certain areas that provide homes for endangered species, regardless of whether these species are ecosystem engineers or not. Thus, little attention has been paid to the ecological influence of organisms on ecosystems when considering conservation problems. Our *a priori* evaluation of the influence of marmots on the ecosystems they inhabit could thus provide insights into how to optimize the performance of ecosystem engineering in a way that is beneficial to ecosystem management.

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