

Local-scale disturbance by Siberian marmots has little influence on regional plant richness in a Mongolian grassland

Takehiro Sasaki · Yu Yoshihara

Received: 5 March 2012 / Accepted: 29 October 2012 / Published online: 8 November 2012
© Springer Science+Business Media Dordrecht 2012

Abstract Our objective was to examine the relative importance of local-scale disturbance by Siberian marmots in increasing regional (landscape-wide) plant richness. We used an additive diversity partitioning framework and quantified species richness patterns of grassland plant communities affected by marmot disturbance across different spatial scales: within and among on- and off-marmot-mound subsites, among sites, and among landscape units (corresponding to α and three levels of β richness). Values of β richness among subsites and β richness among landscape units were similar to those expected by chance. This suggests that plant species are randomly distributed among subsites and among landscape units, despite the prediction based on previous studies that local-scale disturbance by Siberian marmots and its interactive effects with landscape contexts disproportionately influence spatial patterns of plant species. Of the spatial components of regional richness, only the β richness among sites was significantly different from the expected value, probably reflecting the differential

spatial pattern of disturbance by marmots at a site scale. The β richness among landscape units contributed the most to regional richness, whereas β richness among subsites and among sites contributed less. Thus, our results suggest that local-scale disturbance by Siberian marmots has little influence on regional plant richness in a Mongolian grassland.

Keywords Additive partitioning · Arid and semi-arid ecosystems · Beta diversity · Ecosystem engineer · Mongolia · Species richness

Introduction

Understanding the importance of local-scale enhancement of species diversity by disturbances in the maintenance of regional diversity is a key to comprehensive conservation of biodiversity within a region (Whittaker et al. 2001; Ricklefs 2004). Since local-scale disturbance interacts with a range of biotic and abiotic factors across landscapes (Bestelmeyer et al. 2003; Questad and Foster 2007), we need a multi-spatial scale assessment of how local-scale disturbance contributes to regional diversity.

The ecological roles of ground-dwelling rodents in biodiversity maintenance have been a concern among ecologists, as in the case of North American prairie dogs (Ceballos et al. 1999; Kotliar et al. 1999; Miller

T. Sasaki (✉)
Graduate School of Frontier Sciences, The University
of Tokyo, 5-1-5 Kashiwanoha, Kashiwa,
Chiba 277-8653, Japan
e-mail: sasa67123@gmail.com

Y. Yoshihara
Graduate School of Agricultural Science, Tohoku
University, 232-3, Yomogida, Naruko-Onsen,
Osaki, Miyagi 989-6711, Japan

and Cully 2001). Previous studies of grasslands reported that disturbance by rodents enhances the establishment of rhizomatous species and fugitive forbs, which are competitively inferior to dominant grasses, resulting in an increase in species richness at the local (patch) scale (Coppock et al. 1983; Guo 1996; Questad and Foster 2007). However, few studies have examined the relative importance of local-scale disturbance by rodents in increasing regional (landscape-wide) diversity. Empirical studies have shown that the effects of ecosystem engineers at a broad scale are context-dependent (Badano and Cavieres 2006; Crain and Bertness 2006). Landscapes consist of various units that have specific soil structures dependent on the parent materials and pedogenic processes. Thus, it is likely that the effects of soil disturbance by rodents on vegetation differ among landscape units.

Spatial scaling of diversity patterns allows researchers to identify the most important sources of diversity and the existence of processes operating at both small and large spatial scales. Additive partitioning of species diversity provides a useful framework for quantifying the spatial patterns of diversity across hierarchical spatial scales (Lande 1996). Total species diversity in a pooled set of communities (γ) can be partitioned into additive components representing within-community (α) diversity and between-community (β) diversity (Lande 1996). The additive relationship among diversity components (i.e., $\beta = \gamma - \alpha$) enables quantification of the contributions of α and β diversity to overall diversity across a range of spatial scales (Gering et al. 2003; Lande 1996; Veech et al. 2002). Thus, additive diversity partitioning allows the identification of the scale by which diversity is maximized (Lande 1996; Veech et al. 2002). Moreover, a comparison of observed patterns with those predicted by null models gives insights into the existence of ecological processes that may disproportionately differentiate total species diversity (Crist et al. 2003).

Siberian marmots (*Marmota sibirica*) are the most common rodent in Mongolia and are an example of a keystone species acting as an ecosystem engineer. They play many important ecological roles, such as changing species diversity of vegetation and modifying the soil's physical properties through burrowing, grazing, urinating, and defecating (Adiya 2000; Yoshihara et al. 2009; Yoshihara et al. 2010a, b). In this study, we performed hierarchical sampling of plant communities affected by Siberian marmot

disturbance at a local scale in a Mongolian grassland. We quantified species richness patterns of grassland plant communities across different spatial scales using an additive diversity partitioning framework. We then used a randomization approach to test the null hypothesis that plant assemblages are uniform across all spatial scales investigated and that observed β richness among samples is simply a sampling effect (Crist et al. 2003). If local-scale disturbance by Siberian marmots and its interactive effects with landscape contexts disproportionately influence spatial patterns of plant species, we would observe greater β richness at the local and landscape scales than expected by chance, thus rejecting this null hypothesis.

Methods

Study sites

Our study site is located 100 km west of Ulaanbaatar (47°50.0'N, 106°00.0'E), in the 600-km² Hustai National Park (HNP) in Mongolia's forest steppe region (Yoshihara et al. 2010c). 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 1,100 to 1,840 m above sea level (Hustai Mountains). 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 Haplic Kastanozems as identified by the world reference base for soil resources (FAO et al. 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). The present field survey was conducted within the preserved area of HNP. The plant communities within this area are generally dominated by the perennial grasses *Agropyron cristatum*, *Carex korshinskyi*, *Elymus chinensis*,

Koeleria macrantha, and *Stipa krylovii* (Yoshihara et al. 2009, 2010a; nomenclature follows Grubov 1982).

Site selection and vegetation sampling

A hierarchical sampling design was conducted to investigate how the effects of marmot disturbance on plant species richness at a local scale contribute to regional plant richness using additive partitioning of species richness across different spatial scales. We selected sites that covered all typical landscape units from the HNP landscape map (Yoshihara et al. 2010c), except for landscape units that had no marmot mounds. The six sampled landscape units were hill or mountain tops; mountain ridges or south-facing slopes of a mountain; north-facing slopes of a mountain; valleys in a plain; river valleys or riparian areas; and marginal landscape units such as steep cliffs and gullies (Table 1). Although these landscape units had distinctive soil types, all of them had grassland physiognomy.

Field surveys were conducted in July which was the time of peak aboveground biomass and species appearance, in 2007. In each landscape unit, 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). This procedure was done to minimize the effects of initially large disturbance on vegetation and to remove the effects of different lengths of abandonment which would differentiate the stages of succession. In particular, because time of abandonment is difficult to identify in the field, we decided to survey vegetation only on mounds that were in use. Although the exact durations of use were also unknown, plant species composition on the mounds was likely to be stabilized under the subsequent moderate disturbance by marmots after the

initial construction of mounds. At each mound, we established a 1 × 1 m quadrat (about equivalent to the mound size) on the mound and a second one off the mound at a location that received the least influence from animals around the mound (Van Staalduinen and Werger 2007). We visually estimated the percent cover of each species present in the quadrats, but in this study, we used the presence–absence information in the vegetation data for additive partitioning of regional species richness. Consequently, we sampled 10 quadrats (5 paired on- and off-mound quadrats) at each of the 14 sites belonging to six different landscape units (Table 1), for a total of 140 quadrats. Hereafter, we refer to on- and off-mounds (each consisted of 5 quadrats) at each site as the subsites. Each landscape unit included two or three sampling sites (replicates).

Data analysis

We tested the null hypothesis that species richness is uniform at all spatial scales by additive partitioning of total richness (γ richness). In this study, total richness across different landscape units within HNP is the sum of α and β richness (Lande 1996), that is, the average richness within the subsites, average richness among the subsites, average richness among the sites, and average richness among the landscape units.

The PARTITION 3.0 program (Veech and Crist 2009) was used to calculate average richness (α) at each scale, and the differences between them indicate β richness. Although species diversity can be measured as the Simpson or Shannon index (Magurran 2004), recent theoretical analysis of the mathematics of diversity in ecology (Jost et al. 2010) suggested that these indices are not necessarily appropriate in additive partitioning of diversity and that results are often difficult to interpret in a biological sense. This is also the case for our study, and

Table 1 Characteristics of the six landscape units

Landscape unit ^a	Description	Mean elevation (m)	Soil texture ^b
Mountain (2)	Hill or mountain tops	1,530	G
South-facing slope (2)	Mountain ridges or south-facing slope of a mountain or a hill	1,340	G/F
North-facing slope (2)	North-facing slopes of a mountain or a hill	1,440	F
Plain (3)	Valleys in a plain	1,300	G/F/S
Riverbed (2)	River valleys or riparian areas	1,400	G/F
Others (3)	Marginal units such as steep cliffs and gullies	1,330	G/F

^a The number of sampling sites in each landscape unit is indicated in parentheses

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

therefore, we did not use these indices. Total richness across different landscape units can be partitioned into the richness contributed by each scale, as follows:

$$\alpha_1 = \bar{S}_{\text{microsite}}, \quad (1)$$

$$\beta_1 = \bar{S}_{\text{site}} - \alpha_1, \quad (2)$$

$$\beta_2 = \bar{S}_{\text{landscape}} - \bar{S}_{\text{site}}, \quad (3)$$

$$\beta_3 = \gamma - \bar{S}_{\text{landscape}}, \quad (4)$$

where $\bar{S}_{\text{microsite}}$, \bar{S}_{site} , and $\bar{S}_{\text{landscape}}$ are the average richness within a subsite, a site, and a landscape unit, respectively. Thus, regional (total) richness can be described as follows:

$$\gamma = \alpha_1 + \beta_1 + \beta_2 + \beta_3. \quad (5)$$

We used the sample-based randomization procedure in PARTITION to test whether the observed partitions of regional richness could have been obtained by a random allocation of lower-level samples nested among higher-level samples (Crist et al. 2003). To test the significance of α_i and β_i , samples at level $i - 1$ were randomly allocated only to those samples at level i that belonged to the same sample unit at $i + 1$. In this way, to test the significance of α_1 and β_1 , the lowest-level samples (i.e., the quadrat samples, $n = 140$) were randomly assigned to samples aggregated by the on-mound and off-mound subsites ($n = 28$). Then, in separate randomizations, the subsite level samples were randomly assigned to the site level samples ($n = 14$); and the site level samples were randomly assigned to the landscape unit samples ($n = 6$), to test the significance of β richness at each hierarchical spatial scale. Null values of β_i obtained from 1,000 randomizations were used to obtain a P value for the observed β_i at each scale. Deviations of the observed richness from the null expectation indicate a nonrandom spatial distribution of plant species at a given scale. Because the statistical significance of each richness component is tested using a separate set of randomizations, the expected values of α_1 and β_i are not additive to the total richness (Crist et al. 2003).

Results

We recorded a total of 51 species in the entire landscape from the 140 quadrats across six different landscape units. Low regional richness probably reflects the severe aridity and influence of long history

Table 2 Additive partitioning of species richness across hierarchical spatial scales

Richness	Description	Observed	%	Expected	P^a
α_1	Within subsites	10.68	20.94	10.58	NS
β_1	Among subsites	3.27	6.41	3.37	NS
β_2	Among sites	8.66	16.98	7.27	<0.05
β_3	Among landscape units	28.39	55.67	28.68	NS
γ	Total ^b	51		–	

Total richness across different landscape units within Hustai National Park is the sum of α and β richness, that is, the average richness within on- and off-marmot-mound subsites, average richness among on- and off-marmot-mound subsites, average richness among sites, and average richness among landscape units

^a The observed partitions are compared with the expected values as predicted by the null model (level of significance $P < 0.05$; NS not significant)

^b Note that because the statistical significance of each richness component was tested using a separate set of randomizations, the expected values of α_1 , β_1 , β_2 , and β_3 are not additive to the total richness (Crist et al. 2003)

of livestock grazing before the establishment of the national park. The average species richness within all quadrats (i.e., α_0 richness: note that the significance of α_0 richness cannot be tested by the sample-based null model) was 4.43. On-mound quadrats were generally dominated by fugitive forbs such as *Artemisia adamsii*, whereas off-mound quadrats were dominated by perennial grasses such as *S. krylovii* and *C. duriuscula*.

Mean richness within subsites (α_1), mean richness among subsites (β_1), and mean richness among landscape units (β_3) were not significantly different from the null expectations (Table 2). Only the β_2 component (mean among-site richness) was significantly higher than expected. Of these richness components, β_3 richness accounted for a substantial proportion of the total richness.

Discussion

In this study, the β richness among on- and off-mound subsites and that among landscape units were similar to those expected by chance (Table 2). This means

that plant species are randomly distributed among subsites and among landscape units, despite the prediction based on previous studies that local-scale disturbance by Siberian marmots and its interactive effects with landscape contexts disproportionately influence spatial patterns of plant species (Badano and Cavieres 2006; Crain and Bertness 2006; Questad and Foster 2007). Another key finding is that the β richness among landscape units contributed the most to total richness, whereas β richness among subsites and among sites contributed less (Table 2), suggesting that local-scale disturbance by Siberian marmots has little influence on regional plant richness. Previous studies also found that the largest scale contributed most to the regional diversity of beetle assemblages in forest ecosystems (Gering et al. 2003) and that of coral assemblages in coral reef ecosystems (Zvuloni et al. 2010). However, Chandy et al. (2006) found that intermediate scales contained the largest proportion of total diversity of tree and understory species in forest ecosystems.

Of the spatial components of regional richness, only the β richness among sites was significantly different from the expected value, indicating that plant species are not randomly distributed among sites (Table 2). This result points to the importance of biotic or abiotic factors at the site level in determining community composition and richness. One possible explanation for this result is that a differential spatial pattern of disturbance by marmots, such as differences in the disturbance size and in the configuration of disturbance, affects the spatial heterogeneity of vegetation through changes in the disturbance regime at the site level (Adler et al. 2001; Yoshihara et al. 2010a, b), resulting in a nonrandom distribution of plant species among sites. Although differences in abiotic factors such as soil moisture or nutrients among sites might also explain nonrandom distribution of species, we cannot definitively examine the relative importance of these factors from this study.

Additive partitioning of species richness thus allows researchers to identify the most important sources of diversity and the existence of processes operating across hierarchical spatial scales (Crist et al. 2003; Veech et al. 2002). In Mongolian grasslands, Siberian marmots may play a minor role in determining regional plant richness. However, our results do not necessarily suggest that local-scale disturbance by marmots is unimportant in fostering diversity, because

a nonrandom process driven by marmot disturbance is one of the responsible factors for the differences in community composition among sites. Indeed, in the face of the recent sharp decline in marmot populations in Mongolia, the importance of marmot conservation itself needs to be more strongly recognized (Yoshihara et al. 2010c), even though we cannot justify it in terms of the maintenance and enhancement of regional plant richness.

Acknowledgments This work was financially supported by the Sumitomo Foundation for Environmental Research (No. 103117), with additional support from Tohoku University's Global COE program "Ecosystem Adaptability Science for the Future" (No. J03) and a Grant-in-Aid for Young Scientists B (No. 23710278) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

References

- Adiya Y (2000) Mongolian marmots: biology, ecology, conservation, and use in Mongolia. Mammalian Ecology Laboratory, Institute of Biological Sciences, Mongolian Academy of Sciences, Ulaanbaatar
- Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479
- Badano EL, Cavieres LA (2006) Impacts of ecosystem engineers on community attributes: effects of cushion plants at different elevations of the Chilean Andes. *Divers Distrib* 12:388–396
- Bestelmeyer BT, Miller JR, Wiens JA (2003) Applying species diversity theory to land management. *Ecol Appl* 13: 1750–1761
- Ceballos G, Pacheco J, List R (1999) Influence of prairie dogs *Cynomys ludovicianus* on habitat heterogeneity and mammalian diversity in Mexico. *J Arid Environ* 41: 161–172
- Chandy S, Gibson DJ, Robertson PA (2006) Additive partitioning of diversity across hierarchical spatial scales in a forested landscape. *J Appl Ecol* 43:792–801
- Coppock DL, Detling JK, Ellis JE, Dyer MI (1983) Plant–herbivore interactions in a North American mixed-grass prairie. 1. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1–9
- Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* 56:211–218
- Crist TO, Veech JA, Gering JC, Summerville KS (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of alpha, beta and gamma diversity. *Am Nat* 162:734–743
- FAO, ISRIC, ISSS (1998) World reference base for soil resources. World Soil References Reports 84. FAO, Rome
- Gering JC, Crist TO, Veech JA (2003) Additive partitioning of species diversity across multiple spatial scales: implications

- for regional conservation of biodiversity. *Conserv Biol* 17:488–499
- Grubov VI (1982) Key to the vascular plants of Mongolia. Science Publishers, Enfield
- Guo Q (1996) Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia* 106: 247–256
- Jost L, DeVries P, Walla T, Greeney H, Chao A, Ricotta C (2010) Partitioning diversity for conservation analyses. *Divers Distrib* 16:65–76
- Kotliar NB, Baker BW, Whicker AD, Plumb G (1999) A critical review of assumptions about the prairie dog as a keystone species. *Environ Manage* 24:177–192
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13
- Magurran AE (2004) Measuring biological diversity. Blackwell Science, Oxford
- Miller SD, Cully JF (2001) Conservation of black-tailed prairie dogs (*Cynomys ludovicianus*). *J Mammal* 82:889–893
- Questad EJ, Foster BL (2007) Vole disturbances and plant diversity in a grassland metacommunity. *Oecologia* 153: 341–351
- Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. *Ecol Lett* 7:1–15
- Takhi Reintroduction Centre (1998) Inventories and monitoring at Hustain Nuruu National Park. Internal report. Mongolian Association for Conservation of Nature and the Environment, Hustai National Park, Bayankhangai
- Van Staalduinen MA, Werger MJA (2007) Marmot disturbances in a Mongolian steppe vegetation. *J Arid Environ* 69: 344–355
- Veech JA, Crist TO (2009) PARTITION: software for hierarchical partitioning of species diversity, version 3.0. <http://www.users.muohio.edu/cristto/partition.htm>
- Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 93:3–9
- Wallis de Vries MF, Manibazar N, Dügerlham S (1996) The vegetation of the forest-steppe region of Hustain Nuruu, Mongolia. *Vegetatio* 122:111–127
- Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* 28:453–470
- Yoshihara Y, Ohkuro T, Buuveibaatar B, Takeuchi K (2009) Effects of disturbance by Siberian marmots (*Marmota sibirica*) on spatial heterogeneity of vegetation at multiple spatial scales. *Grassl Sci* 55:89–95
- Yoshihara Y, Ohkuro T, Buuveibaatar B, Jamsran U, Takeuchi K (2010a) Clustered animal burrows yield higher spatial heterogeneity. *Plant Ecol* 206:211–224
- Yoshihara Y, Ohkuro T, Buuveibaatar B, Jamsran U, Takeuchi K (2010b) Spatial pattern of grazing affects influence of herbivores on spatial heterogeneity of plants and soils. *Oecologia* 162:427–434
- Yoshihara Y, Ohkuro T, Buuveibaatar B, Jamsran U, Takeuchi K (2010c) Responses of vegetation to soil disturbance by Siberian marmots within a landscape and between landscape positions in Hustai National Park, Mongolia. *Grassl Sci* 56:42–50
- Zvuloni A, van Woesik R, Loya Y (2010) Diversity partitioning of stony corals across multiple spatial scales around Zanzibar Island, Tanzania. *PLoS ONE* 5:e9941