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Research Note

Marmot Disturbance Drives Trait Variations Among Five Dominant Grasses in a Mongolian Grassland

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Abstract

We examined how disturbances by Siberian marmots (*Marmota sibirica*) and associated spatial heterogeneity of foraging patterns and soil properties affect trait variations in five dominant perennial grasses (including sedges) in a Mongolian grassland. Using four continuous traits (leaf height, leaf area, leaf mass per area, and root length) of each grass species, we compared species and plot mean trait values and species' niche breadth (calculated on the basis of species' traits) between sites with and without marmots. At sites with marmots, investment in leaves was not favored, probably because of the prevalence of foraging, with the result that plot mean values of leaf height and area were smaller than at control sites. Niche breadth values for leaf area and leaf mass per area were greater at marmot sites, probably due to the spatially heterogeneous patterns of foraging. We observed greater values of species and plot mean root length values at marmot sites. We suggest that the modification of soil physicochemical properties by marmot burrowing, defecation, and urination might enhance root growth for ensuring physical stability of plant bodies and increasing the rate of nutrient acquisition. Niche breadth value for root length was greater at marmot sites, probably due to the spatial heterogeneity of soil properties. Quantification of trait distributions among plant species may help to explain the different plant adaptive mechanisms in relation to external drivers, such as disturbance.

Key Words: arid and semiarid grasslands, disturbance, Mongolia, niche breadth, soil heterogeneity

INTRODUCTION

Variations in plant traits between and within species in relation to various environmental gradients have been increasingly studied during the last decade (Ackerly and Cornwell 2007; Cornwell and Ackerly 2009). Quantifying such variations helps to explain the different plant adaptive mechanisms and their interactions with external drivers, including climate change and disturbance (Diaz et al. 1998; Ackerly and Cornwell 2007).

In Mongolian grasslands, Siberian marmots (*Marmota sibirica*) modify plant communities and soil physicochemical properties through activities such as foraging, burrowing, defecating, and urinating (Van Staalduinen and Werger 2007; Yoshihara et al. 2010a, 2010b). Foraging disturbance directly damages aboveground plant materials. Leaf traits, such as leaf height, leaf area, and leaf mass area, are negatively affected by foraging (Diaz et al. 2001). In contrast, the ranges of these trait values might be wider under foraging disturbance due to the spatially heterogeneous patterns of foraging (Yoshihara et al. 2010b). Disturbances such as burrowing, defecating, and urinating would indirectly affect belowground plant traits through the modification of soil physicochemical properties. Increases in the number of soil patches with coarser particles and associated large macropores caused by burrowing, as well as soil NO_3-N and K enrichments due to defecation and urination (Sherrod and Seastedt 2001; Yoshihara et al. 2010a), are expected to increase root growth, which enhances physical stability of the plant bodies and increases the nutrient acquisition rate (Day et al. 2003). Consequently, greater values for root traits such as root mass and length would be observed. Modifications of soil properties are also spatially heterogeneous (Yoshihara et al. 2010b), and this may result in wider ranges of root trait values.

Thus, we can expect that species traits respond differently to marmot disturbances but that the ranges of trait values are widened similarly due to the associated spatial heterogeneities of foraging patterns and soil properties created by marmot disturbance. In this study, using four continuous traits (leaf height, leaf area, leaf mass per area, and root length), we compared species and plot mean trait values and species' niche breadth (calculated on the basis of species' traits) between sites with and without marmots to understand the effects of marmot disturbance and associated spatial heterogeneity on trait distributions among five dominant perennial grasses (including sedges) in a Mongolian grassland.

MATERIALS AND METHODS

Study Area

The study area is located in Hustai National Park (HNP), which covers 60 000 ha and is located 100 km west of Ulaanbaatar, Mongolia (lat 47°50.0′N, long 106°00.0′E; elevation 1 100–1 840 m above sea level). The climate is arid and cold, with a short summer. HNP receives 232 mm of precipitation annually and is in the forest steppe region of

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Mongolia. The annual average temperature is 0.2°C, and average monthly temperatures vary between –23°C (in January) and 20°C (in July). More details on the study area are available in Yoshihara et al. (2010a, 2010b). The field survey was conducted in a protected area of HNP where livestock grazing is prohibited.

Site Selection and Vegetation Sampling

We used four sites where the spatial heterogeneity of the vegetation and soils had been explicitly described by previous work (see Yoshihara et al. 2010a, 2010b). These include two 0.25-ha (50×50 m) sites with marmot burrows (hereafter marmot sites) and two 0.25-ha (50×50 m) sites without marmot burrows (hereafter control sites). Yoshihara et al. (2010a, 2010b) demonstrated that disturbance caused by marmots increases the spatial heterogeneity of vegetation and soils within sites. The sites were separated by at least 500 m within the same landscape (valley foot slope) and altitude (about 1 300 m). All sites had the same soil type (Haplic Kastanozems) according to the soil-type layer in the GIS database produced by the HNP.

We established nine spatially evenly distributed circular plots with a 1-m radius within each site. The plant community is dominated by the perennial grasses (including sedges), *Agropyron cristatum*, *Carex korshinskyi*, *Elymus chinensis*, *Koeleria macrantha*, and *Stipa krylovii* (Yoshihara et al. 2010a; nomenclature follows Grubov 1982). These grasses are fairly palatable to marmots (Yoshihara et al. 2010a, 2010b). We chose these five grasses as representative species in the studied grassland and sampled traits on these species where they were present (but it was not necessarily the case that all five species were present within each plot).

In each plot, we measured leaf height (cm), leaf area (mm^2), and leaf mass per area (LMA; leaf dry weight divided by leaf area; $g \cdot cm^{-2}$) as leaf traits and root length (cm) as a root trait in each of the five species present. We selected two individuals per species that were not damaged or senescent in each plot to sample these traits. To calculate LMA, three fully expanded leaves per individual from two individuals per species in each plot were scanned, and their areas were calculated using a scanner and IMAGE J software.[1] The same leaves were used to determine dry weight. Leaf height (cm) was measured from the plant base to the tip of the highest leaf in two individuals of each species in each plot. Fresh roots from two individuals per species were destructively sampled in each plot. Sampled roots were scanned, and root length was measured as a maximum root length of each individual with IMAGE J software. The values of all parameters were determined for each individual and averaged by species in each plot. In addition, we estimated the cover (percent) of each grass species in each plot. The information on the cover value was used to calculate species and plot mean trait values and niche breadth of species (see next section). The fieldwork took place in August 2010.

Data Analysis

We computed three trait-based variables, the species mean trait value, niche breadth, and the plot mean trait value separately across two marmot sites and two control sites using the method proposed by Ackerly and Cornwell (2007). All trait values were $\log_{10}$ transformed to reduce skew before analysis (Ackerly and Cornwell 2007). The species mean trait value is the mean value of each trait in each species, calculated as follows:

$$\bar{t}_i = \frac{\sum_{j=1}^{P} a_{ij} t_{ij}}{\sum_{j=1}^{P} a_{ij}} \quad [1]$$

where t_{ij} is the trait value, a_{ij} is the cover value for species i in plot j, and P is the total number of plots in which traits of species i were sampled. We then calculated the plot mean trait value across all species sampled in each plot as follows:

$$\bar{p}_j = \frac{\sum_{i=1}^{S} a_{ij} t_{ij}}{\sum_{i=1}^{S} a_{ij}} \quad [2]$$

where S is the total species richness in each plot (maximum is five). The niche breadth of a species is defined as the range of p_j values in the plots occupied by that species.

We examined the differences in the species mean trait values and the niche breadth of the five species between the marmot ($n=5$) and control ($n=5$) sites using paired t tests. We also examined the difference in the plot mean trait values between the marmot ($n=18$) and control ($n=18$) sites by using nested analysis of variance (ANOVA) with sites as the highest factor and plots nested within sites. Statistical analyses were performed with R software (version 2.10.1; R Development Core Team 2009).

RESULTS

Differences in species and plot mean trait values and species' niche breadth between marmot and control sites are presented in Figure 1 and Table 1. The contribution of intraspecific trait variation of each species relative to the overall shift in trait values at the community level differed to greater or lesser extent. However, we consistently observed decreasing trends in the plot mean trait values for leaf traits but increasing trends in the plot mean trait value for root length due to marmot disturbances (Fig. 1). Species trait values of *S. krylovii* (most abundant species among the five species) for four functional traits was consistently strongly correlated with plot mean trait values, primarily mirroring the overall shift in trait values at the community level (Fig. 1e). The species mean value of each leaf trait did not differ significantly between marmot and control sites, whereas that of root length was significantly greater at marmot sites (Table 1, parameter a). Niche breadth for leaf height was significantly narrower at marmot sites (Table 1, parameter b). In contrast, niche breadth values for leaf area and LMA were significantly wider at marmot sites. Niche breadth for root length was also slightly wider at marmot sites. The plot mean values of leaf height and area were significantly smaller at marmot sites (Table 1, parameter c). In contrast, the plot mean

[1] http://rsb.info.nih.gov/ij

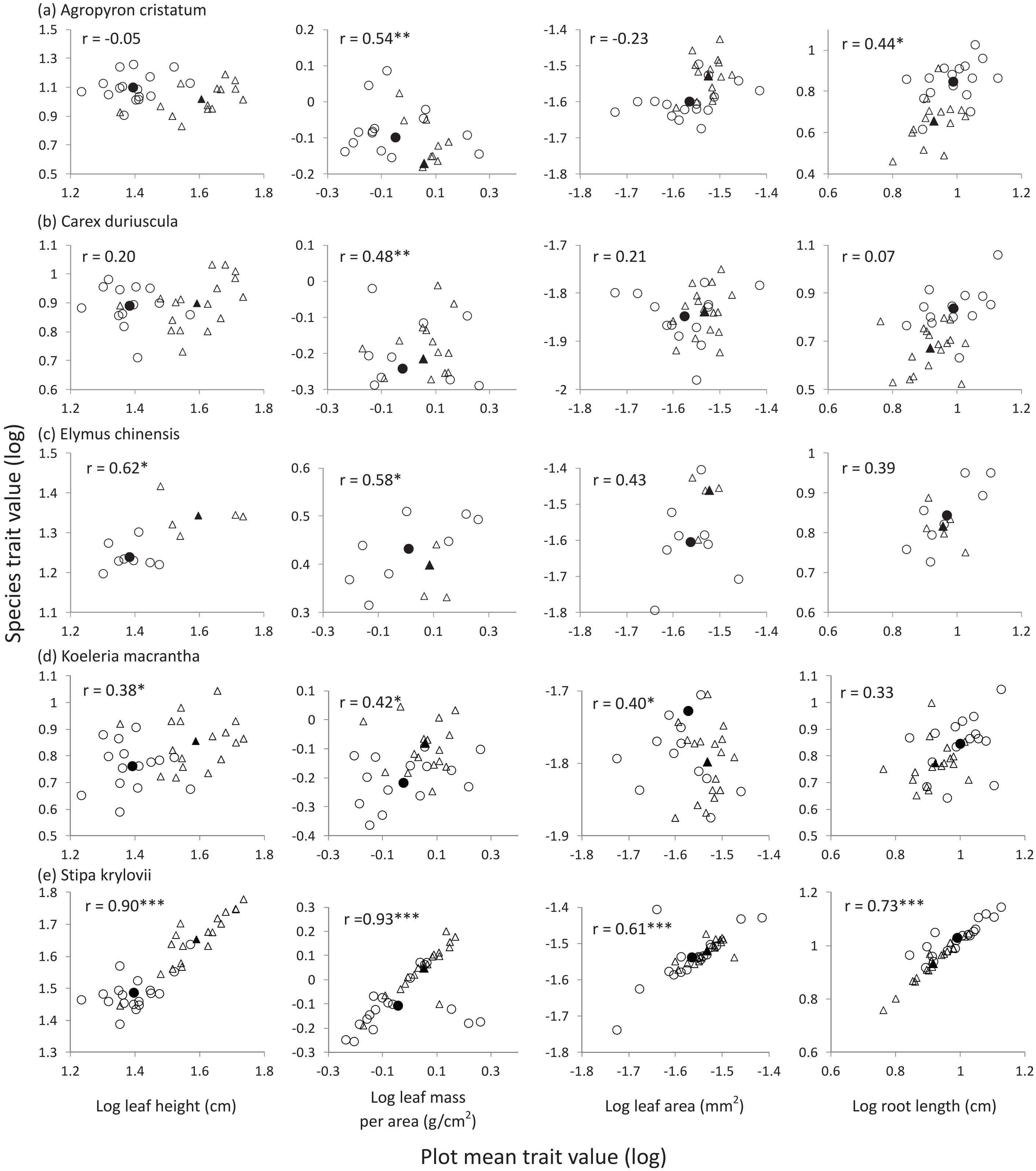

Figure 1. Scatter plots of species trait values versus abundance-weighted plot mean trait values across five dominant perennial grasses (**a**–**e**) for four functional traits (left to right panels for each species; leaf height, leaf area, leaf mass per area, and root length) in Hustai National Park, Mongolia. Both values are expressed in $\log_{10}$-transformed units. The open circle and triangle symbols represent species occurrence at the plots in marmot sites and those in control sites, respectively .The solid circle and triangle symbols represent the intersection of the mean trait value for the plots occupied by each species (on the horizontal axes) and the species mean trait value (on the vertical axes). The niche breadth of a species is represented as the range of plot mean trait values in the plots occupied by that species. Correlation (*r*) values between species trait values and plot mean trait values across marmot and control sites are shown ($^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$). Summary statistics for differences in species and plot mean trait values and species' niche breadth between marmot and control sites are in Table 1.

Table 1. Differences in the species mean trait values and niche breadth of the five species for four plant functional traits between marmot ($n=5$) and control ($n=5$) sites (means across five species with standard deviation [SD] in the parentheses) in Hustai National Park, Mongolia. The significance levels were determined by paired t tests. Differences in the plot mean trait values between marmot ($n=18$) and control ($n=18$) sites (means across 18 plots with SD in the parentheses) are also shown. The significance levels were determined by nested ANOVA with sites as the highest factor and plots nested within sites. All results and measurements of the various components of the trait gradient analysis are expressed in $\log_{10}$-transformed units of the traits. Significant P values ($P < 0.05$) are in bold.

	Functional traits											
	Leaf height (cm)			Leaf area (mm^2)			Leaf mass per area ($g \cdot cm^2$)			Root length (cm)		
Parameters	Marmot	Control	*P*	Marmot	Control	*P*	Marmot	Control	*P*	Marmot	Control	*P*
(a) Species mean trait value	1.08 (0.30)	1.17 (0.35)	0.14	−0.03 (0.28)	0.01 (0.25)	0.52	−1.68 (0.12)	−1.62 (0.19)	0.31	0.88 (0.09)	0.78 (0.11)	**0.04**
(b) Niche breadth	0.30 (0.07)	0.36 (0.06)	< **0.001**	0.48 (0.02)	0.29 (0.08)	< **0.001**	0.28 (0.06)	0.12 (0.02)	< **0.001**	0.28 (0.01)	0.23 (0.06)	0.09
(c) Plot mean trait value	1.39 (0.08)	1.57 (0.10)	< **0.001**	−0.04 (0.15)	0.05 (0.09)	**0.02**	−1.57 (0.07)	−1.53 (0.03)	0.10	0.99 (0.08)	0.93 (0.07)	< **0.001**

value of root length was significantly greater at marmot sites. The plot mean value of LMA did not differ significantly between marmot and control sites.

DISCUSSION

Typical categories of marmot activities are burrowing, foraging, defecation, and urination. The prevalence of foraging within marmot sites might cause each species to invest less in leaves, thus explaining the smaller plot mean trait values for leaf height and leaf area at marmot sites (Fig. 1; Table 1, parameter c). Species mean values for leaf traits tended to be smaller at marmot sites (Table 1, parameter a). Previous studies on colonial, burrowing herbivores in other regions, such as prairie dogs (*Cynomys* spp.), reported that they alter biomass allocation and production, resulting in lower leaf height and leaf area (Stapp 2007; Hartley et al. 2009). Short leaf height and small leaves are typical mechanisms of grazing resistance by grazing avoidance (Diaz et al. 2001). As predicted, niche breadth values for leaf area and LMA were greater at marmot sites (Table 1, parameter b), probably because the degree of grazing avoidance among local patches ranged greatly through the spatially heterogeneous patterns of foraging (Yoshihara et al. 2010b). However, niche breadth for leaf height was narrower at marmot sites. We speculate that foraging pressure by marmots strongly affected leaf height, acting as a convergence filter (i.e., a filter that leads to a restricted range of trait values; Grime 2006) and overwhelming the effects of spatial heterogeneity of foraging patterns in creating niche opportunities. Consistent with this result, Diaz et al. (2001) suggested that leaf height is one of the response variables most affected by domestic herbivores' grazing.

The modification of the soil physical environment (i.e., increases in the number of soil patches with coarser particles and associated large macropores at marmot sites as a result of burrowing) as well as soil NO_3-N and K enrichments due to marmot defecation and urination (Sherrod and Seastedt 2001; Yoshihara et al. 2010a) can increase root growth, which enhances physical stability of the plant bodies and increases the nutrient acquisition rate (Day et al. 2003). Thus, the greater values of species and plot mean root length values observed in this study (Fig. 1; Table 1, parameters a and c) can be explained by this modification. Other colonial, burrowing herbivores can have negative (Holland and Detling 1990), positive (Denyer et al. 2010), or neutral effects (Hartley et al. 2009) on root biomass, which is generally highly correlated with root length (e.g., Chen et al. 2012). Although the responses of root traits varied among studies, the synthetic study (Milchunas and Lauenroth 1993) suggested that the responses are generally positive. The alternation of plant root traits and their control on soil communities and litter decomposition would have important consequences for nutrient cycling (Holland and Detling 1990; Klumpp et al. 2009). As predicted, the niche breadth value for root length tended to be greater at marmot sites (Table 1, parameter b). Spatial heterogeneity of soil physicochemical properties created by marmot disturbance can widen a range of trait value for root length.

IMPLICATIONS

We showed that species traits respond differently to marmot disturbances but that the ranges of trait values are generally widened, probably due to the associated spatial heterogeneities of foraging patterns and soil properties created by marmot disturbance. Spatial heterogeneity of soil properties created by Siberian marmots and of marmot foraging patterns might provide an additional range of niche opportunities for grassland species. Quantification of trait distributions among plant species may help to understand the different plant adaptive mechanisms in relation to external drivers, such as disturbance.

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