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Short communication

Pollinators are attracted to mounds created by burrowing animals (marmots) in a Mongolian grassland

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ABSTRACT

Burrowing by semi-fossorial rodents modifies soil properties and plant communities. The effects of this burrowing on plants, however, are typically evaluated only by assessing changes in photosynthetic or production traits, not pollination traits. Therefore little is known about the indirect effects of burrowing on pollinators through its effects on the emergence of insect-pollinated plants. We recorded the relative elevation, grass cover, and flower height of insect-pollinated plant species; the number of inflorescences; and the number of pollinators in a marmot colony on the Mongolian steppe. We compared these parameters on and off marmot mounds and searched for factors that might explain variations in pollinator biodiversity at the plot and individual-plant levels. Flower numbers and flower visitation frequency per plot were significantly higher in the on-mound plots. The number of pollinators at the plot level was positively correlated with the relative elevation and number of flowers. Species richness of the pollinators was negatively correlated with grass cover. These results demonstrate that mounds created by marmots attracted pollinators by increasing flower numbers and by making flowers more conspicuous by raising them above the surrounding vegetation or removing that vegetation.

1. Introduction

The ecosystem engineering concept focuses on how organisms physically change their landscape and how these changes create feedback mechanisms that affect the biota of these sites (Jones et al., 1994). The concept has recently been integrated with the concepts of trophic interactions and food webs (Hastings et al., 2007; Wilby et al., 2001).

Burrowing semi-fossorial animals such as pocket gophers and prairie dogs have been shown to modify chemical and physical soil properties, and as a result, to affect the plant communities in grasslands (Coppock et al., 1983; Day and Detling, 1994; Holland and Detling, 1990; Kinlaw, 1999; Sherrod and Seastedt, 2001). Disturbed areas on mounds had distinct plant communities that attract frugivores (e.g., annuals) and that differed from surrounding communities away from the mounds, resulting in a heterogeneous landscape with modified trophic interactions (Bangert and Slobodchikoff, 2000; Davidson and Lightfoot, 2006; Hardwicke, 2006; Reichman and Seabloom, 2002; Schooley et al., 2000; Whitford and Kay, 1999).

Although studies of the effects of burrowing on plants are frequently evaluated in terms of photosynthetic or production traits, such as the proportions of C_3 or C_4 plants and plant biomass (Archer et al., 1987; Coppock et al., 1983; Guo, 1996), few studies have examined pollination traits such as the proportions of wind-pollinated and insect-pollinated plants (Hardwicke, 2006). This may be why little attention has been paid to the indirect effects of burrowing on pollinators through the effects on the emergence of insect-pollinated plants.

We hypothesized that the mounds created by semi-fossorial animals would attract pollinators for four reasons. First, insect-pollinated plants are more abundant on mounds in graminoid-dominated grasslands. Most studies of grasslands reported that disturbances by these animals suppress the dominance of graminoids and change the communities to include more forbs, and particularly insect-pollinated plants (Denslow, 1980; Guo, 1996; Martinsen et al., 1990; Peart, 1989; Whicker and Detling, 1988). Second, the proportion of flowering plants will be higher on mounds. Martinsen et al. (1990) showed 15% and 35% higher abundances of flowering plants of two forbs, *Ipomopsis aggregata* and *Penstemon barbatus*, in a pocket gopher colony in an Arizona prairie compared with the abundance of the same species away from the mounds. On Mima-like mounds generated by animal burrowing activity, flower production was greater for plants

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growing on the mounds, and this was explained by improved water and nutrient availability on the mounds (Hill et al., 2005). Third, inflorescences on mounds are likely to attract pollinators because of their larger size. This may result from better nutritional conditions on the mounds as a result of the deposition of dung or urine by the animals, which could promote a plant's growth and increase plant size (Day and Detling, 1990; Hill et al., 2005). Such large inflorescences often attract more pollinators than smaller inflorescences (Harder and Barrett, 1996). Fourth, flowers on mounds may be more conspicuous to pollinators because of their higher position above the surrounding vegetation. Burrowing often creates micro-highlands as a result of gradual accretion of excavated soil. Therefore, plants on the mounds are raised above others located off the mound as the mounds grow taller. In previous studies, the taller plants received more pollinator visits than their nearest neighbors (Donnelly et al., 1998), greater pollen deposition on stigmas (Lortie and Aarssen, 1999), and higher fruit initiation (the proportion of ovaries that became visibly enlarged) than those with flowers positioned closer to the ground (Ehrlen et al., 2002). In addition, frequent disturbance by the burrowing animals would reduce the competition from surrounding plants, which would otherwise obscure flowers on the mounds from the view of pollinators. For example, *Primula farinosa* produced more fruits and seeds when they were surrounded by low vegetation (Torang et al., 2006).

In Mongolia, Siberian marmots (*Marmota sibirica*) play an important role in nutrient recycling through burrowing, grazing, defecating, and urinating, activities that are now recognized as typical of ecosystem engineers (Van Staalduinen and Werger, 2007; Yoshihara et al., 2009). The marmots create rounded mounds with different vegetation types (e.g., *Stipa*, *Leymus*, *Artemisia*), depending on the disturbance history and the local species pool. The activity of the marmots leads to enhanced forage quality on the mounds, as indicated by increased nitrogen concentrations (Van Staalduinen and Werger, 2007). These engineering activities would create habitats and resources for other species, such as pollinators.

In this study, we tested the following predictions using marmot mounds: (1) the abundance of insect-pollinated plants would be greater on mounds than off the mounds, and (2) pollinators would be more abundant on mounds than off the mounds both per unit area and per inflorescence. In testing these predictions, we also tried to identify any characteristics of the mounds might explain the observed variations in pollinator biodiversity.

2. Materials and methods

2.1. Study plots

Our study was conducted in Hustai National Park (HNP), which is located 100 km west of Ulaanbaatar (47°50′N, 106°00′E, elevation 1100–1840 m asl). HNP receives 232 mm of precipitation annually and is situated in the forest-steppe region of Mongolia. The park covers 60 000 ha. About 88% of the area is covered by grassland and shrub steppes, and about 5% is covered by birch-dominated forest. Siberian marmots feed on 60–80 species of plants (Adiya, 2000), but various young and succulent grasses dominate their diet. They prefer to eat seeds, shoots, and flower buds when these are available. Livestock have been excluded from core areas of the HNP for conservation purposes since 1992, thus the effects of these animals on soil properties and plant communities are no longer significant factors in determining vegetation succession. A recent survey showed that 289 insect species are present in the park (Nansalmaa, 1999).

2.2. Field work

Our field work focused on a marmot colony in a typical grassland (2 ha) in the HNP. We established randomly distributed 2 × 2 m plots ($n = 60$) throughout the colony, for a total of 21 plots on marmot mounds and 39 plots away from the mounds. The off-mound sampling points represented areas with minimal marmot disturbance. Each plot and every inflorescence within it were permanently marked at the onset of the flowering period. In each plot, we quantified the relative elevation above the mean soil surface (i.e., the mound height if a plot included mounds). We described the general vegetation structure in each plot by recording the proportion of ground covered by graminoid species found in the plot. We then recorded the number of inflorescences in each insect-pollinated plant species and the mean height of each inflorescence above the soil surface. We observed all potential pollinators that visited the marked flowers for 10 min either directly or through binoculars so as to avoid disturbing them and recorded visitation frequencies. We excluded insects such as ants and larval Lepidoptera that are not considered to be pollinators. When we observed an unknown visitor, we collected it and identified it in the laboratory. We carried out these censuses five times during the day throughout the flowering period of the plant populations (from July to August). In total, we performed 300 censuses, corresponding to 50 h of observation.

2.3. Data analysis

We compared the grass coverage, flower height of the insect-pollinated plant species, number of inflorescences per plot, and number of pollinators between the on- and off-mound plots by means of *t*-tests. We conducted principal components analysis (PCA) on the correlation matrix at the plot level to identify major patterns of variation in pollinator communities, using the PC-ORD software (version 4.0; McCune and Mefford, 1999). We used forward stepwise multiple regressions to investigate which factors (relative elevation, grass cover, total number of flowers, and species richness of insect-pollinated plants) were most strongly related to pollinator abundance and to the number of pollinator families at the plot level in the on- and off-mound plots, and for all plots combined. Because pollinator abundance is affected by the flowering plant species that are present, we also tested against a plant species to determine whether these parameters per individual plant were particularly significant for functional evaluation (Yoshihara et al., 2008). Because the annual forb *Dontostemon integrifolius* (Cruciferae) was the most abundant flowering plants at the study site, we repeated this analysis using that species to determine which factors (relative elevation, grass cover, and flower height) most strongly determined the pollinator abundance and the number of families at the individual-plant level. During the model-fitting process, we set the alpha-to-enter and alpha-to-remove parameters at 0.1, and only included explanatory variables with $p < 0.05$ in the models. All statistical analyses were performed using Statistica 7.0 for Windows (Statsoft Inc.).

3. Results

The grass cover was significantly lower in the on-mound plots than in the off-mound plots ($t = 4.26$, $p < 0.001$, d.f. = 58; Fig. 1). The flower height of *D. integrifolius* did not differ significantly between plots ($t = 1.02$, $p = 0.31$, d.f. = 21). The number of flowers per plot ($t = 3.24$, $p = 0.001$, d.f. = 58) and the flower visitation frequency per plot ($t = 5.23$, $p < 0.001$, d.f. = 58) were both significantly higher in the on-mound plots. A total of 920 flowers (inflorescence) of six flowering species were found in the on-mound plots, versus 449

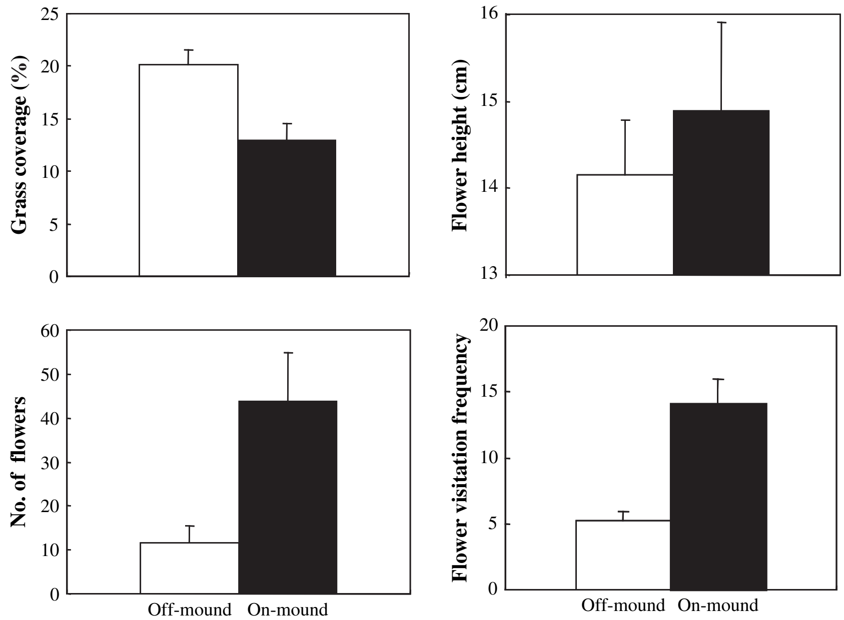

Fig. 1. Grass cover, flower height of *Dontostemon integrifolius*, total number of flowers, and flower visitation frequency per plot (all data represent means ± SD) during the entire study period in the off-mound plots ($n = 39$) and on-mound plots ($n = 21$).

flowers of five flowering species in the off-mound plots. The three most abundant flowering plants in the off-mound plots were *D. integrifolius* (mean inflorescence number = 10.5 per plot), *Ptilotrichum canescens* (0.8), and *Potentilla viscosa* (0.1), and those in the on-mound plots were *D. integrifolius* (27.4), *Panzeria lanata* (9.8), and *Silene repens* (6.0).

We found a total of 500 individual pollinators from 13 families during the study. The number of families was 8 in the off-mound plots and 10 in the on-mound plots. In both types of plot, the pollinators were dominated by species in the Scoliidae (Hymenoptera), Nymphalidae (Lepidoptera), and Bombyliidae (Diptera). The corresponding mean flower visitation frequencies per plot were 1.8, 2.3, and 0.7 in the off-mound plots and 7.0, 4.5, and 2.6 in the on-mound plots. However, PCA analysis did not clearly separate the off-mound plots from the on-mound plots in the ordination space (Fig. 2).

The number of flowers and the species richness of insect-pollinated species were significantly correlated ($r_s = 0.86$, $p < 0.001$, d.f. = 58). In the multiple regressions, species richness of insect-pollinated species was excluded from the models. At the plot level, the number of pollinator families was positively correlated with the relative elevation and number of flowers (Fig. 3, Appendix 1, electronic version). However, the number of pollinators was negatively correlated with grass cover (Fig. 3). At the individual-plant level, neither the number of pollinators nor the number of families was correlated with the explanatory variables.

4. Discussion

Pollinators were more common on marmot mounds than off the mounds, and the number of pollinators was positively associated with the higher number of flowers on the marmot mounds. The three most abundant pollinator families were the same in the on-mound and off-mound plots, even though previous research had revealed distinct communities of ground-dwelling arthropods in off-mound and on-mound plots in a prairie dog town (Bangert and Slobodchikoff, 2006). Our results suggest that pollinators used vegetation on the mounds as an important food resource (Appendix 1, electronic version), whereas the arthropods were more sensitive to differences in environments (e.g., light, humidity) between the on-mound and off-mound plots; some of these arthropods depend strongly on the burrows due to their poor mobility. The present study showed the importance of burrowing animals for increasing the abundance of organisms by providing key resources as a result of their ecosystem engineering in the Mongolian steppe ecosystem. The current study therefore provides important additional information on the contribution of these ecosystem engineers. Burrowing by the rodents and the resulting ecosystem engineering seemed to have a positive association with the biodiversity of invertebrates in this ecosystem.

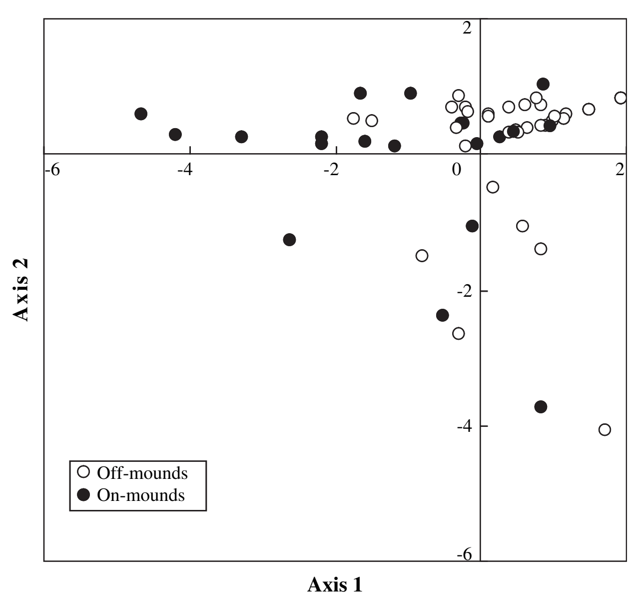

Fig. 2. Principal components analysis of the pollinator community composition for the off-mound and on-mound plots.

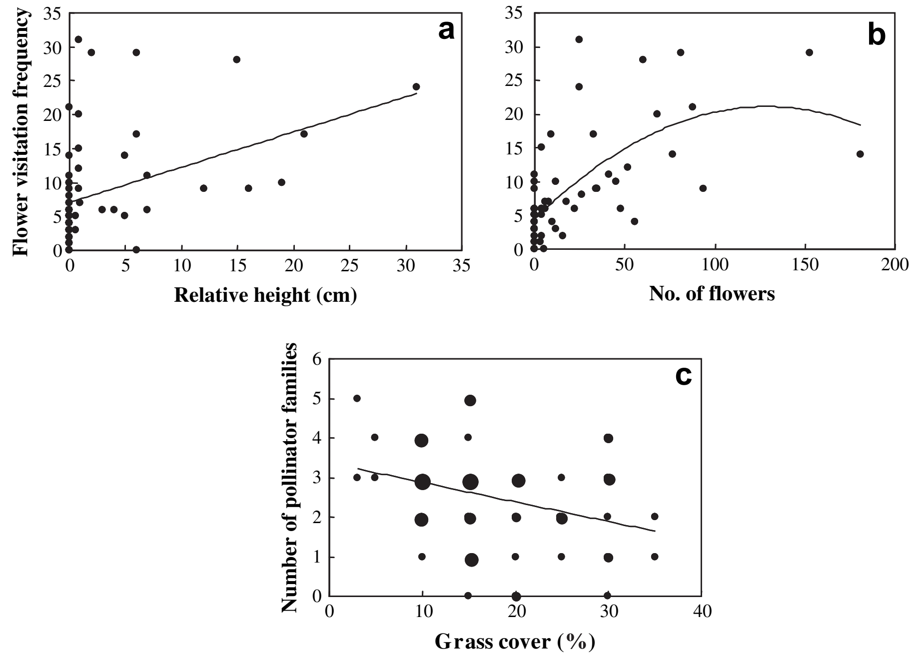

Fig. 3. The relationship between flower visitation frequency per plot and (a) the relative elevation above the ground and (b) total number of flowers. (c) A multivariate bubble-plot of the number of pollinator families as a function of grass cover per plot. The size of the bubbles in (c) is proportional to the sample size (minimum = 1, maximum = 5). Black lines show the best-fit linear regressions for (a) and (c), and the best-fit polynomial curve for (b).

The greater number of on-mound inflorescences compared with the off-mound plots resulted from a change in the species assemblage from graminoids to forbs (Fig. 1). Typically, Mongolian steppes at lower elevations and sites with moderate slopes were rich in wind-pollinated flora (i.e., grasslands), whereas rocky areas such as mountain tops were rich in insect-pollinated flora (i.e., alpine meadows; Wallis de Vries et al., 1996). This general pattern may reflect differences in soil particle size, water or nutrient availability, and seed characteristics. For example, Chambers (2000) reported that at large soil particle sizes, higher numbers of seeds of insect-pollinated plants (forbs and shrubs) were trapped than those of wind-pollinated plants (grasses). Thus, soils with larger particles (e.g., gravels) that are excavated from below the ground by burrowing could have contributed to the greater abundance of flowers in the on-mound plots by creating miniature areas with more coarse particles. At the same time, frequent soil disturbance by the marmots enabled ruderal annuals such as *D. integrifolius* to colonize the on-mound plots.

The significant explanatory variables that we observed were consistent with those in previous studies, in which the abundance of flowers was an important predictor for the diversity of pollinators because it was equivalent to the magnitude of the reward for pollinators (Robertson and MacNair, 1995; Sjodin, 2007; Yoshihara et al., 2008). However, visibility parameters that affect pollinators also determined their diversity. Three visibility parameters had various influences on pollinators (Fig. 2; Appendix 1, electronic version): relative elevation was positively correlated with visitation frequency at the plot level, grass cover was negatively correlated with the number of pollinator families at the plot level, and flower height had no significant influence on this number. The most obvious explanation would be that the relative elevation varied by about 31 cm, and this played a role in advertising of the presence of flowers to pollinators, whereas the subtler difference in flower heights (ca. 9 cm) may not represent a significant height difference. The advantage of being tall for attracting pollinators became apparent for *Verbascum thapsus* at an average height difference of 16 cm (Donnelly et al., 1998) or 92 cm (Lortie and Aarssen, 1999). Our results showed that the higher the surrounding grass cover, the lower the number of pollinator families, as has been reported in past studies (Carvell, 2002; Ehrlen et al., 2002; Torang et al., 2006). Compared to open vegetation communities, inflorescences in communities with a closed vegetation cover should be more difficult to detect for pollinator species that lack a highly sophisticated searching ability, such as bumblebees (Burns and Thomson, 2006; Heinrich, 1979).

Pollinator abundance was greater on the mounds than off the mounds, and this mainly resulted from the greater abundance of flowering plants on the mounds. Yoshihara et al. (2009) demonstrated the possibility of using the Siberian marmots as a conservation tool for plant biodiversity at the landscape level in Mongolian steppes. The present study revealed the ecological value of the Siberian marmot in terms of its ability to increase pollinator abundance. Thus, it is important to remember that conserving marmots in these ecosystems will also promote conservation of the biodiversity of the fauna and flora of the Mongolian steppes. Such information will provide further support for the need to conserve declining populations of the Siberian marmot.

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2009.06.002.

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