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Effects of livestock grazing on pollination on a steppe in eastern Mongolia

Yu Yoshihara^{a,*}, Buyanaa Chimeddorj^b, Bayarbaatar Buuveibaatar^c,
Badamjavin Lhagvasuren^c, Seiki Takatsuki^d

^aDepartment of Ecosystem Studies, School of Agricultural Life Sciences, University of Tokyo, Yayoi 1-1-1, Bunkyo-ku, Tokyo 113-8657, Japan

^bWWF Mongolia Programme Office, Ulanbaatar 210620A, Mongolia

^cInstitute of Biology, Mongolian Academy of Sciences, Ulaanbaatar 51, Mongolia

^dAzabu University, Fuchinobe 1-17-71, Sagamihara, Kanagawa 229-8501, Japan

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ABSTRACT

Widespread degradation of Mongolian grasslands by overgrazing is of global concern. The objective of this study was to reveal the effects of grazing on pollination as an example of interaction biodiversity in Mongolian grasslands. We established three plots according to grazing intensity on the eastern steppe of Mongolia. In each plot, we recorded the numbers of insect-pollinated plants and observed the foraging behavior of pollinators in June and August. The richness of insect-pollinated species was high and these species were most abundant in lightly grazed plots, and formed complex relations with diverse pollinators. But, frequency of flower visitation and pollination index were greater in heavily grazed plots. All pollination properties were poorest in intermediately grazed plots. These results suggest that the forb-biased foraging of sheep and goats reduces the floral diversity of insect-pollinated species, and consequently reduces pollinators in the intermediately grazed plots. In the heavily grazed plots, only limited ruderal species could survive under heavy cattle grazing, and such simple vegetation formed unbalanced but strong bonds with pollinators. Removal simulation showed that the mutual network was more fragile with respect to the extinction of certain species.

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1. Introduction

Grasslands have long been utilized for cultivation and grazing (Samson and Knopf, 1996). Recently, their value in maintaining biodiversity has been recognized as well. Traditionally managed grasslands are characterized by a high biodiversity and a high content of endangered species (Walk and Warner, 2000; Woodcock et al., 2007). But, overuse reduces biodiversity and ecosystem function (Vickery et al., 2001; Darkoh, 2003).

Overgrazing alters plant community structure, biomass, and species composition in grasslands (Huntly, 1991; Freichner, 1994; Hodgson and Illius, 1996; Olff et al., 1999). These changes mostly have detrimental effects on the species richness and abundance of small animals, particularly insects (Dennis et al., 1998; Rambo and Faeth, 1999; Gomez and Gonzalez-Megias, 2002; Kruess and Tschardtke, 2002a,b; Hartley et al., 2003). However, while these studies showed correspondences between plant and insect communities, they did not

* Corresponding author. Tel.: +81 3 5841 5052; fax: +81 3 5841 5072.

E-mail addresses: marmota.sibirica@gmail.com (Y. Yoshihara), chimeddorj@wwf.mn (B. Chimeddorj), buuveibd@yahoo.com (B. Buuveibaatar), ecolab@magicnet.mn (B. Lhagvasuren), takatsuki@azabu-u.ac.jp (S. Takatsuki).

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always clarify the functional aspects – the “interaction biodiversity” of Thompson (1997) – as pointed out by Suominen and Danell (2006).

The plant–pollinator relationship is a good barometer of interaction biodiversity under anthropogenic effects due to its sensibility to habitat change (Inouye, 1978; Kearns and Inouye, 1993, 1997; Tschamntke and Brandl, 2004). For example, pollination decreased owing to habitat fragmentation in several cultivated areas in Europe (Jennersten, 1988) and in arid forests in South America (Aizen and Feinsinger, 1994). Such vulnerability arises from mutual dependence: pollination networks are threatened with the loss of component species on either side (plants or pollinators). A loss may well elicit additional losses, and perhaps even cascades of extinction (Kearns et al., 1998). Nevertheless, studies of the effects of overgrazing by ungulates on plant–pollinator relationships are limited. Overgrazing should affect the relationship indirectly via its effects on the structure of plant communities or on competitive relationships within plant assemblages (Morris, 2000), as seen in forest in Argentina (Vazquez and Simberloff, 2003, 2004) and in Spain (Gómez, 2005).

The phenological patterns of insect-pollinated plants and the activity patterns of pollinators differ temporally, e.g., between seasons (Herrera, 1988; Ashman and Stanton, 1991; Vazquez and Simberloff, 2004), and consequently their relationship may vary. Additionally, the effect of grazing on flowering probability depends on its season (Brys et al., 2004). Thus, the effects of grazing on pollination should differ by season.

The importance of understanding plant–pollinator interactive structures for conservation purposes is mounting (Bascompte and Jordano, 2007). Such structures offer the chance to understand the relative importance of each component (Barrat et al., 2004), the degree of specialization (Olesen and Jordano, 2002), and even the robustness when structural components become extinct (Dunne et al., 2002; Memmott et al., 2004), because the actual impact of pollinator loss on pollination services depends on the degree of specialization (Bond, 1995; Steffan-Dewenter et al., 2006). If we assume that the most specialized relationship is where a single plant species relies on a single pollinator and vice versa, pollination services are at higher risk in the case of extinction of either plant or pollinator than generalized relationships where several plants rely on several pollinators and vice versa.

The Mongolian steppe has been used sustainably for grazing for centuries. However, following the move to a market economy in 1992, livestock populations have been increasing, partly as a response to strong demands for cashmere (Lise et al., 2006). The total population of livestock (cattle, horses, sheep, and camels) was 10 million in the early 1900s, but is currently more than 30 million (Milner-Gulland and Lhagvasuren, 1998; National Scientific Office of Mongolia, 2007). Nevertheless, there has been only limited study of the effects of overgrazing on the steppe ecosystem of Mongolia. These studies have demonstrated vegetational changes (e.g., Fernandez-Gimenez and Allen-Diaz, 2001), but no study has examined the effects of overgrazing on ecosystem functions, especially pollination.

The overall objective of this study was to reveal the effects of grazing on pollination as an example of interaction biodi-

versity in Mongolian grasslands. Specifically, we asked following questions: (1) Would the diversity of insect-pollinated plants and pollinators and the effective pollination decline under overgrazing? (2) How do the effects of grazing on pollination change by season? (3) Is the plant–pollinator interactive structure under overgrazing more vulnerable to loss of components? To answer question 3, we evaluated the robustness of the pollination network structure by simulation of the removal of components. By clarifying the effects of grazing on pollination, we hope to identify good management practice in the face of widespread degradation of Mongolian grasslands.

2. Materials and methods

2.1. Study areas

We selected study plots in Tumentsogt soum (county) (47°39′46.4″N, 112°25′49.8″E), Sukhbaatar province (82,000 km²), 500 km east of Ulaanbaatar. The elevation of the study site is about 1000 m and the site is flat. Because the region receives only 250 mm of precipitation annually, steppe prevails, and forest stands grow only along rivers. According to vegetation zonation, the site is a typical steppe (Hilbig, 1995). About 200 families live in the soum and herd 11,000 livestock, mainly sheep, goats, horses, and cattle. The majority of the people who rely on livestock grazing live in *gers* (tent-type movable houses), but there are offices, shops, and permanent houses in the soum center. Grasslands remain in good condition in the eastern steppes, but the nearby grasslands are deteriorating because of the high density of stocking maintained by herders who now live in permanent houses. The height of grass gradually increases away from the soum center, and tall grasses such as *Stipa grandis* P. Smirn. (Poaceae) and *Agropyron cristatum* (L.) P.B. become more abundant with distance.

2.2. Data collection

In 2005, we established transects in three directions (east, north, and west) from the soum center. The length of the transects varied from about 7 to 14 km, according to the *ger* distribution. We expressed livestock density in terms of the “standard sheep unit” (SSU; Humphrey and Sneath, 1999). Along each transect, we chose three plots (500 m × 500 m, respectively) and defined them as “heavily grazed” (mainly by large livestock; grass height 2–5 cm, 523 SSU per plot), “intermediately grazed” (by small livestock; 5–15 cm, 411 SSU), and “lightly grazed” (>15 cm, 185 SSU) in order the distance from the smallest to biggest to the soum center. We calculated the SSU indexes from dung density in twenty 25-m² quadrats in each plot, in which we counted the number of dung pats or pellets of each species. Then, we calculated total SSU per plot by assuming one SSU per a fecal pellet of sheep or goat, five SSU per a pat of cow or bull, and six SSU per a dung pile of horse.

The nine plots were separated by at least 500 m. Along the center of each, we established a belt measuring 200 m × 3 m for surveys. An investigator walked along the

one side of the belt recording the number of each insect-pollinated plant species and of each pollinator within it, and then returned along the other side, again recording species. Pollinators were identified according to Nakano (2003). When we saw an insect on a flower, we carefully observed it through binoculars so as not to disturb it and recorded its movements between flowers for 1 min to record visitation frequency. We checked for pollination or the touching of a stamen or pistil by the insect by careful observation of its movements, its posture, and the attachment of pollen to its body. After following an insect, we returned to the point where we first saw it, and continued the survey. If we saw several insects simultaneously, we followed them one by one. We excluded insects, such as ants and larval Lepidoptera, that are not considered to be pollinators. When we found an unknown species, we collected it and identified it in the laboratory. A person allocated to each plot on the same transect, and the same person surveyed a belt for 2 hours at a time in the morning (beginning at 09:00), in the afternoon (beginning at 13:00), and in the evening (beginning at 17:00) of the same day. We carried out this series of censuses on three consecutive days along the eastern, northern, then western transects, five times for pollinators censuses and two times for flora censuses between June and August. We performed the censuses so close together because of the dramatic differences in weather (a short rainy season in June) and flora (spring bloomers in June and autumn bloomers in August) at our study site. All transects, plots, and belts were the same in both seasons.

2.3. Data analysis

We performed individual-based rarefaction analysis to calculate expected species richness standardized by number of individuals. Rarefaction allowed us to compare species richness among the plots by controlling for differences in the numbers of individuals sampled (Gotelli and Colwell, 2001). The analysis was carried out with *EstimateS* v. 8.0 software (Colwell, 2007), using a randomization method with 1000 iterations.

Pollinators were categorized into functional groups according to taxonomy, body size, and behavior according to Corbet (1997) as bumblebees (Hymenoptera), other Hymenoptera, Bombyliidae (Diptera), Syrphidae (Diptera), other Diptera, butterflies (Lepidoptera), beetles (Coleoptera), and others.

Mutualism strength can be estimated as the relative frequency of species that interact with a particular species (Bascompte and Jordano, 2006). As an indicator of mutualism strength and effective pollination, we used the pollination index (PI) of Nakano (2003), in which $PI = (\text{visitation frequency}) \times (\text{number of movements among flowers}) \times (\text{touch of stamen or pistil})$, where “visitation frequency” is the frequency of visits of a pollinator among flowers, “number of movements among flowers” is the number of visits between different inflorescences of the same species by a pollinator within 1 min, and “touch” is a categorical variable indicating whether the pollinator touched (1) or did not touch (0) a stamen or pistil.

PI values were summed for each plot and for each species, and averaged for each species per flower. Mean PI values per flower of each species could be compared only between lightly and intermediately grazed plots, because common plant species with enough flowers did not occur in the heavily grazed plots. Nine plant species with more than 30 flowers each were used for the analyses. We used the Mann–Whitney U-test to look for between-plot differences in the PI values per individual of each plant species.

To test for significant differences among plots and between seasons (June and August), we compared log-transformed numbers of insect-pollinated plant species, flower visits, and PI values per plot by repeated measures ANOVA. We set the significance level at 0.05, and used the Bonferroni P-value adjusted for multiple comparisons.

For comparison of the generalization level at the network or counterpart level under different grazing intensities, we calculated connectance (C) and linkage levels (L) in each plot (Olesen and Jordano, 2002):

$$C = I \times 100 / A \cdot P,$$

$$L_a = I / A,$$

$$L_p = I / P,$$

where C is the percentage of all possible interactions within a network that are actually established; I is the total number of interactions in the network; A and P are the total numbers of interacting animal and plant species, respectively, in the habitat ($A \cdot P$ thus indicates the maximum number of observable interactions); and L_a and L_p are the mean numbers of interactions across animal and plant species, respectively.

We simulated secondary extinction by the removal of component species from each pollination network (one per grazing intensity) to determine its robustness when the network is fragmented (Albert et al., 2000). We removed pollinators only or plants and pollinators with equal probabilities from each network one species at a time until the network collapsed (all species disappeared). If removal disconnects a species (plant or pollinator) from its complement species (pollinator or plant), that species is also removed from the network (secondary extinction). This assumes that plant species go extinct upon loss of all their effective pollinators owing to failure of sexual reproduction (Bond, 1995; Memmott et al., 2004). Conversely, loss of floral resources is a key threat facing pollinators (Kearns et al., 1998). For example, if we remove *Allium anisopodium* from the network of the lightly grazed plot in Fig. 3a, *Machimus* sp. is also removed, resulting in a value of 0.2 for both the proportion of removal and for secondary extinction. The robustness of the networks with respect to species loss was judged from the proportion of secondary extinctions: if the proportion of secondary extinctions was higher than that of primary removal, we judged the network to be fragile.

To remove species, we used three widely used removal algorithms (Dunne et al., 2002; Memmott et al., 2004): most connected to least connected, least connected to most connected, and random regardless of the number of links. Random removal was repeated 100 times for each network (Albert et al., 2000). All three removal algorithms are based on the probable extinction sequence seen in the real world (Memmott et al., 2004).

3. Results

3.1. Insect-pollinated flora

The total number of plant species was highest in the lightly grazed plots in both June and August (Table 1). The number increased from June to August in the intermediately grazed plots, but decreased in the heavily grazed plots. When the lightly and heavily grazed plots were rarefied to $N = 243$ individuals (maximum size in intermediately grazed plot), their species richnesses in June were identical among grazing intensities (Fig. 1a). In August, the richness values predicted by rarefaction curves were highest in the lightly grazed plots when the curves reached the plateau (around 1500 individuals, Fig. 1b).

The total number of flowers was highest in the lightly grazed plots and lowest in the intermediately grazed plots in both June and August (Table 1), although the number was not significantly different among plots ($F = 2.64$, $P = 0.15$, $d.f. = 2$). Overall, *Allium* spp., *Bupleurum bicaule* Helm, *Filifolium sibiricum* (L.) Kitam., and *Haplophyllum dahuricum* (L.) G. Don. decreased with increased grazing intensity (Table 1). In contrast, *Convolvulus ammanii* Desr., *Heteropappus hispidus* (Thunb.) Less., and *Saussurea salicifolia* (L.) DC. increased with increased grazing intensity. In the lightly grazed plots, *F. sibiricum* dominated in June (Table 1), but it disappeared in August and *B. bicaule* and *Allium* spp. increased markedly. In the intermediately grazed plots, *Cymbaria dahurica* L. was abundant in June, and *B. bicaule* and *Allium* spp. were abundant in August. In the heavily grazed plots, *Myosotis caespitosa* C.F. Schultz.

Table 1 – Total number of insect-pollinated plant species at each grazing intensity on a steppe in eastern Mongolia in June and August 2005

Plant name	June			August		
	Light	Intermediate	Heavy	Light	Intermediate	Heavy
<i>Adenophora stenanthina</i>	3			65	11	
<i>Allium anisopodium</i>	185		7	944	396	14
<i>Allium odorum</i>				59	36	
<i>Allium senescens</i>	40	5		314	9	
<i>Amaranthaceae</i> sp.	113		85			
<i>Asparagus dahuricus</i>	3		2	1		3
<i>Astragalus</i> sp.					2	
<i>Bupleurum bicaule</i>				5197	706	2
<i>Caragana leucophylla</i>	2					
<i>Caragana microphylla</i>	250	2	16			
<i>Clematis hexapetala</i>	21			118		
<i>Convolvulus ammanii</i>		2	71			4
<i>Cymbaria dahurica</i>	64	120	3			
<i>Ephedra monosperma</i>		2				
<i>Euphorbia discolor</i>	6	3	69			
<i>Filifolium sibiricum</i>	1752	4	6			
<i>Galium verum</i>	28		1	31	6	
<i>Geranium pseudosibiricum</i>						45
<i>Gypsophylla</i> sp.		2	2	106	39	
<i>Haplophyllum</i> sp.	462	89	63	36	20	6
<i>Heteropappus hispidus</i>				87	130	1368
<i>Ixeris</i> sp.	23		7	5		1
<i>Leontopodium ochroleucum</i>	25					
<i>Lithospermum</i> sp.			1			
<i>Medicago</i> sp.				18	1	3
<i>Myosotis caespitosa</i>			1289			
<i>Oxytropis</i> sp.			15			
<i>Polygonum divaricatum</i>	4			113	109	
<i>Potentilla bifurca</i>	18	14	143			
<i>Potentilla tanacetifolia</i>				1		
<i>Ptilotrichum tenuifolium</i>	54	4		13		
<i>Saussurea salicifolia</i>				19	15	1575
<i>Scabiosa comosa</i>				56		
<i>Schizonepeta multifida</i>				324	245	
<i>Sedum purpureum</i>				6	1	
<i>Serratula centauroides</i>	8	1	1	384	16	6
<i>Stellaria chamaejasme</i>	14		20			3
<i>Thymus gobicus</i>	7			10		
<i>Vicia</i> sp.	7					
<i>Youngia</i> sp.	2		6			
Number of flowers	3087	243	1802	7903	1739	3028
Number of species	23	12	19	22	16	12

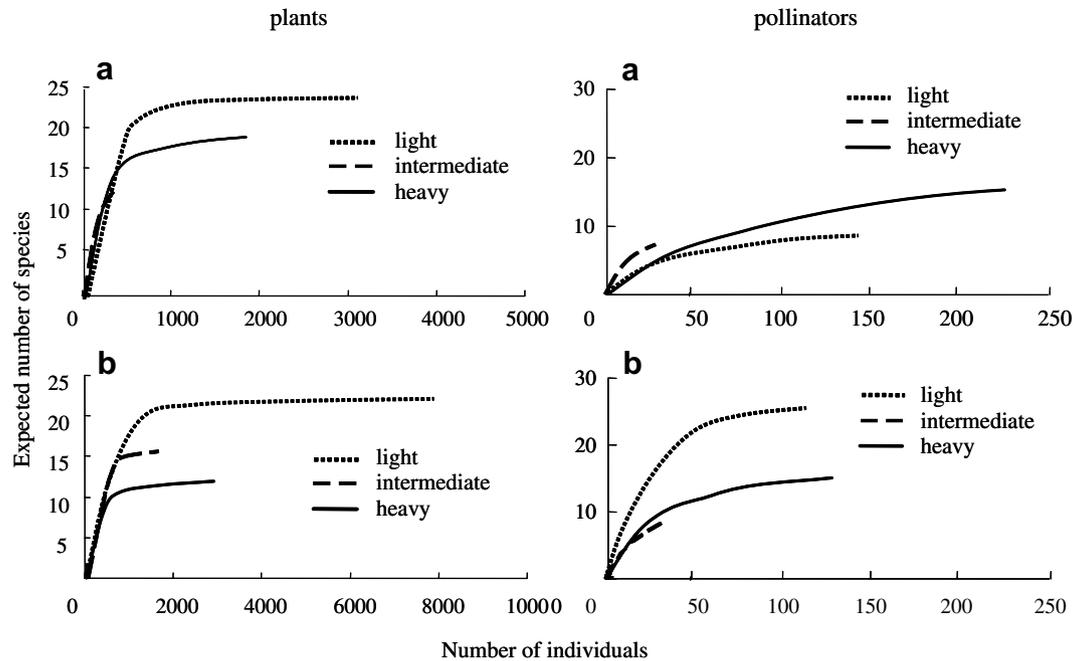


Fig. 1 – Rarefaction curves for each grazing intensity, predicting the expected number of insect-pollinated plant species (left) and pollinator species (right) with increasing number of individuals. (a) June and (b) August.

was dominant in June, but *H. hispidus* and *S. salicifolia* became dominant in August.

3.2. Flower visits

The total number of species visiting flowers increased from June to August in the lightly grazed and intermediately grazed plots, but not in the heavily grazed plots (Table 2). When the lightly and heavily grazed plots were rarefied to $N = 25$ pollinator individuals, their species richness in June was lower than in the intermediately grazed plot (Fig. 1). In August, the richness of the lightly grazed plot predicted using the rarefaction curves exceeded that predicted in the other plots.

The number of pollinator visits to flowers were marginally significantly different among grazing intensities ($F = 4.60$, $p = 0.06$, $d.f. = 2$). The total number of flower visitors was lowest in the intermediately grazed plots (Fig. 2, $p < 0.01$). Likewise, every insect type except syrphids showed the lowest abundance in the intermediately grazed plots and the highest in the heavily grazed plots. In June, the pollinators were dominated by the Coleoptera (Table 2). No Bombyliidae or Syrphidae (Diptera) were observed. Among the Coleoptera, *Epicauta* sp. appeared commonly in all plots, and *Melasoma* sp. was abundant in the heavily grazed plots. The species composition changed in August: the Coleoptera decreased from 328 to 55 species, while the Hymenoptera increased from 9 to 68

Table 2 – Total numbers of observed flower visitors at each grazing intensity on a steppe in eastern Mongolia in June and August 2005

Orders of insects	June				August			
	Light	Intermediate	Heavy	Total	Light	Intermediate	Heavy	Total
Diptera	30	7	26	63	31	11	55	97
Bombyliidae					18	7	48	73
Syrphids					10	1		11
Other Diptera	30	7	26	63	3	3	7	13
Hymenoptera	2		7	9	23	7	38	68
Bumblebees			1	1				
Honey bees	1		1	2	1		2	3
Other Hymenoptera	1		5	6	22	7	36	65
Coleoptera	116	21	191	328	30	3	22	55
Lepidoptera	1	1	12	14	11	6	8	25
Total number	149	29	236	414	116	27	128	271
Total species	8	7	15	30	26	10	15	41

Italicized numbers represent the total for each insect order.

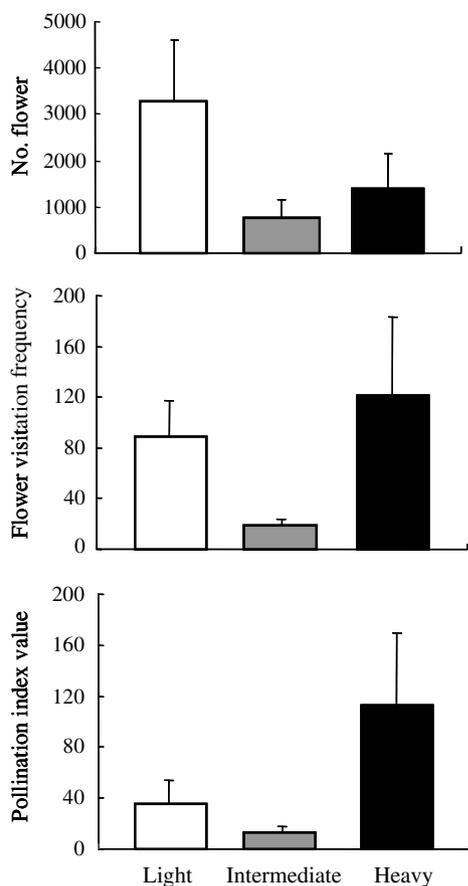


Fig. 2 – Mean numbers of flowers, mean flower visitation frequency, and mean PI values per plot (+SE) at different grazing intensities.

species. Among the Diptera, the Bombyliidae, which did not occur in June, dominated, particularly in the heavily grazed plots, while other Diptera decreased.

3.3. Pollination index

3.3.1. Pollination index at plot level

Pollination index values were marginally significantly different among grazing intensities ($F = 4.79$, $p = 0.06$, $d.f. = 2$). In June, total PI values were highest in the heavily grazed plots, and interactions between pollinators and insect-pollinated species were weak in the lightly and intermediately grazed plots (Fig. 3a). The numbers of interactions between pollinator species and plant species were 4, 1, and 18 in the lightly, intermediately, and heavily grazed plots, respectively (Fig. 3a). The PI values were small, except for that between *C. ammannii* and *Epicauta* sp. (14) in the heavily grazed plots.

In August, the PI values increased greatly in all three plots (Fig. 3b). Total PI values were highest in the heavily grazed plots, as in June. The numbers of interactions between pollinator species and plant species were 32, 11, and 20 in the lightly, intermediately, and heavily grazed plots, respectively. Although the number of interactions was greatest in the lightly grazed plots, the PI value was not. In the intermediately grazed plots, a tight association was found only between *H. hispidus* and Bombyliidae sp. 1 (PI = 19). In the heavily

grazed plots, associations between *H. hispidus* and Bombyliidae sp. 1 (PI = 55) and between *S. salicifolia* and Scoliidae sp. (PI = 74) were strong. Connectance and linkage at the network level (L) were highest in heavily grazed plots (Table 3).

3.3.2. Pollination index at the individual plant level

Because PI values are affected by the number of flowers, the higher PI values in the lightly grazed plots may have resulted from the greater abundance of flowers. Therefore, we additionally calculated the PI per individual plant for functional evaluation (Table 4). The difference was large only for *Gypsophila* sp. Values were higher for three species and smaller for four species in the lightly grazed plots than in the intermediately grazed plots (Table 4). Therefore, there was no significant difference in PI per individual between the lightly grazed and intermediately grazed plots ($P = 0.93$).

Overall, there were no significant effects of the interaction between grazing intensity and season on the number of flowers ($F = 0.05$, $P = 0.94$, $d.f. = 2$), pollinator visits ($F = 0.16$, $P = 0.84$, $d.f. = 2$), or PI values ($F = 0.06$, $P = 0.93$, $d.f. = 2$).

3.4. Simulated secondary extinction

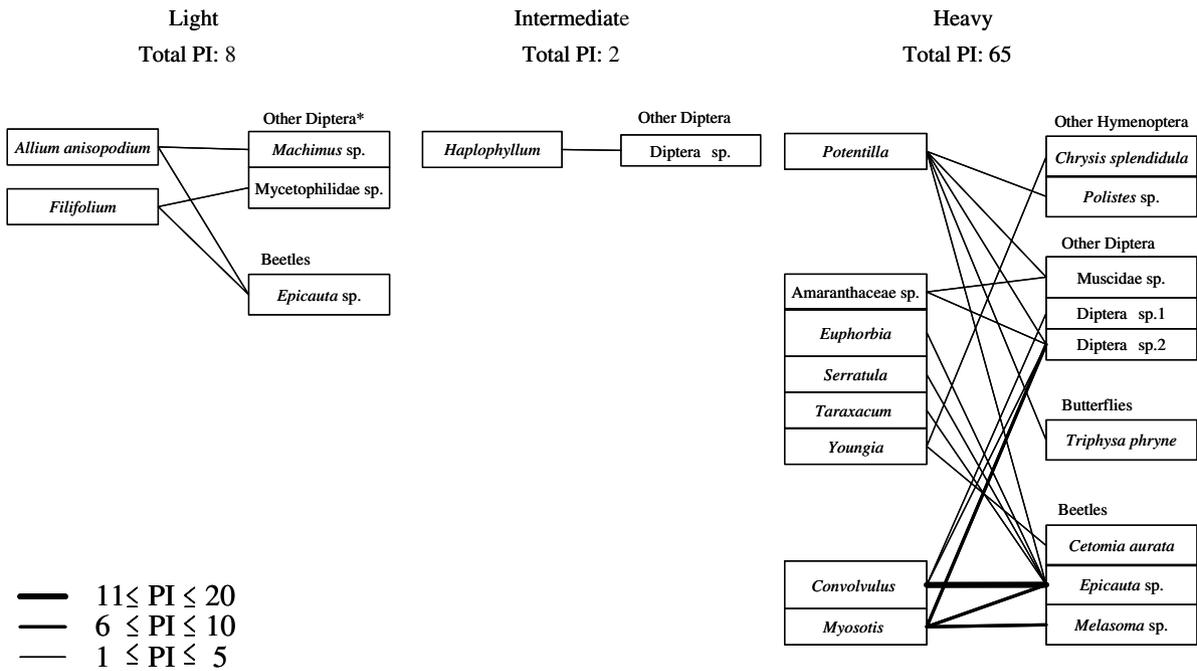
In the removal of pollinators only, the proportions of secondary extinctions were similar, especially between the lightly grazed and heavily grazed plots, in all algorithms (Fig. 4). In the removal of plants and pollinators with equal probabilities, the proportion of secondary extinctions was higher in intermediately grazed and heavily grazed plots than in the lightly grazed plots (Fig. 4). For instance, the lightly grazed plots did not collapse upon removal of 50% of the topmost linked species, but the heavily grazed plot collapsed upon removal of only 28%. Compared with the removal of pollinators only, the difference in secondary extinctions among algorithms was greater on removal of both plants and pollinators in all three plots.

4. Discussion

4.1. Effects of grazing on plant species

Various forbs flowered in the lightly grazed plots only; examples include tall forbs such as *Polygonum divaricatum* (L.) H. Gross And *Scabiosa comosa* Fisch. ex Roem et Schult. (Table 1). There were more species (species richness) in the heavily grazed plots than in the intermediately grazed plots in June, which were simply a consequence of a higher amount of individuals (Fig. 1a). However, same tendency was seen in flower number (more flowers in the heavily grazed plot), the opposite to results seen in Mediterranean shrublands (Vulliamy et al., 2006). This is probably because Mongolian nomads herd mainly sheep and goats, which are browsers or selective herbivores (Hofmann, 1988), and consequently forbs were eaten selectively (though not eliminated) in the intermediately grazed plots. This selective foraging was supported by the fact that the feces of sheep and goats are dominated by forbs in an eastern steppe of Mongolia, whereas those of cattle and horses are dominated by grasses (Yoshihara et al., 2008). Flowering of perennial forbs is often size dependent (Kachi

a



b

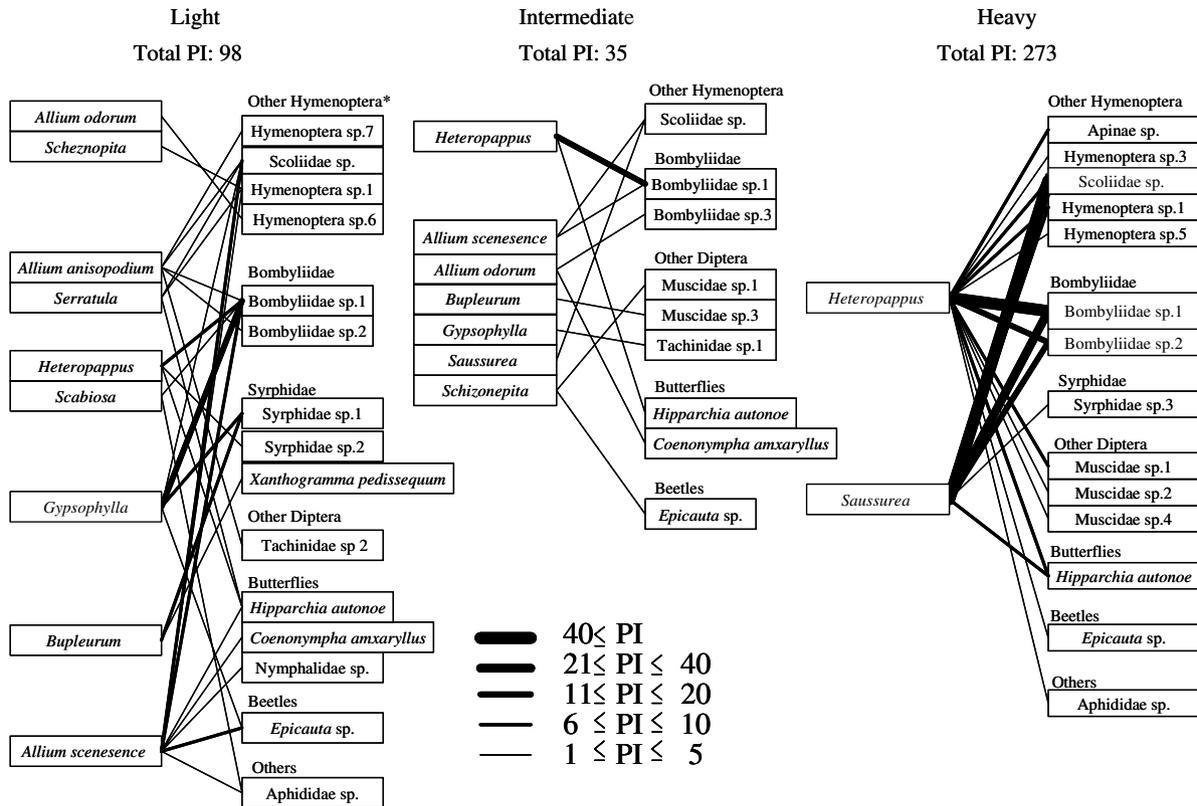


Fig. 3 – Combinations of plants and pollinators at different grazing intensities on the steppe in eastern Mongolia in (a) June and (b) August 2005. The strength of a plant–pollinator combination is indicated by the PI value. Boxes on the left show plants; those on the right show pollinators; line thickness indicates the PI value. *, The classification of pollinator types was based on function (see text for details).

Table 3 – Characteristics of the network structure at each grazing intensity

	Light	Intermediate	Heavy
A, no. animal species	33	24	25
P, no. plant species	31	12	27
M, network size (A × P)	1023	288	675
I, no. interactions recorded	36	12	38
C, connectance	3.52	4.17	5.63
L_a , mean no. interactions across animal species	1.09	0.50	1.52
L_p , mean no. interactions across plant species	1.16	1.00	1.41

Table 4 – Total numbers of flowers (N), total pollination index (PI), and PI values per flower (PI/N) of each species in both seasons compared between lightly and intermediately grazed plots

Plant name	Light			Intermediate			Difference
	N	PI	PI/N	N	PI	PI/N	$PI/N_{Light} - PI/N_{Intermediate}$
<i>Allium anisopodium</i>	944	8	0.0085	396	0	0	+0.0085
<i>Allium odorum</i>	59	1	0.0171	36	3	0.0845	-0.0674
<i>Bupleurum bicaule</i>	5197	10	0.0019	706	1	0.0014	+0.0005
<i>Cymbaria dahurica</i>	64	0	0	120	0	0	0
<i>Gypsophylla</i> sp.	106	20	0.1887	39	1	0.0260	+0.1627
<i>Haplophyllum</i> sp.	462	0	0	89	2	0.0226	-0.0226
<i>Heteropappus hispidus</i>	87	8	0.0920	130	22	0.1699	-0.0779
<i>Polygonum divaricatum</i>	113	0	0	109	0	0	0
<i>Scheznophyta multiphyta</i>	324	1	0.0031	245	2	0.0082	-0.0051

Common species were not found in the heavily grazed plots.

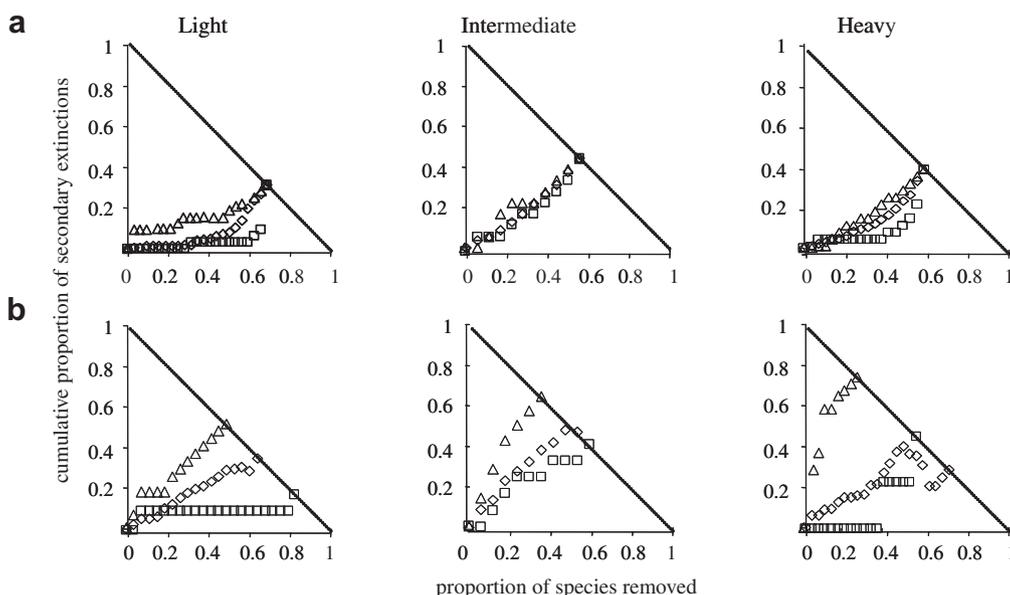


Fig. 4 – Proportion of species lost to secondary extinction as a function of species removed (primary extinction) under different grazing intensities. Three different removal algorithms were used: most connected (triangles), least connected (squares), and random removal (diamonds). Species were removed until the data series reached the dashed diagonal line, where primary removals + secondary extinctions = all species gone. In (a), pollinators alone are removed, and only plants experience secondary extinctions. In (b), plants and pollinators are removed with equal probability.

and Hirose, 1983), so defoliation likely reduces or prevents flowering.

Plants common in the lightly and intermediately grazed plots did not grow in the heavily grazed plots, in which only a few forbs were dominant: *M. caespitosa* in June and *H. hispidus* and *S. salicifolia* in August (Table 1). Despite the low biomass, these plants flowered more abundantly than they did in the intermediately grazed plots. This can be explained by several factors. People graze their cattle near the *soum* center because they need milk, and the cattle eliminate the tall grasses. This results in a relative increase in rosette or prostrate forbs by the removal of their competitors. Low-growing forbs are generally not favored by grazers (Gimingham, 1951; Crofts and Jefferson, 1999). *Myosotis caespitosa* is unpalatable to livestock because of hairs on the plant body. *Heteropappus hispidus* is a prostrate species and *S. salicifolia* is a rosette species, allowing both to escape grazing.

4.2. Pollination

The rarefaction curves for insect sampling did not reach a plateau in the intermediately grazed plot, indicating that more sampling effort is needed to better represent species richness.

However, the visitation frequency and pollinator richness in August were low in the intermediately grazed plots, in which insect-pollinated plant species had a low abundance. The diversity of pollinators reflects the flora and the abundance of flowers (Erhardt, 1985; Carvell, 2002; Sjodin, 2007).

Contrary to expectation, total PI values in the lightly grazed plots were not the highest, even though the visitation frequency was high (Fig. 2). The presence of insects does not guarantee a PI value. For example, the visitation frequency was higher in June than in August, but the PI value was lower, because most of the insects were beetles which are not effective pollinators (e.g., moved little from flower to flower). In contrast, PI values increased in August because of an increase in Diptera and Hymenoptera, which are effective pollinators. Similarly, the PI value in the lightly grazed plots in June was smallest despite a high frequency of pollinator visits, because the insects attracted to *Serratula centauroides* L. flowers, which accounted for about half of the total visits, moved little from flower to flower, probably owing to abundant nectar production by the young flowers. Abundant nectar is available immediately after blooming of *Echium vulgare*, which is protandrous (Klinkhamer and Dejong, 1990). Therefore, our PI value may underestimate the effective pollination in the lightly grazed plots if the higher availability of nectar leads to more efficient pollination. The lower PI of the lightly grazed plots may also be a product of a lower probability of encounter of pollinators with flowers of the same species owing to the diverse flora and high abundance of graminoids in the plots.

The higher PI values in the heavily grazed plots can be attributed to the following causes. First, if the number of flowers were the same, the PI values would be higher in the heavily grazed plots, where the flora was less diverse. Second, most of the dominant plants in the heavily grazed plots (e.g., *C. ammanii* and *S. salicifolia*) tended to be clumped, which tends to attract more visitors because of display effects (Sih and Baltus, 1987). Third, the dominant plants in the heavily grazed plots (e.g., *H. hispidus* and *S. salicifolia*) bore dish-

shaped flowers and were visited by pollinators for shorter times than were the complex-shaped flowers that were often found in the lightly grazed plots. Fourth, the vegetation was short and not diverse in the heavily grazed plots; consequently, pollinators could find flowers more easily than in the other plots (Ehrlen et al., 2002). Thus, our PI value may overestimate the effective pollination in the heavily grazed plots if a surplus of visits has no effect on reproductive success of plants.

Both the PI values and the number of flower–pollinator interactions were lowest in the intermediately grazed plots (Fig. 3). However, the PI values of individual flowers were not always smaller than those in the lightly grazed plots (Table 4), suggesting that the low total PI is attributable not to the pollination rate, but rather to the decline in the number of flowers.

The connectance and linkage at the network level were highest in the heavily grazed plots (Table 3). This result indicates that increased grazing pressure leads to a shift from oligolectic to polylectic pollinator species, and from plants depending on specialized pollinators to plants depending on generalized pollinators. This generalization is valid perhaps worldwide in anthropogenic ecosystems (Johnson and Steiner, 2000). In general, generalized relationships between plants and pollinators are more robust under fragmentation (Dunne et al., 2002; Steffan-Dewenter et al., 2006). However, an unbalanced structure due to a strong dependency on limited species (*H. hispidus* and *S. salicifolia*) produced different results: in the worst scenario (most-connected species removed first), the mutual network was fragile with respect to the extinction of certain species owing to the strong dependence of pollinators on these limited plant species (Figs. 3, 4). In such a simple pollination system, it is probable that the loss of dominant plants will result in serious effects on their partners and lead to the collapse of the network (Bascompte and Jordano, 2006).

As inferred from our results, pollination properties can be partially explained by grazing intensity. However, other factors relevant to our methods need to be recognized. We used a gradient of grazing intensity, but this is linked with different types of browsers. So we could not clearly separate the two factors. In addition, we did not measure soil quality or plant fitness in each plot. To control for grazing quality and environment, it is better to change livestock density at the same soil condition with fenced plots, and then compare plant fitness among plots in addition to the surveys we did (Gómez, 2005). Further experimental research is needed to determine how pollination services respond to grazing intensity.

4.3. Conservation implications for the Mongolian steppe

Since the regime change in 1992, nomads and livestock have become more concentrated in *soum* centers, resulting in an expansion of overgrazed areas. Our intermediately grazed plots were grazed mainly by sheep and goats, which feed selectively on forbs, resulting in a decrease in insect-pollinated flora and, consequently, pollinators (Fig. 2). It is noteworthy that both insect-pollinated plant species and pollinators were least diverse in the intermediately grazed plots, which were dominated by typical grasses (Fig. 1). This

is problematic from the viewpoint of ecosystem function, because grazing is common in Mongolia, and the number of goats is increasing faster than that of other livestock (National Scientific Office of Mongolia, 2007). In future work, we need to show whether the pollination services limit many plant species in the intermediately grazed plots.

In the heavily grazed plots, the invasion of ruderal and exotic plants such as *M. caespitosa* caused the concentration of pollinators limited to these plants. The failure of a botanist in our group to find *M. caespitosa* here until this survey indicates that the recent overgrazing would provide safety site (e.g. bare ground) for exotic plants brought in on vehicles. Thus, although the total PI values were highest in the heavily grazed plots, this may only encourage these unfavorable plants to increase their sexual reproduction. Moreover, the plants growing there and the plant–pollinator interactions were quite different from those of the natural Mongolian steppe.

In conclusion, overgrazing weakens ecological function through the impoverishment of forbs and consequent pollination over a wide area, and by unexpectedly weakening the flower–pollinator mutual structure around *soum* centers in eastern Mongolia. Although the PI values were highest in the heavily grazed area, this paradoxically reflects a decrease in interaction diversity. This is not necessarily characteristic of the traditional Mongolian steppe, but may be a biological fact.

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