

Climate change and grazing interact to alter flowering patterns in the Mongolian steppe

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Abstract Socio-economic changes threaten nomadic pastoralism across the world, changing traditional grazing patterns. Such land-use changes will co-occur with climate change, and while both are potentially important determinants of future ecosystem functioning, interactions between them remain poorly understood. We investigated the effects of grazing by large herbivores and climate manipulation using open-top chambers (OTCs) on flower number and flowering species richness in mountain steppe of northern Mongolia. In this region, sedentary pastoralism is replacing nomadic pastoralism, and temperature is predicted to increase. Grazing and OTCs interacted to affect forb flowering richness, which was reduced following grazing removal, and reduced by OTCs in grazed plots only. This interaction was directly linked to the soil moisture and temperature environments created by the experimental treatments: most species flowered when both soil moisture and temperature levels were high (i.e. in grazed plots without OTCs), while fewer species flowered when either temperature, or moisture, or both, were low. Removal of grazing increased the average number of graminoid flowers produced at peak flowering in Year 1, but otherwise grazing

removal and OTCs did not affect community-level flower composition. Of four abundant graminoid species examined individually, three showed increased flower number with grazing removal, while one showed the reverse. Four abundant forb species showed no significant response to either treatment. Our results highlight how climate change effects on mountain steppe could be contingent on land-use, and that studies designed to understand ecosystem response to climate change should incorporate co-occurring drivers of change, such as altered grazing regimes.

Keywords Climate manipulation · Grazing abandonment · Land-use change · Open-top chamber · Pastoralism

Introduction

Different components of global change are likely to act in concert to affect biodiversity and ecosystem functioning (Sala et al. 2000), potentially interacting in complex ways (Post and Pedersen 2008; Hoover et al. 2012). Climate change and land-use change are among the factors expected to affect ecosystems and the services they provide in the coming decades (MEA 2005; IPCC 2007). Both factors are particularly likely to affect parts of the world that support traditional nomadic pastoralism, amounting to over 25 % of land area (FAO 2001), as land-use change in these regions is increasingly manifested as altered grazing patterns due to socio-economic changes affecting the number and movements of pastoral people (Namgail et al. 2007; Dong et al. 2011). In such regions, climatic change must be considered in the context of altered grazing regimes to gain a more realistic picture of its ecological significance and likely impacts.

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Numerous studies have examined the effects of changing climatic factors on vegetation in grazed systems (see reviews in Rustad 2008; Elmendorf et al. 2012). However, few have specifically considered interactive effects of climate change and grazing on plant communities (Klein et al. 2004; Post and Pedersen 2008; Olofsson et al. 2009), and only one, to our knowledge, has experimentally manipulated both climate and grazing by large herbivores (Post and Pedersen 2008; Post 2013). Grazers have been recognised for decades as important agents of disturbance affecting plant community composition through trampling, depositing dung and urine, and removing live and dead plant material (Ellison 1960; Grime 1973; Facelli and Pickett 1991). The specific nature of the disturbance, and hence its impact on plant communities, will depend on grazer identity, abundance, and seasonality. Winter grazers reduce plant litter, with direct and indirect repercussions for the physical microenvironment and nutrient cycling. Accumulated litter can reduce light availability, increase soil moisture and decrease temperature (Facelli and Pickett 1991; Deutsch et al. 2010), and ultimately influence the composition of the plant community (Lamb 2008; He et al. 2011). Microclimatic effects caused by changes in grazing regime will be super-imposed upon those induced by climatic change.

The Mongolian steppe is part of the Eurasian steppe, the largest herbaceous biome in the world, and is threatened by both changes in pastoralism and climate. Northern Mongolia has warmed significantly over the past 50 years (+1.7 °C; Namkhajantsan 2006), and predicted temperature increases over the next century are among the highest in the world, while precipitation predictions for the area have no consensus (IPCC 2007; Sato et al. 2007). At the same time, traditional nomadic pastoralism in the region is shifting to more sedentary pastoralism and is threatened by urbanisation and employment opportunities in the rapidly growing mining industry (Morris and Bruun 2005; Batima et al. 2008). These socio-economic trends simultaneously create areas where grazing intensity has increased and areas where grazing has been abandoned.

We present results from a 3-year experiment, conducted in mountain steppe of northern Mongolia, in which we manipulated both climate and grazing by large herbivores. Because the site is usually used as winter pasture, we employed two grazing treatments, the usual scenario of winter grazing, and the removal of grazing by fencing plots year round. Climate manipulation was achieved by deploying passive warming devices (open-top chambers, OTCs) in the summer growing season. We investigated the combined and independent effects of grazing regime and climate manipulation on number of flowers at peak and flowering species richness of the steppe plant community. Flowering phenology has received considerable attention as a biotic variable affected by climate change (Wolkovich et al.

2012). Responses in flower number are far less commonly documented in natural systems. The number of flowers produced is a key plant character because it contributes to reproductive success, maintenance of genetic diversity, and the long-term viability of populations (Clark et al. 2007; Jacquemien et al. 2010). In addition, flowers provide particular ecosystem services, producing resources supplied to pollinators (Hegland and Boeke 2006), constituting a component of plant biomass (La Pierre et al. 2010), and contributing to the aesthetic qualities of the environment (Tielbörger et al. 2010).

Specifically, we asked how climate manipulation with OTCs and/or grazing regime affected flowering species richness and flower number at peak flowering for both the community as a whole and of individual species. Since vegetative growth in the mountain steppe is co-limited by temperature and water availability (Yu et al. 2003), we hypothesized that, compared to the control conditions of winter grazing and no OTC:

1. OTCs would reduce flowering species richness and flower number due to incurring drought stress by increasing temperatures while decreasing soil moisture; and
2. Flowering species richness and individual and community-level flower number would be lower on ungrazed plots due to litter accumulation.
3. An interaction between climate manipulation and grazing would occur, mediated by their effects on key abiotic variables (soil and air temperature and soil moisture).

Materials and methods

Study site

The study was conducted June–August, 2009–2011, on the lower south-facing slope of the Dalbay Valley (elevation ~1,670 m a.s.l. with a flat to gentle incline) in northern Mongolia (51°01.405'N, 100°45.600'E), part of the Lake Hövsgöl International Long Term Ecological Research Site (ILTER). The climate of the Hövsgöl region is 'harsh continental' with large annual and diurnal temperature ranges. Air temperatures averaged -4.5 °C annually, with monthly averages ranging from -21 °C (Jan) to 12 °C (July) (Nandintsetseg et al. 2007). Regionally, average annual precipitation over the last 40 years was 265 mm (Namkhajantsan 2006). An on-site meteorological station (HOBO U30 Station; Onset Computers, Bourne, MA, USA) recorded annual rainfall (August–August) of 270 mm (2008–2009), 246 mm (2009–2010), and 207 mm (2010–2011), and summer rainfall (June–August) of 201 mm (2009), 178 mm (2010), and 137 mm (2011).

The bedrock consists of Cenozoic volcanic deposits, and the soil is sandy loam of alluvial origin and classified as a non-carbonated Dark Kastanozem (Aridic Boroll or Typic Ustolls). While the north-facing slope is forested, predominantly by *Larix sibirica*, the vegetation of the south-facing slope is mountain steppe, a mixture of sedges (e.g. *Carex pediformis*), grasses (e.g. *Festuca lenensis*, and *Koeleria macrantha*) and short forbs (e.g. *Aster alpinus*, *Potentilla acaulis*, and *Artemisia commutata*). Average vascular plant cover of the lower south-facing slope is 95 %, and is dominated by *Carex pediformis* (Online Resource 1, Fig. S1). The site is winter pasture, normally grazed in autumn until spring by yaks, cows, horses, sheep, and goats, as part of the traditional seasonal movement of nomadic herders.

Experimental design

We had eight experimental blocks, each consisting of a 9 × 9-m section fenced to exclude livestock throughout the year ('ungrazed'), and a 3 × 9-m section fenced only during the growing season, June–August ('grazed'). Therefore, grazing in grazed plots occurred from September to May, when most of the plant material had senesced.

Each grazed and ungrazed section held a plot in which climate was passively manipulated with an open-top chamber (OTC), and a control plot without an OTC; thus, the grazing and climate manipulation treatments were fully factorial. The temporal separation of OTC placement and grazing avoided confounding effects of OTCs serving as obstacles to grazers (Wookey 2008). OTCs were hexagonal and followed the ITEX design (Marion et al. 1997): 1.0 m wide at the top and 1.5 m at the bottom, 40 cm tall, and made of Sun-Lite® HP fibreglass glazing mounted on a clear Lexan frame. Control plots had the same footprint as OTCs. The same plots were used in all years of the study. The chambers were in place for three summers, 2009–2011, but data are presented here for 2010 and 2011 only because the grazing treatment did not start until the autumn/winter of 2009. The OTCs reduce photosynthetically active radiation at ground level by 16 % relative to plots without OTCs in the ungrazed section of blocks (Liancourt et al. 2013).

Abiotic variables

Soil temperature and volumetric water content (%VWC) were measured in all plots in 2011. Measurements were taken once daily (between 1000 and 1200 hours) for 7–9 days during early, mid-, and late season (June, July, and August, respectively) using a WET-2 sensor (Delta-T Devices, Cambridge, UK) at a depth of approximately 6 cm. Additionally, air temperature was measured at 10-min intervals throughout the 2011 growing season in all plots of four experimental blocks using HOBO dataloggers

(Pro v2; Onset Computers). We calculated air temperature at mid-day during the same early, mid-, and late season periods as for soil temperature and moisture, by averaging readings between 1215 and 1415 hours, corresponding to 1 h before and after the sun's zenith. Values of the three abiotic variables were averaged for each plot within each seasonal period.

Treatment effects on each of the three abiotic variables (soil moisture, soil temperature, and air temperature) were tested using repeated-measures ANOVA with fixed effects of seasonal period as the repeated measure, climate manipulation as a split-plot within grazing treatment, and all interactions. Block and all the interactions with block were treated as random effects and estimated by REML procedures using the *lme4* package (Bates et al. 2012) in R 2.15.2 (R Development Core Team 2011). *F* ratios and *P* levels were calculated using car package (Fox and Weisberg 2011) using Type II sums of squares. The Greenhouse-Geisser estimates of Box's epsilon (GGe) was applied as a correction factor to degrees of freedom to account for violation of the sphericity assumption. GGe apply to treatments that are split-plot or repeated measures, but GGe = 1 with $n = 2$ factor levels. GGe were calculated using the *ez* package (Lawrence 2012).

Measurement of plant litter

Plant litter was quantified in June 2010 and 2011. On grazed plots, it corresponded to litter biomass remaining after winter grazing, while on ungrazed plots it measured litter that had accumulated in the absence of grazing over 1 or 2 years, respectively. All dead plant biomass, including standing material, was collected from within two randomly positioned 40 × 40-cm areas in both the grazed and ungrazed section of each block but outside the experimental plots. Litter was air-dried and the mass from the two areas averaged to provide litter quantity (g m^{-2}) for each section. Litter quantity was compared between grazed and ungrazed sections of blocks using repeated-measures ANOVA with fixed effects of Year as the repeated measure, grazing treatment and its interaction with Year. Block and all the interactions with block were treated as random effects and estimated using REML procedures as described above. This analysis does not consider litter levels in OTC plots, however, it is representative of the plots as a whole as we found no significant difference in litter biomass between plots with and without OTCs at harvesting in 2012 (unpublished data).

The extent to which litter mediated the effect of grazing treatment on soil moisture and soil temperature was examined for 2011 data using repeated-measures ANCOVA. The model included grazing treatment, season (early, mid-, and late) as the repeated measure, and litter biomass as the

covariate. There was no interaction between litter biomass and grazing treatment in their effects on soil moisture or temperature, confirming the assumption of homogeneity of slopes. Block and all the interactions with block were treated as random effects and estimated using REML procedures. The GGe correction was applied as described above.

Measurement of flower number and richness

The number of flowers per species was assessed weekly in 2010 and 2011 by counting flowers within a 50 × 100-cm quadrat in the centre of each plot. The quadrat was positioned with its short edges parallel to the north- and south-facing sides of each hexagonal plot. For forbs, fully-opened flowers, or inflorescences with at least one fully-open flower, were counted (Online Resource 1, Table S1). For graminoids, inflorescences were counted as ‘flowering’ from the beginning of the transition to reproductive stage (i.e. bolting stage) through, but not after, the anthesis stage. Weekly assessments were conducted 11 times each year, ranging from Julian days 155 to 223 in 2010, and days 156 to 226 in 2011. These data were used for measures of flowering species richness and flower number per species. Throughout these weekly censuses, we saw no evidence of inflorescence or flower herbivory, even though small herbivorous mammals were present in the system. A survey of leaf herbivory conducted in summer 2011 found no differences among experimental treatments (unpublished data).

Our measure of flowering species richness is the number of species on each plot with at least one fully-opened flower in at least one weekly census. Flowering species richness was quantified separately for forb and graminoid species each year. The effect of grazing and climate manipulation on forb and graminoid flowering richness was analyzed using repeated-measures ANOVA with fixed effects of year as the repeated measure, climate manipulation as a split-plot within grazing treatment, and all interactions. Block and all the interactions with block were treated as random effects and estimated using REML procedures. In addition, the relationship between soil abiotic conditions and forb and graminoid flowering richness in 2011 only was examined using regression models, which included mid-season soil moisture and soil temperature as main effects, their interaction, and block as a random factor. Flowering species richness data was not transformed, despite being count data, as the residuals in these analyses were normally distributed.

Our measure of flower number per species is the number of flowers produced at time of peak flowering, weighted by vegetative cover on each plot in each year (‘flower number at peak’ hereafter). We weighted our measure by vegetative cover to account for relative abundance and to provide a

standardized measure. Vegetative cover of each species in each quadrat was measured in mid-July each year. Cover was determined using the same quadrat as for the flowering census, divided into 50 cells of 10 × 10 cm. Percentage cover per species was estimated in each cell and averaged to estimate percentage cover per plot. Inflorescence counts and cover of three co-occurring *Carex* spp. were combined due to the difficulty in distinguishing them vegetatively.

Flower number at peak was calculated for each species on each plot using the procedure given in Liancourt et al. (2012b) and is as follows. First, the date of peak flowering was calculated as $\sum_j F_{ij}T_j / \sum_j F_{ij}$ where F_{ij} is the number of flowers produced by species i on a given plot in week j , and T_j is the Julian day on which the count of week j was performed. Then, flower number at peak was based on the 3-week period centred on the week with the largest (i.e. peak) number of flowers for each species on each plot. Flower number at peak was calculated as the number of flowers in the week of peak flowering, plus the number 1 week before and 1 week after the peak, divided by the percent vegetative cover. Species present but not flowering were given a peak flower number value of zero.

Community-level flower number at peak was analysed using canonical analysis of principal coordinates (CAP; see Anderson and Willis 2003) conducted separately for graminoids (10 species) and forbs (29 species; Online Resource 1, Table S1), and for both 2010 and 2011. Data were analysed separately by year because of the strong difference between years in absolute flower production that dominated the first CAP axis if data from the 2 years were combined. Data matrices contained 32 objects (corresponding to 32 separate plots) by species. Distances were calculated using Gower’s dissimilarity using package FD (Laliberté and Legendre 2010; Laliberté and Shipley 2011), which allows including plots in which some species were not present. Permutation ANOVAs with 999 permutations were used to examine community-level flower number at peak for effects of grazing, climate manipulation, and their interaction. The package *vegan* was used (Oksanen et al. 2013).

Flower number at peak was also examined at the species-level for four forbs and four graminoids. These species occurred on at least half of the plots each year and had the highest average correlation with the site scores from the first two CAP axes. All eight species are perennial. Separate repeated-measures ANOVAs were performed for each species and included main effects of year as the repeated measure, and climate manipulation as a split-plot within grazing treatment. Block was treated as a random effect, but interactions of fixed effects with block were not included because of unbalanced design. F ratios and P values were calculated using the *car* package as described above. P values were corrected using a sequential Bonferroni procedure (Sokal and Rohlf 2012) with $k = 8$.

Table 1 Seasonal differences in air temperature at mid-day, soil temperature, and soil moisture for Grazing treatment (grazed vs. ungrazed) and climate manipulation (control vs. open top chamber, OTC)

Treatment	Season		
	Early	Mid	Late
Air temperature (°C)			
Grazed	19.4 ± 0.5	25.0 ± 0.6	18.9 ± 0.4
Ungrazed	19.6 ± 0.6	25.5 ± 0.8	18.9 ± 0.6
Control	18.4 ± 0.3	24.2 ± 0.5	17.8 ± 0.3
OTC	20.8 ± 0.2	26.4 ± 0.4	19.7 ± 0.3
Soil temperature (°C)			
Grazed	17.1 ± 0.3	22.5 ± 0.3	17.0 ± 0.2
Ungrazed	18.8 ± 0.5	23.8 ± 0.2	17.8 ± 0.1
Control	17.4 ± 0.3	22.8 ± 0.3	17.1 ± 0.2
OTC	18.5 ± 0.5	23.4 ± 0.3	17.7 ± 0.2
Soil moisture (%VWC)			
Grazed	16.4 ± 0.6	8.4 ± 0.5	15.6 ± 0.5
Ungrazed	15.8 ± 0.7	7.5 ± 0.6	15.2 ± 0.4
Control	17.9 ± 0.5	9.2 ± 0.3	17.1 ± 0.4
OTC	14.4 ± 0.4	6.8 ± 0.3	13.7 ± 0.3

Values are mean ± SE ($n = 8$ for soil temperature and soil moisture data, $n = 4$ for air temperature data). For results of ANOVA, see Online Resource 1, Table S4; there was no significant interaction between grazing and climate manipulation treatments

%VWC is percent volumetric water content

Results

Abiotic factors and litter accumulation

Soil temperature was significantly lower on ungrazed compared to grazed plots ($P = 0.001$, repeated-measures ANOVA; Online resource 1, Table S2), while OTCs increased soil temperature ($P = 0.008$). Treatment effects were consistent across the season, although soil temperatures did vary among seasonal periods ($P < 0.001$), being predictably highest in mid-season. Mid-day air temperature was not affected by grazing or OTCs (Online resource 1, Table S2). Grazing did not affect volumetric soil water content (%VWC), while OTCs significantly decreased %VWC ($P < 0.001$; Online resource 1, Table S2), more so in mid-season ($P = 0.007$). Grazing and climate manipulation treatments did not interact to affect air or soil temperature or soil moisture. See Table 1 for mean values of abiotic variables within each experimental treatment.

There was more litter on ungrazed plots. Litter biomass was significantly higher in the ungrazed portion of blocks than in the grazed portions ($P = 0.001$; repeated-measures ANOVA; Online resource 1, Table S2), an effect that was consistent across the 2 years (mean ± SE in g m^{-2} for litter biomass in grazed vs. ungrazed plots: 72.7 ± 17.4 vs.

155.4 ± 37.2 in 2010 and 104.2 ± 15.8 vs. 209.4 ± 21.0 in 2011). When included as a covariate in an analysis of soil temperature in plots without OTCs in 2011, litter biomass was negatively correlated to soil temperature ($P = 0.004$, repeated-measures ANCOVA; Online Resource 1, Table S2), while the grazing treatment as a main effect was not significant. However, litter quantity did not significantly affect soil moisture.

Flowering richness

The grazing and climate treatments interacted to affect forb flowering richness ($P = 0.033$, repeated-measures ANOVA; Online Resource 1, Table S4). The nature of interaction was the same in both years: forb flowering richness was lower on ungrazed plots, while OTCs reduced forb flowering richness on grazed plots and increased forb flowering richness on ungrazed plots (Fig. 1b). Grazing and climate treatments did not affect graminoid flowering richness, although there was a non-significant trend for OTCs to reduce graminoid flowering richness in 2010 ($P = 0.068$; Fig. 1a). Both forb and graminoid flowering richness was higher in 2010 than 2011 ($P = 0.021$ and $P = 0.020$, respectively; Online Resource 1, Table S4).

Soil moisture and soil temperature significantly interacted to affect flowering richness of forbs ($r^2 = 0.68$, $P = 0.001$, mixed-effects regression) and graminoids ($r^2 = 0.67$, $P = 0.001$) in 2011. Forb and graminoid flowering richness increased with soil temperature if soil moisture was high but decreased with soil temperature if soil moisture was low (Fig. 1c, d).

Flower number at peak for the community and individual species

At the community-level, flower number at peak was affected by experimental treatments in 2010 only. The grazing treatment significantly affected graminoid flower number at peak in 2010, but did not affect forbs (Table 2). Comparison of centroids with the overlain contour lines showing the gradient in averages of peak flower number for all included graminoid species indicate that graminoid flower number at peak was higher on ungrazed plots (Fig. 2a). There was a non-significant trend for OTCs to affect forb flower number at peak in 2010 (Table 2). We did not detect an effect of OTCs on graminoid flower number (Table 2; Fig. 2a, c). Grazing and climate manipulation treatments had no effect on community-level flower number in 2011 and did not interact (Fig. 2b, d).

At the individual species-level, grazing affected flower number at peak for all four graminoid species examined but none of the forbs (Online Resource 1, Table S6; Fig. 3). Flower number at peak was higher on ungrazed plots for

Fig. 1 Treatment differences in number of **a** graminoid and **b** forb species flowering in each year. Ungrazed plots are indicated by *circles* connected by *solid lines* and grazed plots by *squares* connected by *dashed lines*, 2010 data has *open symbols* while 2011 symbols are *filled*. Climate manipulation treatment indicated as *CON* (control) and *OTC* (open-top chamber). *Points* are mean \pm SE. Contour plots show number of **c** graminoid and **d** forb species predicted to be flowering based on soil temperature and soil moisture values

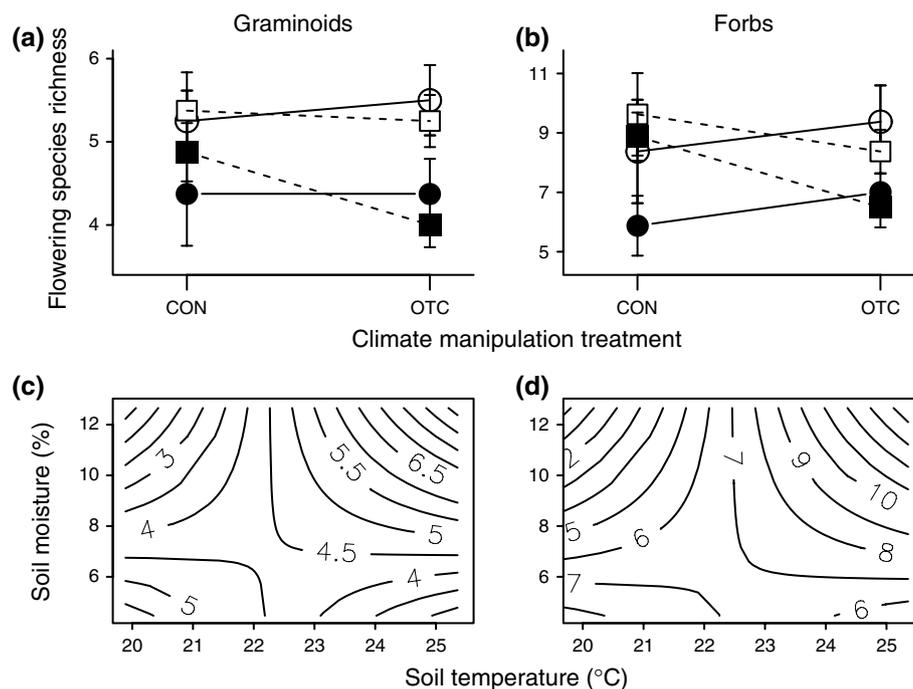


Table 2 Results of permutation tests (*P* values) in the community-level CAP analysis of graminoid and forb flower production at peak in response to treatments for 2010 and 2011

Treatment	Graminoids		Forbs	
	2010 (12.6 %)	2011 (9.3 %)	2010 (10.9 %)	2011 (9.0 %)
Grazing	0.002	0.19	0.71	0.59
Climate	0.82	0.67	0.067	0.33
Climate \times grazing	0.52	0.66	0.39	0.68

Values in parentheses are percentage of variance explained by the constrained axes

Festuca lenensis ($P = 0.013$; repeated-measures ANOVA) with the effect strongest in 2010 ($P = 0.035$), for *Helictotrichon schellianum* in 2010 only ($P = 0.019$), and for *Hierochloe odorata* ($P = 0.047$). In contrast, flower number at peak for *Koeleria macrantha* was lower on ungrazed plots ($P = 0.033$).

In contrast, only one species, the graminoid *Festuca lenensis*, showed a significant response to climate treatment either as a main effect or in interaction with year. OTCs decreased flower production at peak for *F. lenensis* ($P = 0.012$); an effect that was larger in 2010 than 2011 ($P = 0.021$; Fig. 3a). Grazing and climate treatments significantly interacted to affect flower number at peak for *Koeleria macrantha* ($P = 0.034$) such that OTCs reduced flower number on grazed plots, but had no effect on ungrazed plots (Fig. 3d).

Discussion

Flowering patterns in the mountain steppe of northern Mongolia responded rapidly to the removal of winter grazing and to climate manipulation by open-top chambers (OTCs), showing differences within 2 years. The Mongolian steppe, therefore, appears sensitive to two pressures likely to occur in coming decades: climate change and land-use change (Namkhajantsan 2006; Batima et al. 2008). In addition, removal of the winter grazing modified the effect of OTCs on the number of forb species flowering. These results indicate the need to conduct climate manipulation experiments within the context of changing land-use (Sala et al. 2000).

The differing effects of grazing and climate manipulation on flowering species richness may be explained by their relative effects on abiotic factors that apparently co-limit plant growth in this system: temperature and water availability (Yu et al. 2003). The decrease in soil temperature caused by the removal of grazing is most likely due to persistent litter that increases shading and albedo (Facelli and Pickett 1991; Deutsch et al. 2010). These abiotic soil changes are similar to those observed between sites with high and low grazing histories in alpine meadow (Klein et al. 2005) and with clipping in tallgrass prairie (Wan et al. 2002). In contrast, OTCs predominantly increase air temperature and reduce soil moisture due to complex modifications of evaporation, transpiration, and rainfall interception (Marion et al. 1997; Liancourt et al. 2012a). The reduced flowering richness observed in ungrazed plots without

Fig. 2 Results of CAP ordination for flower number at peak of **a** graminoids in 2010, **b** graminoids in 2011, **c** forbs in 2010, and **d** forbs in 2011. *Circles* represent control plots, and *squares* open-top chamber (OTC) plots; *crosses* represent grazed plots. The overall pattern is visualised by overlaying the plots of the first two CAP axes on contour lines indicating average peak flower number for all graminoid, or forb species used in the analysis. *Points* are mean \pm SE. Percentages indicate how much of the total explained variation (see Table 1) is attributable to each axis

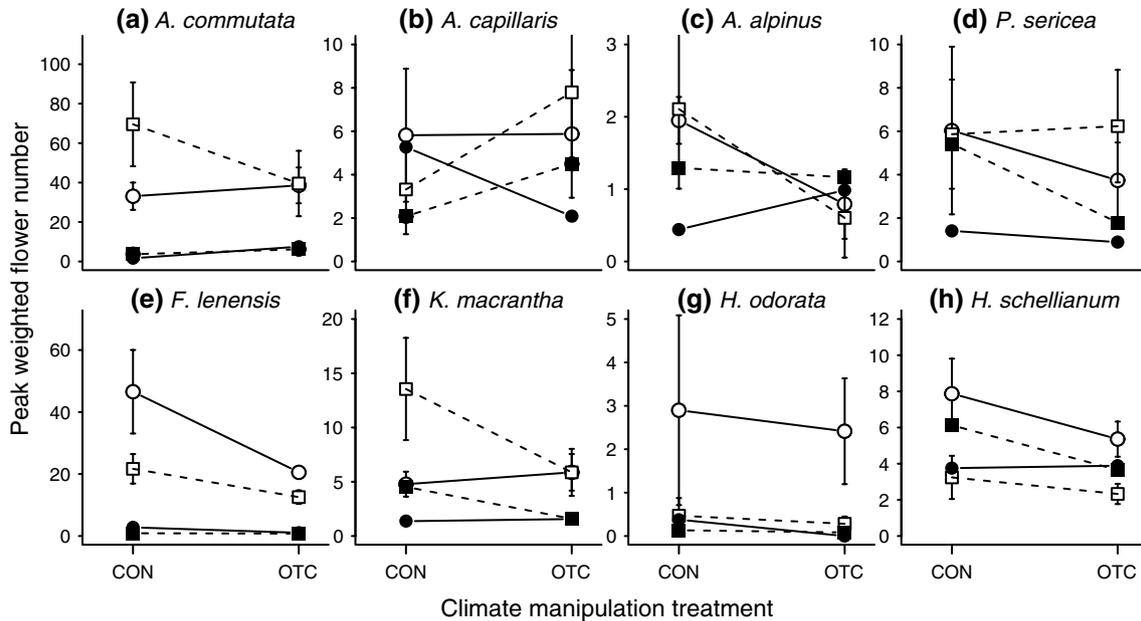
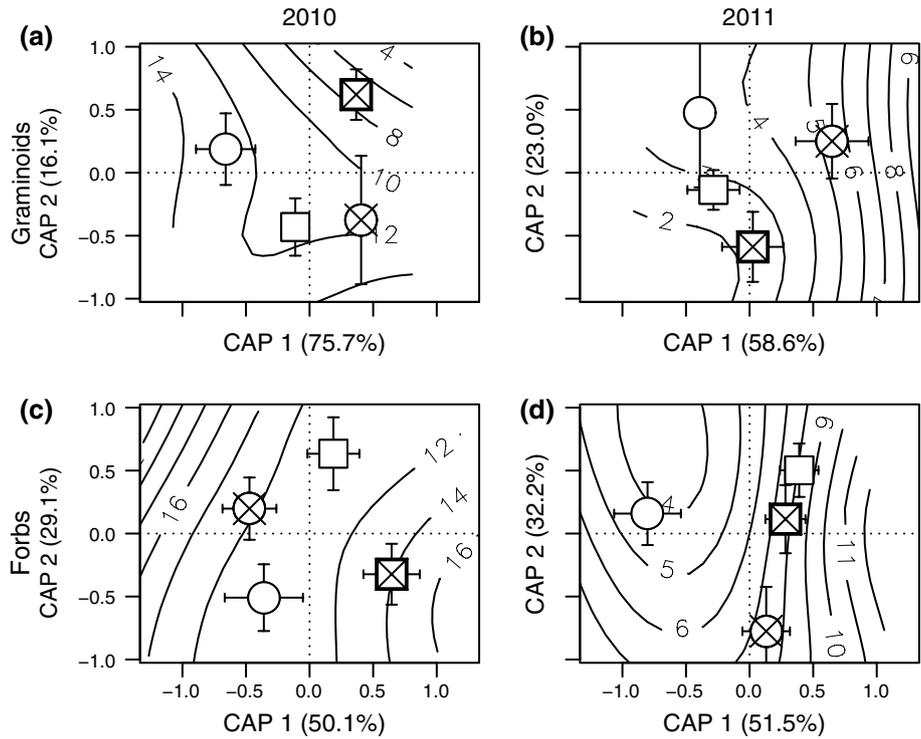


Fig. 3 Flower number at peak weighted by species abundance for eight species used in these analyses **a–d** forb species; **e–h** graminoid species. Ungrazed plots are indicated by *circles* connected by *solid*

lines and grazed plots by *squares* connected by *dashed lines*; *open symbols* are 2010, and *filled symbols* are 2011. *Points* are mean \pm SE. Full species names can be found in Online Resource, Table S1

OTCs may result from lower soil temperature and thus cold stress. Conversely, when OTCs are present on grazed plots, the combination of increased soil temperature and reduced soil moisture may well create water stress (Llorens and Peñuelas 2005; Liancourt et al. 2012b), thereby eliminating

the otherwise positive effect of winter grazing on the number of species flowering.

The interplay between winter grazing and climate that affects soil abiotic factors and flowering species richness is particularly notable because most climate change

experiments do not explicitly manipulate grazing by large herbivores. The only other study, to our knowledge, examining the combined effects of OTCs and large herbivores on vegetation took place in low-shrub arctic tundra (Post and Pedersen 2008). Post and Pedersen (2008) reported plant community responses similar to those observed in long-term exclosures (Olofsson et al. 2009; Hofgaard et al. 2010), namely that the plant community appears to respond to OTCs or warmer temperatures mainly when grazing does not occur, a result contrasting with ours where OTCs affect the plant community mainly when large herbivore grazing *does* occur. This difference may be because the arctic tundra studied had a palatable shrub component that can come to dominate if temperature increases and the system is released from grazing. There are only relatively unpalatable sub-shrubs in the Mongolian steppe flora such as *Thymus* and *Artemisia*. In general, tundra sites are not always limited by moisture (Walker et al. 2005, but see Elmendorf et al. 2012), and increasing temperature may even increase water availability through permafrost melting (Oberbauer et al. 2007). The Mongolian steppe, in contrast, is semi-arid and our system has very sandy soil, therefore increasing temperature may exacerbate water stress.

An explanation for the stronger, and often positive, response of graminoids to the removal of grazing, in comparison to forbs, is not clear. It may be that tissue senescence has not progressed as much in graminoids as it has in forbs before autumn grazing begins, resulting in grazers removing tissue that still contained extractable nutrients and/or carbohydrates and reducing storage reserves that would support flowering the following year. This effect might be exacerbated if grazers are selective and more likely to choose graminoids before senescence is complete (Schwartz and Ellis 1981).

Our findings that graminoids and forbs, as functional groups, differed in their flowering responses to grazing contrasts with some other studies where there were no such broad patterns and responses were species-specific (Hollister and Webber 2000; Dunne et al. 2003; Primack et al. 2009). Regardless, the application of functional leaf and plant traits (Lavorel and Garnier 2002), that often separate forbs and graminoids, may be of primary importance for developing adequate predictions of plant community responses, including flowering, to global change.

The larger effect of experimental treatments on flowering in 2010 may be explained by there being 30 % more summer rainfall than in 2011. These interannual differences in the effects of experimental treatments suggest that changes in climate or land use might act to reduce the quality of more favourable years rather than making unfavourable years worse. At the individual-species level, more graminoid species responded to the grazing treatment than the climate manipulation. This might be because the effects

of our climate manipulation fell within the range of natural year-to-year variation, in contrast to our grazing treatment, which may also have modified disturbance patterns, the light environment, and carbon storage and allocation. Three of the graminoid species examined showed increased flowering with the removal of grazing, perhaps because autumn grazing removed plant material before senescence causing plants to lose carbon that would be used for flowering the following year (Schwartz and Ellis 1981). In addition, an altered light environment through litter accumulation may modify competitive interactions among graminoid species, whereas the OTCs have been shown not to affect interspecific competition (Liancourt et al. 2013).

Flower production in mountain steppe appears sensitive to even small changes in abiotic conditions, resulting from either future climate change and/or grazing abandonment. This is pertinent for Mongolia, where the warming climate (IPCC 2007; Namkhajantsan 2006) is occurring alongside a changing economy that could cause nomadic pastoralism to be replaced by other lifestyles (Batima et al. 2008). Reduced soil moisture, as caused by the OTCs, is also a possible scenario because reduced, or more infrequent, precipitation is predicted for the region by some climate models (Sato et al. 2007), and is a change perceived to be happening by Mongolian herders (Marin 2010). The greater responsiveness of graminoid than forb species in this study may mean that certain ecosystem services affected by flower production, such as the provision of forage for animals, may be more vulnerable to climate change and grazing abandonment in this environment than others, such as pollination resources.

We believe that climate manipulation studies should incorporate co-occurring drivers of global and local change relevant to the study system, in just the same way that local studies of conservation management should consider regional climatic change impacts (e.g. Maalouf et al. 2012). In our system, we find that predicted climate change could strongly affect flowering in a scenario where historic land-use practices continue. However, even stronger effects on flowering could be caused by grazing cessation, in which scenario, predicted climate change would have a lesser effect. Our results highlight the need for further studies of land-use and climate interactions in other pastoral systems around the world, in which there are similar demographic and social trends that could significantly affect vegetation and how it responds to climate change.

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