



Large scale experimental effects of three levels of sheep densities on an alpine ecosystem

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Plant–herbivore dynamics is a major topic in ecological research, but empirical knowledge on the ecological effects of different densities of large grazers from fully replicated experiments is rare. Previous studies have focused on grazing vs no grazing, and our understanding of the extent to which different levels of grazing alter vegetation composition, and how quickly such effects can be measured, is therefore limited. We performed a fully replicated, short-term (four-year) experiment using large enclosures (each $\sim 0.3 \text{ km}^2$) with three different sheep densities (no grazing, low grazing and high grazing, respectively) in an alpine environment with summer grazing in southern Norway to address these issues. Sheep grazing mainly affected plant species at high densities of sheep as compared to no sheep after a four-year treatment; few effects of low sheep densities were detectable. Highly selected herbs, herbs suggested vulnerable to trampling, and woody species decreased, while most graminoids, one ruderal, one prostrate species and two bryophyte taxa increased at high sheep densities. We found contrasting responses within main functional groups highlighting that fine details of plant life histories need to be known for responses to grazing to be successfully predicted. Vascular plant cover and bare soil responded to sheep density after two years of treatment, but only for one of the species was frequency change observed at this stage. Overall, plants in low grazing plots were found to be almost unaffected. Changes in abundance were mainly found at the no grazing and high grazing treatments. Plant species that decreased at high grazing generally increased at no grazing and vice versa, suggesting a response to both cessation of grazing and enhanced grazing respectively. Our study demonstrates, beyond a simple comparison of heavily grazed and non-grazed sites, that herbivore effects on plants are typically non-linearly related to herbivore density, and that the speed of plant responses will depend both on the plant property examined and the grazing pressure.

Herbivores can strongly affect plant community patterns by favouring resistant and tolerant plants to the detriment of less tolerant, highly selected species (Crawley 1997, Hester et al. 2006). Although the outcome of direct and indirect herbivore effects in terms of (change in) overall species composition appears more or less predictable for the alpine tundra (Van Der Wal 2006), these are mostly qualitative patterns for main growth-form groups. Exactly how high herbivore intensity is required for different species in alpine communities to trigger abundance change over time has rarely been examined experimentally. The effect of herbivory has mainly been studied by small-scale enclosure experiments (Mulder 1999) or by use of spatial contrasts in herbivore density (rather than following grazing over time in one area) in quasi-experiments at coarse scales (Bråthen et al. 2007, Ims et al. 2007). Empirical knowledge of the shape of the density-effect function of large grazers on plant community patterns is thus limited. Studies on browsing effects of depleted species in boreal forests along

gradients of deer densities (Horsley et al. 2003, Tremblay et al. 2006) or indirect studies of browsing by manipulating moose browsing (Persson et al. 2005) show no consistent pattern. Different levels of browsing intensity cause non-linear decreases (Tremblay et al. 2006), thresholds and then a linear decrease (Persson et al. 2005) or no response at all (Horsley et al. 2003) on a short-term scale (three years). However, effects of herbivory over time result from complex interactions depending on environmental factors such as site productivity, herbivore history as well as spatial scale. Knowledge of how such environmental factors mediate the effect of herbivores on vegetation dynamics is thus essential for determining the grazing intensity thresholds that separate continuous and reversible versus discontinuous and non-reversible processes in different environments (Briske et al. 2005).

Arctic and alpine grazers generally prefer herb species, and grazing frequency among palatable herbs increase from low to high sheep densities (Evju et al. 2006). On a time

scale of two decades, high reindeer density reduced the abundance of palatable herbs in productive habitats as compared to areas of low reindeer density (Bråthen et al. 2007). In contrast, graminoids, which dominate in terms of biomass in arctic and alpine habitats and in general provide the main diet during summer (Bråthen and Oksanen 2001), are generally promoted by grazing, and some graminoid species may increase rapidly in response to increased grazing (Jonsdottir 1991, Steen et al. 2005). The exception is some highly selected palatable graminoids which also are found to decrease at high grazing levels (Bråthen and Oksanen 2001, Austrheim et al. 2007). Dwarf shrubs constitute an important part of the grazer's diet, especially for reindeer during wintertime. *Salix* spp. are highly depleted in areas of high reindeer densities (Bråthen et al. 2007), and also sheep eat woody plants such as *Salix* spp. during summer (Kausrud et al. 2006). Finally, bryophytes which hardly are foraged by large herbivores in alpine environments, are disturbed by trampling which may cause short-term negative responses, while indirect competitive effects from graminoids are expected to have a negative effect on a long term scale (Virtanen 2000).

We performed a fully replicated, short-term (four-year) experiment with three levels of sheep densities (no grazing, low and high) at a landscape scale (2.7 km²) in an alpine environment with summer grazing in southern Norway to address whether plants respond differently to varying levels of grazing intensity. As large herbivores are also expected to have indirect effects on plants due to interactions with small herbivores (Evans et al. 2006), we also examine if sheep grazing affects rodent grazing as measured by a rodent sign index (Lambin et al. 2000, Evans et al. 2006). The predictions that we aimed to test are summarised in Table 1. Grazing effects are in general expected to be faster at high than at low grazing intensity of sheep compared to no grazing, and on plant communities selected by sheep, such as snow-bed and graminoid dominated communities (grass-

land) compared to less selected vegetation types such as dwarf-shrub heaths and lichen ridges (heathland) (Kausrud et al. 2006). However, many of the selected species growing in successional environments, such as the low alpine zone, may depend on grazing since this system has a history of grazing by wild herbivores as well as by livestock dating back to prehistoric times (Austrheim and Eriksson 2001, Körner 2003). Especially graminoids and herbs may decrease with cessation of grazing, suggesting an abundance optimum at intermediate disturbance (Crawley 1997), but the mechanisms for predicted disturbance responses (i.e. grazing) and their temporal effects is expected to vary among plant groups (P₁₋₅; Table 1). The above predictions on the effect of sheep grazing on plants are, however, also expected to depend on whether sheep affect rodent densities (P₆; Table 1).

Methods

Study site

The study was conducted in Hol municipality, Buskerud county, southern Norway (7°55'–8°00'E, 60°40'–60°45'N) in the low alpine region (1050–1300 m a.s.l.). The vegetation of the study area is dominated by dwarf shrub heaths (51%) with e.g. *Vaccinium* spp., *Betula nana*, *Empetrum nigrum*, *Deschampsia flexuosa*, lichen ridges (17%) with *Cetraria nivalis*, *C. cucullata*, *C. islandica*, *Cladonia rangiferina*, *C. arbuscula*, snow-beds (12%) with graminoids *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Carex bigelowii*, *Alchemilla alpina* and alpine meadow communities (9%) dominated by graminoids and herbs such as *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Agrostis capillaris*, *Carex* spp., *Geranium sylvaticum*, *Ranunculus acris*, *Rumex acetosa*, *Viola biflora* (Rekdal 2001). A total of 104 vascular plants (Austrheim et al. 2005a) and 58 bryophytes (Austrheim et al. 2005b) were recorded in 2001

Table 1. A review of predicted responses of the effect of grazing on plants groups (P₁–P₅) and rodent disturbance (P₆), their main mechanisms and the predicted time scale of responses.

	Examined variables	Predicted response	Main mechanism	Response time scale	References
P ₁	Herbs	–/+	(a) highly selected herbs get a reduced opportunity for resprouting. (b) small (less foraged) and less competitive herbs increase due to increased biomass of large competitive plants	Intermediate	(a) Crawley 1997, Olofsson et al. 2002, Evju et al. 2006, Hester et al. 2006 (b) Olofsson et al. 2002
P ₂	Graminoids	+	High resprouting ability and efficient use of mineralized nutrients	Intermediate	Olofsson et al. 2001, Stark et al. 2002, Van Der Wal 2006
P ₃	Woody species	0	Shoots persistent and vegetative reproduction slow at a short term scale	Long	Tolvanen 1994, Tolvanen and Laine 1997
P ₄	Cryptogams	–	Trampling, shading and resource depletion from graminoids	Intermediate	Virtanen 2000
P ₅	Plant community parameters	–	Biomass depletion exceeds plant compensation and reduces vascular plant height, vascular plant and cryptogam cover, while bare soil increases.	Short	Crawley 1997, Hester et al. 2006
P ₆	Rodent disturbance (i.e. sign index of winter activity)	–/+	(a) competitive or (b) facilitative depending on sheep density	Short	(a) Steen et al. 2005, (b) Austrheim et al. 2007, Bråthen et al. 2007

and ranked mean frequencies for the most common plants are shown in Table 2. Before fencing, grazing pressure by sheep was low (<10 sheep km⁻²). The total grazing pressure in Hol municipality has decreased continuously since 1949 (22% decrease in metabolic grazing rate up to 1999; Austrheim unpubl.) and, although moose browsing probably has more or less compensated for the reduced grazing by large domestic herbivores in sub-alpine areas (Austrheim unpubl.), moose only occasionally enters the low alpine zone for foraging during summer.

Experimental design

We used a block-wise randomised design. A large enclosure (2.7 km²) was split into nine fenced sub-enclosures so that three replicates of three levels of treatment could be run. Within each of three blocks consisting of three sub-enclosures, one sub-enclosure was randomly selected as 'no grazing' (no sheep), one as 'low' (25 sheep km⁻²) and one as 'high' (80 sheep km⁻²) density (Fig. 1), which represents the variation in densities of sheep grazing on mountain pastures in Norway. Non-grazeable habitats (lakes, streams, rocks or other habitats dominated by bryophytes and lichens) were excluded when densities were calculated. Gross densities were thus slightly lower; 19, 19, 21 and 56, 69, 72 for low and high densities respectively. All sheep were the 'Kvit Norsk sau' breed (formerly called 'Dala breed'). Ewes averaged 83 kg (live weight in spring) and lambs 19 kg in spring and 42 kg in autumn (Mysterud unpubl.). Distribution of habitat types were similar among enclosures (Rekdal 2001). Experimental grazing started 2002, with grazing seasons that lasted approx. two months from late June to late August/early September every year since.

Vegetation data

Twenty plots (each 0.25 m²) were placed by a stratified balanced procedure among altitudinal levels (Fig. A1) and

habitats (Table A1) within each enclosure giving a total of 180 plots (Austrheim et al. 2005a). Allocation of plots to vegetation types were: grassland (graminoid-dominated snow-beds (30%) and grasslands with a varying cover of willows (21%)) and heathland (dwarf-shrub heath with *Vaccinium* spp. (29%) and ridge vegetation with lichens (20%)) We recorded the abundance of all vascular plants (in the summers of 2001, 2003 and 2005) and of bryophytes (in the summers of 2001 and 2005) in each plot as subplot frequency based on recordings of presence-absence within 16 subplots (0.0156 m²). Furthermore, we recorded the percent coverage of vascular plants, bryophytes, and bare soil. Plant height was recorded as the average height of the dominating strata of vascular plants in each plot. We aggregated closely related species to avoid effects of possible misidentifications when comparing bryophyte abundances from 2001 and 2005. Thus *Barbilophozia* included *B. barbata*, *B. floerkei*, *B. hatcheri*, *B. kunzeana* and *B. lycopodioides*; *Brachythecium* included *B. reflexum*, *B. glaciale*, *B. oedipodium*, *B. salebrosum* and *B. starkei*; *Dicranum* included *D. flexicaule*, *D. fuscescens*, *D. majus*, *D. scoparium* and *D. spadiceum*; *Lescurea* included *L. incurvata*, *L. plicata*, *L. radicata*, and *L. saxicola*; *Lophozia* included *L. badensis*, *L. heterocolpos*, *L. obtusa*, *L. silvicola*, *L. sudetica*, *L. ventricosa* and *L. wenzelii*; *Mnium* included *M. spinosum* and *M. ambiguum*; *Scapania* included *S. irrigua*, *S. paludicola* and *S. paludosa*; *Polytrichum* included *P. commune*, *P. hyperborum*, *P. juniperum*, *P. piliferum*, *P. strictum*, *P. formosum*, *P. longisetum* and *P. alpinum*; and *Plagiothecium* included *P. nemorale*, *P. denticulatum* and *P. laetum*. Nomenclature follows (Lid and Lid 1994) for vascular plants and Frisvoll et al. (1995) for bryophytes.

Rodent grazing

Rodent grazing pressure was recorded as the frequency of subplots visibly affected (by tunnels, nests or faeces) within each plot (0.25 m²) in 2005. Rodent populations are normally cyclic and root vole *Microtus oeconomus* and field vole *Microtus agrestis* dominated in the study area during

Table 2. Ranked frequencies (frequency of all plots; n=180) for vascular plants and bryophytes. Main growth-form type is given for all species. Abundance values are based on 2001 data prior to the experimental grazing.

Vascular plants	Growth-form	Mean abundance	Bryophytes	Growth-form	Mean abundance
<i>Deschampsia flexuosa</i>	Graminoid	0.76	<i>Barbilophozia</i> coll.	Liverwort	8.10
<i>Vaccinium myrtillus</i>	Woody	0.69	<i>Polytrichum/Polytrichastrum</i> agg	Acrocarpous moss	5.88
<i>Empetrum nigrum</i>	Woody	0.68	<i>Dicranum</i> coll.	Acrocarpous moss	5.46
<i>Vaccinium uliginosum</i>	Woody	0.52	<i>Brachythecium</i> coll.	Pleurocarpous moss	2.84
<i>Vaccinium vitis-idea</i>	Woody	0.50	<i>Ptilidium ciliare</i>	Liverwort	2.40
<i>Trientalis europea</i>	Herb	0.43	<i>Pleurozium schreberi</i>	Pleurocarpous moss	1.20
<i>Salix herbacea</i>	Woody	0.40	<i>Sanionia uncinata</i>	Pleurocarpous moss	1.13
<i>Anthoxanthum odoratum</i>	Graminoid	0.39	<i>Mnium</i> coll.	Acrocarpous moss	0.78
<i>Betula nana</i>	Woody	0.33	<i>Pohlia nutans</i>	Acrocarpous moss	0.56
<i>Rumex acetosa</i>	Herb	0.32	<i>Lescurea</i> coll.	Pleurocarpous moss	0.34
<i>Bistorta vivipara</i>	Herb	0.28	<i>Aulacomnium palustre</i>	Acrocarpous moss	0.33
<i>Viola biflora</i>	Herb	0.25	<i>Lophozia</i> coll.	Liverwort	0.33
<i>Carex bigelowii</i>	Graminoid	0.24	<i>Hylocomiastrum pyrenaicum</i>	Pleurocarpous moss	0.27
<i>Geranium sylvaticum</i>	Herb	0.24	<i>Rhodobrym roseum</i>	Acrocarpous moss	0.22
<i>Nardus stricta</i>	Graminoid	0.24	<i>Syntrichia ruralis</i>	Acrocarpous moss	0.22
<i>Luzula multiflora</i>	Graminoid	0.23	<i>Hylcomium splendens</i>	Pleurocarpous moss	0.20
<i>Hieracium</i> coll.	Herb	0.23	<i>Tritomaria quinqueidentata</i>	Liverwort	0.17
<i>Alchemilla alpina</i>	Herb	0.21	<i>Racomitrium canescens</i>	Pleurocarpous moss	0.15
<i>Solidago virgaurea</i>	Herb	0.21	<i>Desmatodon latifolius</i>	Acrocarpous moss	0.06
			<i>Plagiothecium</i> coll.	Pleurocarpous moss	0.06

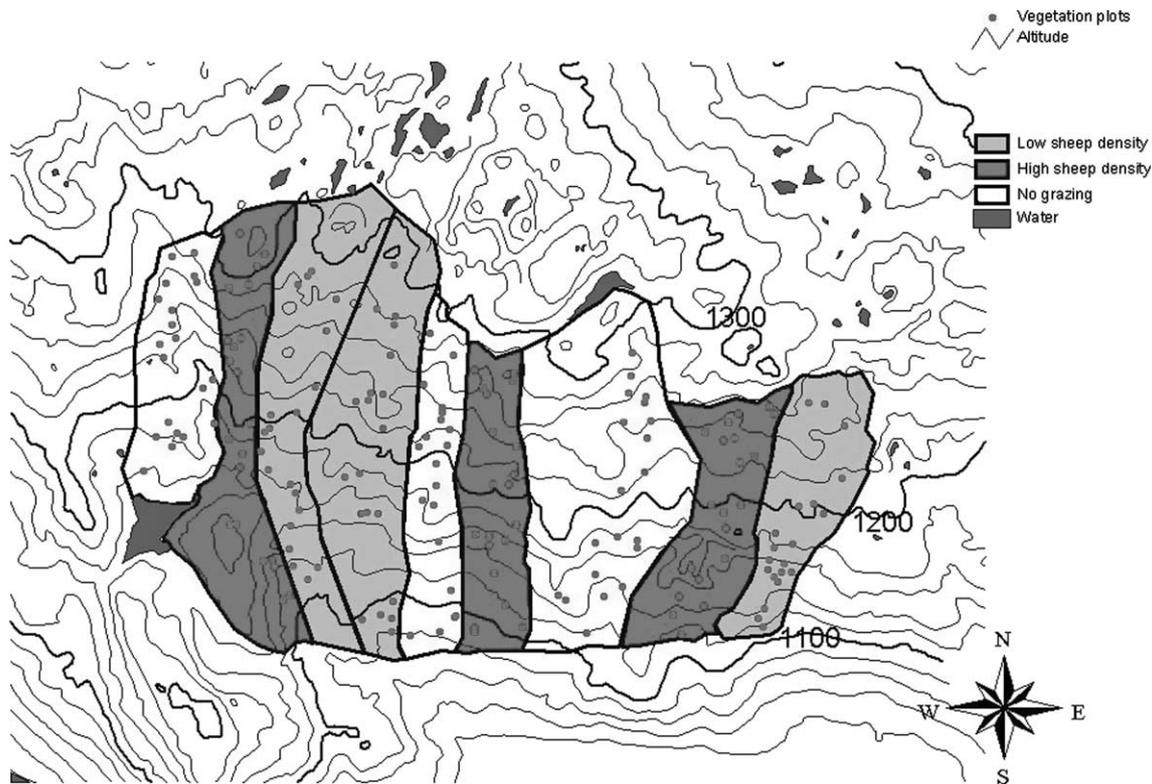


Fig. 1. The experimental design at the study site in Hol municipality, southern Norway. Dark greys enclosures = high densities of sheep, light grey = low densities and white = no sheep. Dots represent permanent plots for vegetation recordings.

population peaks in the summers of 2003 and 2004 (Steen et al. 2005). The plots showed only sparse signs of rodent activity in year 2001 and 2003 due to low grazing in previous winters (summer grazing is in general hardly noticeable), and frequency of affected subplots was not recorded those years.

Statistical analysis

We examined the effect of sheep grazing on abundances of individual plant species, vascular plant height and coverage, bryophyte coverage, percent bare soil, and vascular plant and bryophyte species richness. We used linear mixed models (LME) based on a repeated measures design with year, grazing, blocks, altitude and relevant two-way interactions (grazing \times time) as fixed factors, while nesting of plots in enclosures was included as a random factor. In addition, we examined for effects within the habitat subset of plots which were found to be preferred by sheep (i.e. grassland, $n=93$; Kausrud et al. 2006). Model selection with the AIC criterion was first performed in linear fixed-factor models, since AIC is not meaningful when using LME with REML (Crawley 2003). Only the most parsimonious models (i.e. with the lowest AIC values) were then re-analysed by LME.

To minimize the problem with non-normal distribution of species responses due to a large number of zeros, rare species (i.e. species that occurred in < five plots in 2001 and for all years) were excluded prior to analysis leaving 51 herbs, 21 graminoids, 15 woody species and 22 bryophytes.

Because the study area is heterogeneous, with plots covering a wide altitudinal range and spanning a range of different habitats, we used Detrended correspondence analysis (DCA; Hill 1979) and global non-metric multi-dimensional scaling (GNMDS; Kruskal 1964) to reveal main gradients in vascular plant and bryophyte community patterns prior to the grazing treatment. Multivariate plant species responses (plant community matrices with plot frequencies) over time were examined by distance-based, nonparametric MANOVA (Legendre and Anderson 1999) with treatment (three sheep density levels), time (three levels for vascular plants (2001, 2003, 2005), two levels for bryophytes (2001, 2005)) and habitat (two levels [grassland, heathland]) as fixed factors and sub-enclosure (three levels nested within each grazing level) and plot (20 levels nested within each sub-enclosure) as random factors together with all relevant interactions in a repeated measures design in the program DISTLM ver. 5 (Anderson 2004). The analyses are based on Euclidean distances. The program XMATRIX (Anderson 2003) was used to construct design matrices corresponding to factors or interaction terms in the ANOVA design. Construction of test statistics follows the same principle as for univariate analyses (Underwood 1997); mean square denominators (error terms) are listed in Table 3. Since an unbalanced variable (habitat) is included in the model, we used type III sums of squares and denominators of the multivariate F-ratios (Legendre and Anderson 1999) were adjusted as shown in Supplementary material Appendix 1 (Table A2). Permutation tests with 499 permutations provided the p-values (Anderson 2001, McArdle and Anderson 2001).

Table 3. Repeated measures MANOVA on vascular plant species frequencies (n = 87) from the years 2001, 2003, and 2005 in a balanced experimental design with three treatment levels: high density of sheep, low density of sheep and no sheep (n = 180 plots yr⁻¹).

Source of variation	Error term	DF	Type III SS	F	p	Variance explained (%)
Grazing [G]	E(G)	2	435192498.8	0.90	0.574	1.0
Habitat [H]	P(E(G))	1	3299574120.0	18.51	<0.002	7.8
Grazing × habitat [GH]	P(E(G))	2	726120093.5	2.04	0.004	1.7
Enclosure (grazing) [E(G)]	P(E(G))	6	1444702251.1	0.88	0.708	3.4
Plot within treatment combinations [P(E(G))]		168	29951841837.1			70.9
Time [T]	T(E(G))	2	80125457.6	1.74	<0.002	0.2
Grazing × time [GT]	T(E(G))	4	532970.1	0.58	0.992	0.0
Time × habitat [TH]	Residuals	2	47257466.9	1.37	0.118	0.1
Grazing × time × habitat [GTH]	Residuals	4	71689696.4	1.04	0.382	0.2
Time × enclosure (grazing) [TE(G)]	Residuals	12	275196698	1.33	0.014	0.7
Residuals		336	5779335195.8			13.7
Total		539	42222294369.2			100

Since rodent grazing effects only occurred at the last time-point (2005), we analysed for the effect of rodents on changes in vascular plant community patterns and species abundances, $\ln [(N_{2005} + 1)/(N_{2003} + 1)]$ or bryophyte plant cover and bryophyte species abundances, $\ln [(N_{2005} + 1)/(N_{2001} + 1)]$. We also tested for possible sheep × rodent interaction effects on plants.

All data were \ln transformed prior to analyses except for frequency data (plant frequencies and vegetation coverage) that were arcsine transformed to avoid heteroscedasticity. All analyses except for MANOVA, were performed in S-Plus ver. 6.2.

Results

Analyses of plant–environment relationships prior to the grazing treatment revealed a strong gradient from ridge plots to snow-beds [negatively correlated to nitrogen-content ($r = -0.501$, $p < 0.001$) and pH ($r = -0.475$, $p < 0.001$)] along DCA-axis 1 (eigenvalue 0.53), while DCA-axis 2 correlated with altitude ($r = 0.401$, $p < 0.001$). These patterns were in general corroborated by parallel use of GNMDS (results not shown).

Plant species responses to sheep grazing

High densities of sheep had significant negative effects on plant abundances for five herb species after four years as compared to no grazing (Fig. 2a, Table A3a); *Solidago virgaurea*, *Omalotheca norvegica*, *Euphrasia frigida*, *Melampyrum sylvaticum*, *Sagina procumbens* (both in 2003 and 2005), while two species increased at high densities of sheep in 2005 as compared to no grazing; *Cerastium fontanum*, *Omalotheca supina* (marginally non-significant; $p = 0.056$). *Pedicularis lapponica* increased at high densities of sheep vs no grazing [$p = 0.038$ in 2003 and marginally non-significant ($p = 0.071$) in 2005]. Only two graminoid species were significantly affected by the sheep grazing treatment (Fig. 2b, Table A3b); *Carex bigelowii* and *Poa alpina* increased at high densities vs no grazing in 2005, while *Phleum alpinum* showed a marginally non-significant increase ($p = 0.057$). *Carex vaginata* decreased at high densities in 2005. More surprisingly, sheep grazing also affected abundances of four dwarf-

shrub species (Fig. 2c, Table A3c); *Salix glauca* (2005) and *Vaccinium uliginosum* (2003, 2005) decreased with high sheep densities vs no grazing, while *V. uliginosum* also had lower frequencies at low grazing in 2003. *Betula nana* and *Juniperus communis* increased at low densities vs no grazing in 2005. Only two bryophytes responded significantly to grazing. Both *Plagiothecium* coll. and *Rhodobryum roseum* increased at high sheep density in 2005 (Fig. 2d, Table A3d). All effects are consistent between years and treatments. Analyses of sheep grazing effects within the selected grassland plots only, showed few differences compared to the overall effects. As high grazing may differ from low grazing, this contrast was examined for all species without finding any significant differences (results not shown).

Plant community responses to sheep grazing

High densities of sheep grazing reduced vascular plant height after four years and vascular plant cover both after two and four years (Fig. 3, Table A4). Percent bare soil decreased less at high levels of grazing than at no grazing. We found no effect of sheep grazing on total cryptogam cover, or on lichens or bryophytes when analysed separately. Neither vascular plant nor bryophyte species richness was affected by grazing ($p = 0.535$ for all possible time × grazing interactions; see Table A5 for mean values and SE). However, plant community patterns were not affected by a four-year grazing treatment neither for vascular plants (n = 87), bryophytes (n = 22) nor vascular plant subgroups [herbs (n = 48), graminoids (n = 20), woody species (n = 15)]. Results are shown only for the vascular plant group (Table 3). Habitat contributed strongly to the explained variation in all data sets. However, the grazing × time × habitat interaction was not significant for any plant community responses. Alternative multivariate analyses examining temporal changes in species composition along axes using principal component analysis (PCA; Pearson 1901) and movements of plots along main ordination axes using detrended correspondence analysis (DCA) supported the above results; none of the temporal changes along the main axes could be related to the grazing treatment (results not shown).

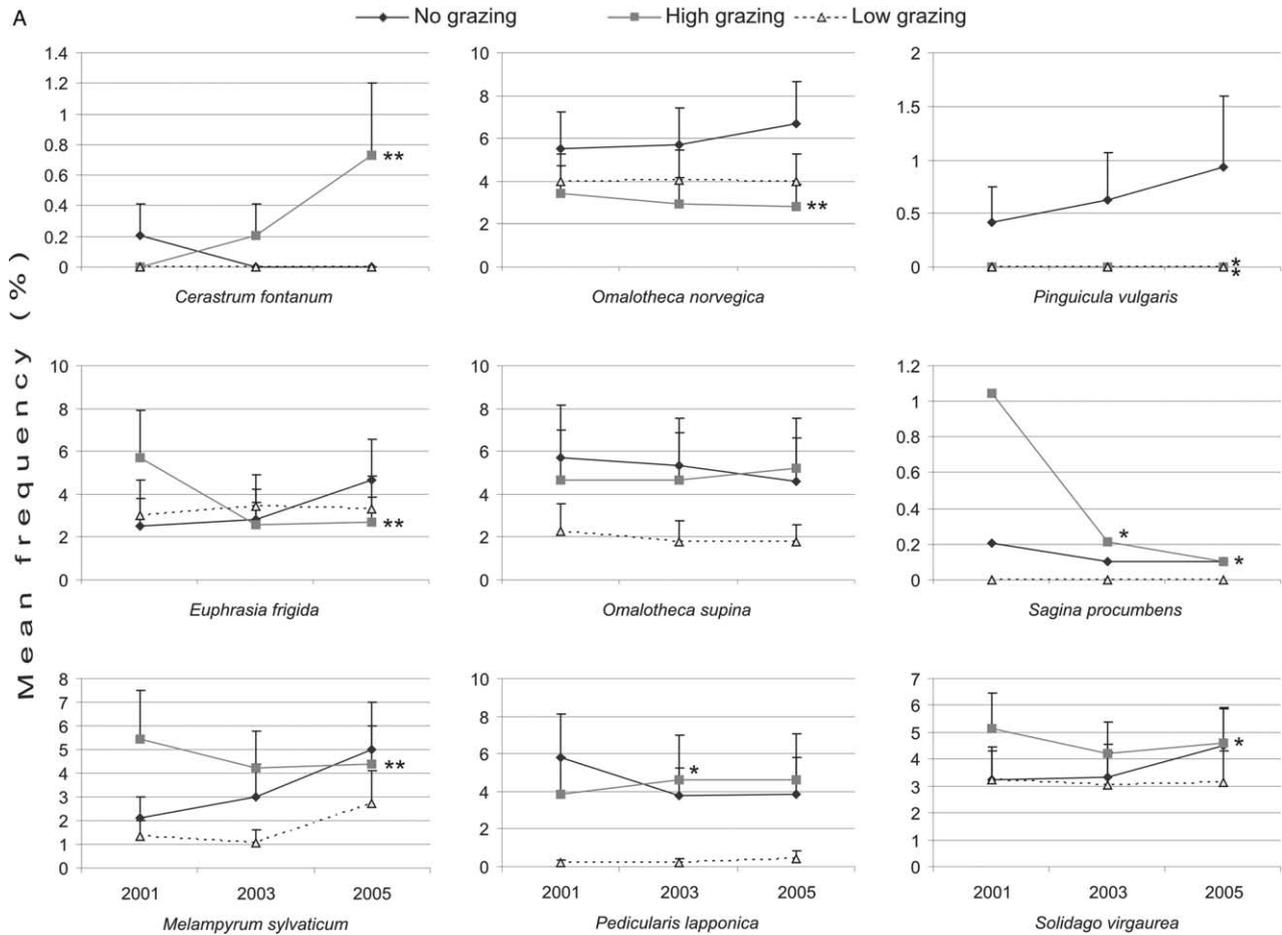


Fig. 2 (Continued)

Effects of sheep grazing on rodent grazing

Rodent grazing could be traced in 46% of all plots in 2005, but levels were not significantly related to treatment ($t = 1.20$, $p = 0.275$ and $t = 1.07$, $p = 0.322$ for no grazing compared to low and high sheep density, respectively). Rodent grazing was negatively related to changes in bryophyte plant cover from 2001 to 2005 ($t = -2.17$, $p = 0.031$) and positively related to changes in percent bare soil from 2003 to 2005 ($t = 3.30$, $p = 0.001$), but did not correlate with vascular plant height or cover, or lichen cover (from 2003 to 2005). The effect of rodent grazing was not found to be affected by sheep grazing for any variable. Changes in vascular plant abundances ($\ln [(N_{2005} + 1) / (N_{2003} + 1)]$) or bryophyte abundances ($\ln [(N_{2005} + 1) / (N_{2003} + 1)]$), were only related to rodent grazing for *Potentilla erecta* ($t = -5.09$, $p < 0.001$).

Discussion

The impact of large grazers on plant communities clearly depends on herbivore density (Crawley 1997, Hester et al. 2006), but the relative importance of different grazing levels are difficult to access experimentally. This fully replicated study at a landscape scale revealed consistent short-term (four-year) effects of high sheep density on plant frequen-

cies (predictions P_1 – P_4 ; Table 1), but few effects of low sheep density compared to temporal development at no grazing. Two biomass properties (vascular plant cover and percent bare soil) responded also after two years as predicted (P_5 ; Table 1). Our study thus highlights that herbivore effects on plants are typically non-linearly related to herbivore density; treatment effects were found both in plots with high grazing and at no grazing, with contrasting effects on the responding species. Plots treated with low grazing were mostly unaffected. Moreover, the speed of plant responses to grazing will depend on both the plant characteristic examined and the grazing pressure. No effect of sheep grazing on rodent grazing signs (mainly as an effect of winter grazing; Grellmann 2002) was found (P_6 ; Table 1), despite that capture studies recorded higher field vole population growth rates during summer at low grazing as compared to high grazing (Steen et al. 2005). As the rodent sign index is found to be linearly related to estimates derived from live trapping (Lambin et al. 2000), this suggests that the effects of sheep grazing on rodent winter grazing might differ from the effects on rodents during summer.

Functional groupings of plants represent a preferred approach in grazing studies, but the level of detail required to successfully predict responses of functional groups to grazing is debated (Lavorel et al. 1997). Our experiment suggests that quite some level of detail is necessary.

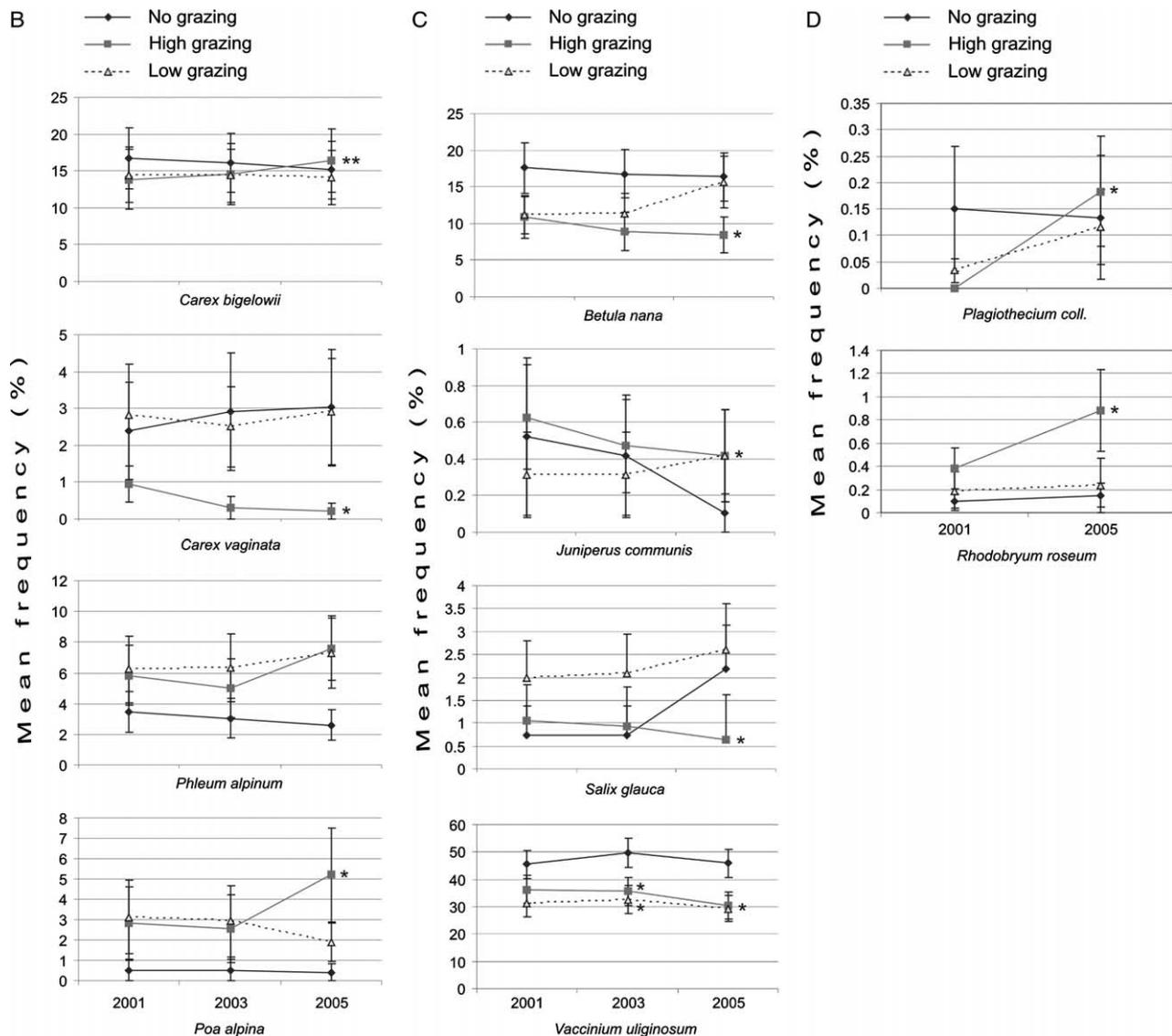


Fig. 2. Mean frequencies and SE for plant species at three levels of sheep grazing in 2001, 2003 and 2005: (a) herbs, (b) graminoids, (c) woody species, (d) bryophytes. The asterisks indicate which grazing level that is significantly different from the no grazing treatment in 2003 and 2005. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Although selected herbs (i.e. *Solidago virgaurea*, *Omalotheca norvegica* and *Melampyrum sylvaticum*) decreased as predicted (P_{1a}), none of the small species (*Euphrasia frigida*, *Sagina procumbens*) which decreased at high sheep density levels were expected to be grazed and might be negatively affected by trampling. Surprisingly, some herbs responded positively to the high sheep density treatment, suggesting three different strategies that might have benefits at high grazing levels; such as colonising ruderals (*Cerastrium fontanum*), prostrate low competitive species (*Omalotheca supina*; P_{1b}) and early flowering species growing among non-selected dwarf-shrubs (*Pedicularis lapponica*). Some variation is also present among the graminoids, as three species increased at high grazing pressure as predicted (P_2), while *Carex vaginata* decreased. Interestingly, two non-selected shrubs (*Juniperus communis* and *Betula nana*), presumably vulnerable to competitive interactions in ungrazed plots, peaked at low sheep grazing suggesting that

they benefit from an intermediate disturbance. Cryptogam cover was not affected by the grazing treatment as predicted (P_4), and only two stress tolerant moss taxa responded and positively so. Thus, plant responses to grazing can be qualitatively different within the 'functional plant groups' examined (Table 1), indicating that detailed knowledge of life history strategies is needed to predict responses to grazing.

Another important component of successful predictions is the time scale of responses. Four woody species were affected by sheep grazing in the predicted direction already after two years, while such changes were predicted only in the longer term (P_3). A decrease of the highly selected *Salix glauca* at high grazing treatment could be expected on a longer term, while *Vaccinium uliginosum* is not selected by sheep (Kausrud et al. 2006), but could be expected to decrease as dwarf-shrubs in general at high grazing on a longer term (Olofsson 2006). Grazing effects are expected

to be strengthened on longer time scales, since several species and community variables showed a response to the grazing treatment from 2003 to 2005, and there are no indications of a stable-state development on a four-year time scale. Transplant experiments indicate that short-term effects are good indicators of long-term effects at the species level in arctic systems with enhanced grazing (Olofsson 2006), and an accumulative effect of grazing intensity on biomass and species richness was found on longer time scales in the eight-year study of del Pozo et al. (2006). If this is the case in our study, we could expect a continuous decrease for palatable herbs and an increase in graminoid abundances at high grazing which thus brings about decreased availability of high-quality fodder. However, low to middle alpine ecosystems in Scandinavian mountains have shown to be far from stable (Cairns and Moen 2004). A strong reduction in human impact (collection of fuelwood and winter-fodder as well as livestock grazing) in the subalpine and alpine region during the 20th century, and a rise in temperature (IPCC 2007), is expected to cause a gradual expansion of sub-alpine forest in this taiga-tundra ecotone if grazing ceases totally. In the long term, such successional processes may confound experimental grazing effects, as indicated in our study area even in a short term. All selected herbs that decreased at high grazing increased in the no grazing treatment, the graminoids that increased at high grazing decreased with no grazing, while plots treated with low grazing were mostly unaffected. This indicates that selected alpine herbs are able to persist while graminoids are suppressed at low grazing levels on short time scales (four years).

An important question for the interpretation of grazing effects in this heterogeneous alpine vegetation (Rekdal 2001) is whether other environmental variables interact with the grazing effects. Habitat and altitude were the two main gradients in these ecosystems prior to grazing treatment. Sheep are highly selective with a preference for grassland habitats (Kausrud et al. 2006), and the affected plants are mainly grassland species. However, no interaction between the effects of sheep grazing pressure and habitat is found in the multivariate analysis. Secondly, studies on sheep grazing activity along the altitudinal gradient in our study area do not indicate no strong preference for specific altitudinal levels during summer (Myrsterud and Austrheim 2005, Myrsterud et al. 2007). Possible effects related to an unbalanced distribution of plots between habitats or along the altitudinal gradient are not likely, as shown in Supplementary material Appendix 1., Fig. A1 and Table A1 respectively.

Studies on ecosystem effects of herbivory have generally concluded that herbivores may have a profound impact on ecosystem structure and processes which is mainly mediated by grazing impacts on plants (Mulder 1999). Although several individual species responded to the grazing treatment, the lack of strong grazing effects on plant community patterns indicate that effects on plant frequencies at short time scales are in general moderate. However, few treatment effects on plants so far do not necessarily imply that the sheep grazing levels used in this experimental design have low effects in an ecosystem perspective. The short term grazing effects on several plant species in this study corresponds with a reduction in sheep body mass (at high

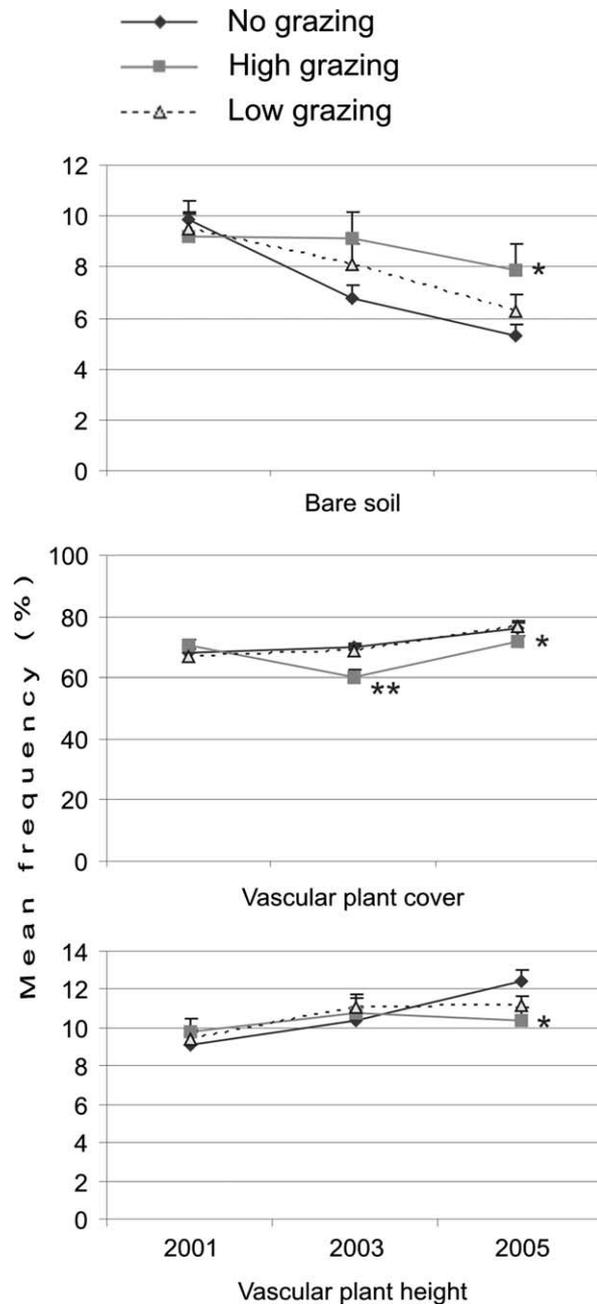


Fig. 3. Mean frequencies and SE for plant community patterns at three levels of sheep grazing in 2001, 2003 and 2005. The asterisks indicate which grazing level that is significantly different from the no grazing treatment in 2003 and 2005. * <math>< 0.05</math>, ** <math>< 0.01</math>, *** <math>< 0.001</math>.

vs low grazing) and invertebrate diversity for plant eating beetles (for both high and low grazing vs no grazing; Myrsterud and Austrheim 2005) and a lower field vole population growth rate during summer after three years (at high grazing vs low grazing; Steen et al. 2005), which all are directly linked to grazing impact on plants; i.e. arguably the availability and quality of fodder plants which is affected on a short terms scale at this study site (Evju et al. 2006). In addition, a higher bird diversity at high grazing as compared to no grazing after a four-year treatment (Loe et al. 2007) clearly indicates short term effects of sheep on important

ecosystem components at the same study site, and these effects might (at least indirectly) be related to plant effects (i.e. field-layer density which was reduced by high grazing of sheep or other aspects of plant structure). This broad range of ecological studies conducted at the same experimental site suggests that sheep grazing mainly affects ecosystem functioning through a change of plant quality, structure and biomass on a short term scale as detected by Evju et al. (2006), and to a minor extent through changes in plant species ramet frequency which is the main plant response in our study, and thus more specifically indicate how changes in plant communities affect ecosystem properties (cf. Pastor et al. 2006). Our study confirms the short term negative effect of high grazing on plant biomass (two-year) while frequencies of specific plant species responded only after four-years at high grazing. The fact that all these effects of high grazing appear in contrasts to no grazing indicates that both cessation of grazing and enhanced grazing are important mechanisms for understanding plant–grazing interactions in low-alpine systems.

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Supplementary material (available online as Appendix O16543 at <www.oikos.ekol.lu.se/appendix>). Appendix 1.