Interactions between sheep, rodents, graminoids, and bryophytes in an oceanic alpine ecosystem of low productivity[1]

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Abstract: Large herbivores directly affect plant communities in alpine ecosystems. In addition, they may compete with, or facilitate foraging by, small herbivores and also cause strong indirect effects on plants. We used an exclosure experiment to examine short-term (5-y) effects of cessation of sheep grazing on rodent grazing and plant communities in an oceanic alpine environment of low productivity with a long history of heavy sheep grazing. Exclusion of sheep significantly impacted plant communities. Vascular plant height increased, but *Deschampsia flexuosa* was the only vascular plant species that increased in sheep exclosures. Changes in the frequency of graminoids, herbs, and dwarf shrubs in exclosed plots were not related to cessation of grazing, but 6 bryophyte species significantly increased or decreased in response to exclusion of sheep. The absence of large grazers thus brought about a change in the species composition in favour of successional bryophytes and the preferred fodder plant. Neither vascular plant nor bryophyte species richness, nor the total cover of bryophytes and lichens, were affected. Cessation of sheep grazing reduced the level of rodent grazing. Rodent grazing correlated with changes in plant communities that led to reduced height and cover of vascular plants, reduced cryptogam cover, and reduced frequencies of 3 bryophyte species. A strong correlation between sheep fodder value index and rodent grazing indirectly indicated additive herbivory. In addition, some of the rodent effects were compensatory; *e.g.*, *Nardus stricta*, which is not grazed by sheep, was significantly reduced by rodents. Our study points to a more central role of facilitation in structuring herbivore assemblages in the short term, with direct implications for the joint effects of large and small herbivores on the cover and frequency of graminoids and bryophytes.

Keywords: ecosystem effects, herbivore communities, herbivory, trophic cascades, ungulates.

Résumé : Les grands herbivores ont un effet direct sur les communautés de plantes dans les écosystèmes alpins. De plus, ils peuvent être en compétition ou faciliter le broutement des petits herbivores et aussi avoir des effets indirects importants sur les plantes. Nous avons utilisé une expérience d'exclusion afin d'examiner les effets à court terme (5 ans) de l'arrêt du broutement par les moutons sur le broutement par les rongeurs et sur les communautés de plantes dans un environnement alpin océanique de faible productivité ayant un long historique de fort broutement par les moutons. L'exclusion des moutons a eu un impact significatif sur les communautés de plantes. La hauteur des plantes vasculaires a augmenté mais la seule espèce ayant vu sa fréquence augmentée dans les exclos à moutons était *Deschampsia flexuosa*. Les changements dans la fréquence des graminées, des herbes et des arbustes nains dans les exclos n'étaient pas reliés à l'arrêt du broutement alors que 6 espèces de bryophytes ont augmenté ou diminué significativement en réponse à l'exclusion des moutons. L'absence de grands herbivores a donc causé un changement dans la composition en espèces en faveur d'une succession chez les bryophytes et en faveur de la plante fourragère préférée. Ni la richesse en espèces des plantes vasculaires et des bryophytes ni la couverture totale des bryophytes et des lichens n'ont été affectées par l'arrêt du broutement alors que le niveau de broutement par les rongeurs a diminué. En présence de broutement par les moutons, le broutement par les rongeurs était corrélé avec des changements dans les communautés de plantes tels qu'une diminution de la hauteur et de la couverture des plantes vasculaires, un réduction de la couverture des cryptogames et une fréquence moindre de 3 espèces de bryophytes. Une forte corrélation entre l'index de valeur du fourrage des moutons et le broutement par les rongeurs indiquait indirectement un effet additif de l'herbivorie. De plus, certains effets des rongeurs étaient compensatoires, *e.g.*, *Nardus stricta* qui n'est pas broutée par les moutons était fortement réduite par les rongeurs. Notre étude démontre le rôle central de la facilitation dans la structuration des assemblages d'herbivores à court terme avec des implications directes pour les effets conjoints de grands et petits herbivores sur la couverture et la fréquence des graminées et des bryophytes.

Mots-clés : cascades trophique, communautés d'herbivores, effets sur l'écosystème, herbivorie, ongulés.

Nomenclature: Lid & Lid, 1994; Frisvoll *et al.*, 1995.

Introduction

Grazing is a complex ecological process, and its impact on plant communities and the outcome depends on a variety of environmental factors and herbivore characteristics, as well as the scale of observations (Milchunas & Lauenroth, 1993; Jefferies, Klein & Shaver, 1994; Augustine & McNaughton, 1998; Mulder, 1999; Austrheim & Eriksson, 2001). In alpine and arctic systems with an evolutionary history of grazing (Oksanen & Virtanen, 1995; Körner, 2003), the species pool is dominated by grazing-tolerant graminoids, grazing-resistant dwarf shrubs, and bryophytes (Olofsson *et al.,* 2001). Interactions among species and their specific ability to tolerate or resist grazing depend in part on climatic factors. For example, grazing generally favours graminoids relative to dwarf shrubs in oceanic systems, while the converse tends to be true in more continental tundra heaths (Oksanen & Virtanen, 1995; Olofsson *et al.,* 2001). Graminoids respond rapidly to nutrient enrichment (Grellmann, 2002; Nilsson *et al.,* 2002), and both mammalian waste products and enhanced nutrient cycling mediated by grazing have been found to bring about an increase of graminoids and a decrease in bryophyte abundances in arctic-alpine tundra (Olofsson *et al.,* 2001; Stark, Strömmer & Tuomi, 2002).

Semi-domestic and wild reindeer (*Rangifer tarandus*) and domestic sheep (*Ovis aries*; summer season only) have been the main large herbivores in Scandinavian alpine tundra since prehistoric times (Austrheim & Eriksson, 2001). However, the effects of rodents on tundra plant communities may be strong and may even exceed those of reindeer in northern Scandinavia (Olofsson *et al.,* 2004). Graminoids and herbs are the preferred fodder of reindeer and sheep (Mysterud, 2000), as well as of rodents such as lemmings (Batzli, 1993) and voles (Hansson, 1983; Henttonen & Hansson, 1984), but we have currently very limited information on whether reduced grazing by large herbivores reduces grazing by smaller rodents or *vice versa*.

Based on a 5-y replicated experiment, we examined the effects of excluding a large grazer (sheep) on vascular plants, bryophytes, and rodent grazing in an oceanic alpine environment of low productivity, situated in a region with a tradition for using outlying mountain pastures for sheep grazing since prehistoric times.

A conceptual model for the main short-term, plant–herbivore interactions is presented in Figure 1. The following vegetational changes are predicted as effects of cessation of sheep grazing: (P_1) Graminoids are expected to decrease due to reduced establishment in denser bryophyte carpets (Virtanen, Henttonen & Laine, 1997). However, graminoid responses are predicted to depend on plant life history. Highly preferred fodder plants with high ramet turnover, such as *Deschampsia flexuosa*, are expected to increase at sites from which sheep are excluded ($P_{1.1}$), while plants resistant to grazing (*e.g., Nardus stricta*) are predicted to decrease ($P_{1.2}$) due to competitive exclusion (Pakeman, 2004). Because of the long history of high grazing pressure in the region, we expect a positive effect of sheep exclusion on the total grazing index value, quantified as the herbivore selection scores for each species multiplied by the frequency of each species. Herbivore-selected plant species with a

stronger dependence on sexual reproduction, such as herbs, are not expected to be capable of rapid increases in frequency in the absence of grazing due to strong limitation of both seeds and safe sites (Austrheim, Evju & Mysterud, 2005).

(P_2) Heavy grazing decreases dominance of bryophytes and lichens in both oceanic and continental areas, favouring resistant bryophytes such as members of the Polytrichaceae and *Dicranum* spp. (Helle & Aspi, 1983; Väre, Ohtonen & Mikkola, 1996; Virtanen, 2000; Olofsson *et al.,* 2004). Bryophyte abundances are in general expected to increase mainly as a consequence of reduced trampling (Jónsdóttir, 1991; van der Wal *et al.,* 2003), especially in oceanic areas where soil moisture is not limiting (Økland, 1997). However, the effect of sheep grazing on vascular plants and bryophytes and the competitive interactions among plant groups are expected to be strongly dependent on the response of the rodent community to reduced levels of sheep grazing.

Two alternative predictions for effects of cessation of sheep grazing on rodent grazing pressure are proposed: (P_{3a}) If there is competition between sheep and rodents for forage (and herbivore densities are high relative to resource levels; Steen, Mysterud & Austrheim, 2005), grazing by rodents is expected to increase within sheep exclosures. (P_{3b}) If, in contrast, sheep grazing facilitates grazing by rodents (which might be expected at low sheep densities; Steen, Mysterud & Austrheim, 2005), exclusion of sheep will likely reduce rodent-grazing pressure. Plant ecological effects of these 2 alternative scenarios for sheep–rodent interactions are likely to depend on whether grazing is actually additive (both herbivores consume the same plants) or compensatory (con-
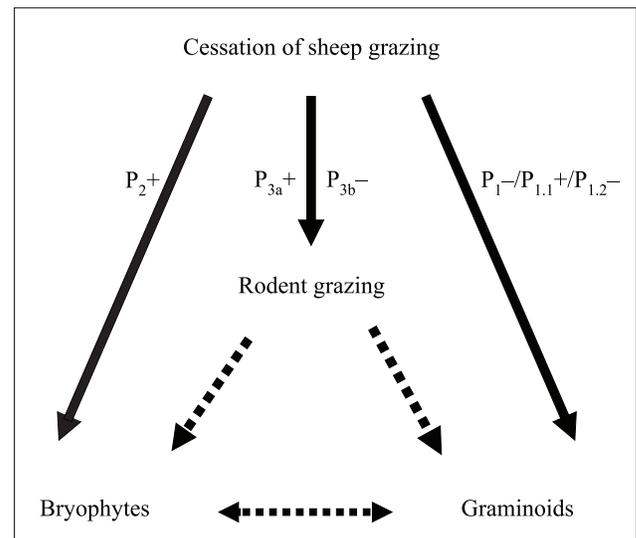

FIGURE 1. Conceptual model of predicted herbivore–plant interactions in our exclosure experiment in a low productive oceanic alpine environment. The model does not represent a complete outline of the general interactions among relevant ecosystem components in a grazed alpine system, but focuses instead on the predictions that could directly or indirectly be examined by our experimental design. Hence, solid lines refer to predictions that were experimentally tested (corresponding to the P_1, $P_{1.1}$, $P_{1.2}$, P_2, P_{3a}, and P_{3b} predictions in the introduction), while the broken lines refer to interactions examined by correlations. Signs refer to predicted effects of cessation of sheep grazing.

sumption of different plants) and thus are more difficult to predict (*cf.* Ritchie & Olff, 1999).

Methods

Study area

The study was performed in the low-alpine region (900–1000 m asl) of Setesdal Vesthei (Sirdal municipality, Vest-Agder county and Valle municipality, Aust-Agder county) in the southern part of Norway (58° 59' N, 6° 58' E). The climate is harsh, with a relatively short growing season and an annual precipitation between 1170 and 1760 mm (recorded at the 2 weather stations situated closest to the study site; Førland, 1993). The bedrock of Precambrian granite is resistant to weathering and gives rise to acidic mineral soils poor in nutrients (Holtedahl, 1969; Austrheim, Evju & Mysterud, 2005). Soil environmental data collected in 2000 revealed high soil moisture and low nutrient contents, which explain the low productivity of the vegetation (Austrheim, Hassel & Mysterud, 2005). Trees (*Betula pubescens* ssp. *czerepanovii*) and shrubs (*Salix lapponum*) occur sparsely. The position of the present treeline, which exceeds 800 m asl only locally, is heavily affected by livestock grazing; the climatic treeline is considered to be 100–200 m higher (Moen, 1998).

Ten pairs of plots (each 20 × 50 m) were established on southerly exposed slopes in the early summer of 2000 (*i.e.,* prior to the release of sheep), with treatment (sheep exclosure) and grazed control randomly allocated within each pair. The minimum distance between exclosure and control plots (within each pair of plots) was set to 30 m in order to avoid the effects of fencing on the vegetation of control plots. All 10 pairs of plots were chosen within habitats considered to be preferentially selected by sheep; thus peatlands, late snow patches (dominated by bryophytes), and areas with a high stone cover (> 10%) were excluded (*cf.* Kausrud *et al.,* 2006). The distance between pairs of plots varied between 0.3 km and 14 km, but they were all situated within an area of 124 km².

Living vascular plants covered 74% (mean for 200, 50 × 50 cm quadrats in 2000), of which *Nardus stricta* contributed nearly one half (34%), as well as 14% of litter cover (visual cover estimates of randomly selected quadrats in each plot; Austrheim, Evju & Mysterud, 2005). Only 50 vascular plant species were found in the study area in 2000. Graminoids dominated (22 species), while herbs and woody species (mainly dwarf-shrubs of the genus *Vaccinium*) were more sparse (14 species each). Species with the ability to produce long-lived genets dominated the local species pool; their abundances were higher than those of sexually regenerating species (Austrheim, Evju & Mysterud, 2005). Bryophytes covered 25% (mean for 200 quadrats), and lichens 6%. Fifty-one bryophyte species were recorded in 2000, and long-lived species dominated (61%; Austrheim, Hassel & Mysterud, 2005). Bryophyte abundances were positively correlated with longevity and humidity, but negatively correlated with the ability to produce asexual propagules (gemmae). No significant relationships between soil variables (pH, Ca, Mg, Na, K, P, loss on ignition, soil dry matter; data collected 2000) and the abundances of vascular plants and bryophytes were found (Austrheim, Evju &

Mysterud, 2005; Austrheim, Hassel & Mysterud, 2005; G. Austrheim, unpubl. data). Ranked mean abundances for vascular plants and bryophytes are shown in Table I.

Sheep are the most abundant large herbivore in the region; in 2004 between 150 000 and 200 000 ewes and lambs (of the breed called "Norsk kvit sau"; Drabløs, 1997) grazed over an area of *ca* 7000 km² (Mysterud & Mysterud, 1999). Gross densities varied between 10 and 50 sheep·km⁻², which were among the highest densities in Norwegian outlying pastures (Anonymous, 2004). The grazing season is from late June to the beginning of September. The majority of sheep were transported into the region from coastal lowlands where outlying pastures are limited, following a tradition that dates back to *ca* 1840 (Mysterud & Mysterud, 1999). The region also hosts the southernmost population of wild reindeer in Europe, with a population size of around 2500 (Bevanger & Jordhøy, 2004). Rodent populations in alpine habitats of southern Scandinavia typically show cyclic behaviour (*cf.* Framstad *et al.,* 1997; Stenseth *et al.,* 1998; Korpimäki *et al.,* 2004), and species such as lemming (*Lemmus lemmus*), root vole (*Microtus oceonomus*), field vole (*Microtus agrestis*), and bank vole (*Clethrionomys glareolus*) show population peaks in certain years, at which time their grazing effect is evident (Andersson & Jonasson, 1985).

Vegetation data

Ten quadrats (each 0.5 × 0.5 m) were placed randomly within each exclosure and control plot (50 × 20 m), giving a total of 200 quadrats. We recorded frequencies of vascular plants (summers of 2000, 2002, and 2004) and bryophytes (summers of 2000 and 2004) in each quadrat, based on presence–absence within 16 sub-quadrats (each 0.125 × 0.125 m), and percent cover (visual estimate) of total vascular plants, bryophytes, *Nardus stricta* (both living plants and litter), and exposed soil. Plant height was recorded as height of the dominant plant species at inter-

Table I. Rank frequency (mean frequency for all quadrats) of the most frequent vascular plants (> 5%) and bryophytes (> 1.7%). Mean frequency values (FRE, %) are based on a data collection in 2000 from 200 quadrats. Selection score (SS) denotes forage preferences of the sheep (data from Kausrud *et al.*, 2006). See text for details on FRE and SS measurements.

Vascular plants	FRE	SS	Bryophytes	FRE
Vaccinium myrtillus	78.9	0.3	*Dicranum scoparium*	36.8
Deschampsia flexuosa	74.2	3.0	*Barbilophozia floerkei*	35.6
Nardus stricta	69.9	0.5	*Polytrichum* coll.	35.1
Empetrum sp.	35.4	0	*Barbilophozia lycopodioides*	25.6
Vaccinium uliginosum	30.3	0.2	*Pleurozium schreberi*	24.9
Trientalis europaea	24.3	0	*Sphagnum girgensohnii*	7.6
Vaccinium vitis-idaea	21.4	0	*Brachythecium* coll.	6.6
Carex bigelowii	19.7	2	*Rhytidiadelphus squarrosus*	5.1
Anthoxanthum odoratum	19.4	2.2	*Sphagnum capillifolium*	4.6
Carex brunnescens	18.8	2	*Pohlia nutans*	3.8
Andromeda polifolia	17.2	0	*Polytrichum strictum*	3.6
Molinia caerulea	8.1	0.6	*Plagiothecium* coll.	3.6
Rubus chamaemorus	7.3	0	*Sphagnum russowii*	2.8
Juncus filiformis	7.3	0.4	*Ptilidium ciliare*	2.7
Viola palustris	7.1	2.0	*Sphagnum compactum*	2.1
Agrostis capillaris	6.6	1.3	*Dicranum fuscescens*	2.0
Trichophorum cespitosum	5.3	0.4	*Polytrichum juniperinum*	1.8

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vals of 5 cm. A fodder value index was calculated for each quadrat by multiplying a herbivore-selection score by the frequency of that species. Fodder plants and their selection ranks were estimated from data of diet selection and species frequency, as identified by Kausrud *et al.* (2006) from an alpine habitat in southern Norway that contained all vascular plant species in the species pool of Setesdal except 2 rare herbs (*Narthecium ossifragum* and *Cornus suecica*). This information on sheep dietary selection was derived from direct observations of individual sheep in an alpine habitat (Kausrud *et al.,* 2006). When a sheep was observed grazing, grazed plants and the percent coverage of all plant species within a 1- × 1-m frame were recorded. Selection is defined as use by the herbivore that is higher than expected based on availability (Thomas & Taylor, 1990). Since selection of a given species will depend on the species pool in the area (*cf*. Aebischer, Robertson & Kenward, 1993), we ranked species from the most to least selected; this selection rank is not expected to change substantially between similar plant communities.

RECORDING OF HERBIVORE DENSITIES

We used pellet group counts (Neff, 1968) to estimate relative densities of sheep use in all 10 control plots in order to be able to correct for possible differences in grazing pressure among control plots. We counted faeces at the end of July every year (except in 2004 when counts were made in September). Faeces were counted on a large scale (circles of 10 m^2 at every 10 m along transects north [25 circles] and south [25 circles] of each control plot). The faeces were not removed when recorded since the fertilization effect was expected to be an important part of the total grazing effect. Faeces counts thus denote the accumulated number of faeces. Sheep grazing intensity was estimated as mean number of faeces for 5 y (2000–2004) on a small and large scale. Rodent grazing pressure was recorded as the frequency of sub-quadrats affected (tunnels, nests, or faeces) within each quadrat (50 × 50 cm) in 2004. The quadrats showed only sparse signs of rodent activity in 2000 and 2002, and consequently rodent grazing pressure was not recorded in those years.

STATISTICAL ANALYSIS

We examined treatment effects (categorical variable, excluding sheep grazing), rodent grazing (continuous), and possible interactions on both univariate (plant frequencies, vascular plant height and coverage, bryophyte coverage, percent exposed soil, *Nardus stricta* [biomass and litter] cover, and fodder value indices) and multivariate (species frequency matrices) response variables using relative temporal change (ln [{N$_{2004}$ + 1}/{N$_{2000}$ + 1}]). Sheep grazing was assumed to be equal among control plots. This was justified by the mean number of sheep faeces per control plot for all years (14.74 ± 0.43 SE), which differed as much between years as between plots (ANOVA: $F_{4, 486}$ = 2.67, P = 0.031 and $F_{9, 486}$ = 2.54, P = 0.007, respectively). For both univariate and multivariate modelling, a covariance approach was used by which the main effects of all available explanatory variables and their two-way interactions were included in the initial model as defined by the conceptual model (Figure 1). Thus, for bryophyte responses

(species group or single species), sheep and rodent grazing were used as predictors. The effect of herbivores on relative changes in multivariate responses (vascular plants and bryophytes) and interactions among specific plant groups and herbivores were examined using 2 alternative linear multivariate approaches. First, we used the constrained ordination technique Redundancy Analysis (RDA; Rao, 1964) to examine the direct relations between multivariate response variables (all vascular plants and bryophytes) and both of the herbivores (sheep and rodents). In addition, we examined other possible vegetation–herbivore relations using specific sub-groups of plants (all plants, graminoids, woody species, and herbs) as responses. Forward selection with statistical testing by unrestricted Monte Carlo permutation tests (499 permutations) was used initially to examine the contribution of each variable. The unique contribution (marginal effect) of one variable was found by specifying other relevant variables as covariables in partial RDAs (the effects of covariables on the model were thereby removed). A variation partitioning approach using partial RDA (Borcard, Legendre & Drapeau, 1992; Økland, 2003) was used to calculate variation shared among variables. The variation components are given as relative variation explained (divided by the total variation explained by all significant variables), instead of absolute fractions of variation explained (divided by total inertia), in accordance with Økland (1999). Secondly, a Principal Component Analysis (PCA; Pearson, 1901) was used to reduce the number of response variables within graminoids, bryophytes, woody species, and herbs. For each set of response variables, we tested for relative effects of sheep and rodent grazing as covariables in linear mixed models (LME). Typical mire species were excluded from matrices used in RDA and PCA since wet habitats are usually avoided by sheep (Kausrud *et al.,* 2006). We excluded the bryophytes *Sphagnum* spp., *Aulacomnium palustre*, *Mylia anomala, M. taylorii*, *Odontoschisma denudatum*, and *Polytrichum strictum* and the graminoids *Eriophorum vaginatum* and *E. angustifolium*. Both RDA and PCA were based on a correlation matrix since the component plot scores were used further in the linear model analysis (Quinn & Keough, 2002). Nonlinearity for the multivariate responses was not likely since gradient lengths were < 1.5 SD units (in detrended correspondence analysis, DCA; Hill, 1979) for all axes (Økland, 1990). For all univariate responses, LME were used with site included as a random variable to account for non-independence of plots within sites. Exceptions were models with a convergence problem in the iterative restricted maximum likelihood method (REML), for which site was included as a fixed factor in the ANOVA. We also examined the spatial structure in all response variables that were found to be significantly related to either sheep or rodent grazing and concluded that the spatial structure was negligible at all relevant scales. Model selection with the AIC criterion was performed in linear models since AIC (Akaike information criterion) is not meaningful when using LME with REML (Crawley, 2003). Only the most parsimonious models were then included in LME. The problem of a large number of zeros in matrices of plant frequency data was minimized by excluding all rare species (occurred in < 5 quadrats) prior to analysis, leaving the following number of species:

15 bryophytes, 13 graminoids, 11 herbs, and 8 woody species. Closely related species were aggregated to increase the frequencies for taxa and to avoid effects of possible misidentification when comparing bryophyte frequencies in 2000 and 2004. *Polytrichum* coll. included *Polytrichum commune, Polytrichastrum formosum, P. longisetum,* and *P. alpinum. Plagiothecium* coll. included *P. nemorale, P. denticulatum,* and *P. laetum,* and *Brachythecium* coll. included *B. reflexum, B. salebrosum,* and *B. starkei.* We did not exclude quadrats with no species occurrences in 2000 and 2004 since the absence of species could be a treatment response, especially for bryophytes. Differences in bryophyte species-richness were only analyzed between grazing treatments within years, based on the species recorded on each occasion.

All data were ln transformed prior to analyses except for percentage data (plant frequencies and vegetation coverage) that were arcsine transformed to avoid heteroscedasticity. All analyses were performed in S-Plus version 6.2, except for RDA analyses that were performed in CANOCO 4.5 (ter Braak & Šmilauer, 2002).

Results

ECOLOGICAL EFFECTS OF SHEEP GRAZING CESSATION

Cessation of sheep grazing had a significant effect on the relative changes in the plant community (vascular plants and bryophytes) from 2000 to 2004 as quantified by RDA (Table II). Splitting the plant community into distinctive functional groups according to Figure 1 revealed no effect of sheep grazing on change in graminoid frequencies (contrary to the P_1 prediction), while bryophytes were affected in accordance with P_2 (Table II). Changes in the frequency of woody species, herbs, and all vascular plants taken together were not related to sheep grazing. These RDA results were supported by results of the PCA. Significant effects of cessation of sheep grazing were found for bryophyte PCA axes 1 and 4 ($t_{189} = 1.99$, $P = 0.048$ and $t_{189} = 2.09$, $P = 0.037$, respectively), but excluding sheep had no effect on graminoids, woody species or herbs. PCA axes 1–4 explained 39% and 44% of the total variation for bryophytes and graminoids, respectively, while woody species and herb axes 1–4 only explained 25%. No axis was significantly related to sheep grazing in the PCA when all plant taxa were included, and only 17% of the total variation was explained by axes 1–4.

Vascular plant height increased more in exclosed plots than in sheep grazed plots ($t_{188} = 2.86$, $P = 0.0047$), while exposed soil increased more in grazed plots than in exclosed plots ($t_{188} = 2.22$, $P = 0.028$). Cryptogam coverage ($t_{188} = -0.33$, $P = 0.739$) and vascular plant coverage ($t_{188} = 0.64$, $P = 0.522$) were unaffected by treatment (Table III). The fodder value index increased continuously over time in exclosures, and change in relative fodder value was positively related to exclosure treatment ($t_{189} = 2.14$, $P = 0.034$). Vascular plant species-richness was not affected by exclusion of sheep. Bryophyte species-richness was significantly higher at ungrazed sites in 2004, but a similar difference was also found in 2000 (Table III).

As predicted from $P_{1.1}$, *Deschampsia flexuosa* (Figure 2a, Appendix I) increased over time in response to exclusion of sheep ($t_{189} = 2.84$, $P = 0.0058$), but it was the only vascular plant species to do so. However, in contrast to $P_{1.2}$, 2 of the most common graminoids, *Nardus stricta* (Figure 2b, Appendix I) and *Carex brunnescens* (Figure 2c, Appendix I), decreased independently of grazing ($t_{589} = -2.64$, $P = 0.0085$ and $t_{589} = -3.18$, $P = 0.0016$, respectively). The amount of litter (dead *Nardus stricta*) increased with time, independent of grazing ($t_{589} = 2.50$, $P = 0.0127$). In accordance with P_2, several bryophyte taxa responded significantly to cessation of sheep grazing (Table IV and Appendix I). *Plagiothecium* coll. and *Brachythecium* coll. were negatively affected by the exclosure treatment, while *Polytrichum* coll. increased in plots that were sheep grazed. *Barbilophozia floerki* decreased in sheep grazed plots, whereas *Straminergon stramineum, Pohlia nutans*, and *Cephalozia bicuspidata* increased with cessation of sheep grazing.

We found a significant negative effect of excluding sheep on rodent grazing ($t_{189} = -2.32$, $P = 0.021$), suggesting additive effects on plants (*cf*. P_{3b}). Rodent activity (nests, tunnels, or faeces) could be traced in 70% of all quadrats in 2004: 76% of the quadrats that were sheep grazed (mean 4.75 sub-quadrats per quadrat) and 64% of the quadrats that were ungrazed (mean 3.39 sub-quadrats per quadrat).

INTERACTIONS BETWEEN RODENT GRAZING AND PLANT COMMUNITY PATTERNS

Rodent grazing was related to changes in the plant community as revealed by RDA, both for vascular plants and for bryophytes (Table II). This effect of rodents was supported by the PCA, as PCA axis 2 was related to rodent grazing ($t_{189} = 2.23$, $P = 0.027$). Plant height was negatively related to rodent grazing ($t_{188} = -4.85$, $P < 0.0001$), as were vascular plant cover ($t_{189} = -7.51$, $P < 0.0001$) and cryptogam cover ($t_{189} = -3.98$, $P < 0.0001$), while exposed soil increased with increasing rodent grazing ($t_{189} = 6.88$, $P < 0.0001$) from 2000 to 2004 (Table III). *Nardus stricta* was the only vascular plant that responded significantly to rodent grazing; its coverage decreased from 2000 to 2004 ($t_{188} = -2.07$, $P < 0.040$). The frequencies of 3 bryophytes (*Pohlia nutans, Straminergon stramineum,* and *Cephalozia*

TABLE II. Variation partitioning by RDA of relative changes in plant community patterns for all plant species (46 taxa) and bryophytes (15 taxa). Only explanatory variables with an initial significant variation were included. S | R denotes variation explained by sheep (S) but not shared by rodents (R), R | S denotes variation explained by R but not shared by S, S ∩ R denotes shared variation, S ∪ R denotes total variation. *P*-values were obtained by a Monte Carlo permutation test with 499 permutations (see text for details).

Variance components	Variation explained	Relative variation explained	*F*-value	*P*-value
All species (46 taxa)				
S | R	0.01	53	2.045	0.002
R | S	0.008	42	1.573	0.044
S ∩ R	0.001	5		
S ∪ R	0.019	100	1.875	0.002
Bryophytes (15 taxa)				
S | R	0.012	55	2.482	0.016
R | S	0.009	41	1.753	0.104
S ∩ R	0.001	4		
S ∪ R	0.022	100	2.181	0.014

TABLE III. Mean and ± SE for main plant community parameters in grazed (G) and ungrazed (U) habitats for the years 2000, 2002, and 2004. Vascular plant height (VPH; cm), vascular plant cover (VPC; %), cryptogam layer cover (CLC; %), exposed soil (ES; %), *Nardus stricta* cover (NSC; %), *Nardus stricta* litter cover (NSLC; %), fodder index (FI; ln-scale), vascular plant species richness (VPSR), and bryophyte species richness (BSR). Statistical testing (LME) of sheep (S), rodents (R), and sheep × rodents (S × R) effects refers to temporal changes of variables using (ln [N_{2004} + 1]/[N_{2000} + 1]) except for VPSR and BSR, where effects of sheep grazing on ln(species-richness) were examined within years. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. See text for details.

Variables	2000		2002		2004		Effects of herbivores		
	G	U	G	U	G	U	S	R	S × R
VPH	14.04 ± 0.50	13.75 ± 0.56	14.38 ± 0.48	15.85 ± 0.52	15.96 ± 0.46	17.50 ± 0.50	*	***	ns
VPC	72.10 ± 1.23	74.15 ± 1.35	71.13 ± 1.43	74.10 ± 1.31	69.70 ± 1.36	72.85 ± 1.28	ns	***	ns
CLC	27.80 ± 2.10	34.80 ± 1.99	–	–	27.20 ± 2.29	33.62 ± 2.30	ns	***	ns
ES	17.55 ± 1.11	15.92 ± 1.29	–	–	20.43 ± 1.89	16.10 ± 1.51	*	***	ns
NSC	32.35 ± 2.46	35.81 ± 2.80	33.47 ± 2.66	36.30 ± 2.92	31.07 ± 2.38	32.27 ± 2.66	ns	*	ns
NSLC	12.35 ± 1.14	14.85 ± 1.39	13.05 ± 1.22	16.28 ± 1.50	16.12 ± 1.24	17.43 ± 1.45	ns	ns	ns
FI	6.15 ± 0.04	5.95 ± 0.05	6.16 ± 0.04	6.02 ± 0.04	6.15 ± 0.04	6.05 ± 0.04	*	ns	ns
VPSR	8.27 ± 0.19	8.52 ± 0.24	8.02 ± 0.24	8.37 ± 0.24	8.31 ± 0.22	8.75 ± 0.25	ns	–	–
BSR	5.06 ± 0.19	5.66 ± 0.20	–	–	5.53 ± 0.23	6.30 ± 0.22	*	–	–

bicuspidate) were negatively related to rodent grazing. Rodent grazing was positively related to the fodder value index in 2002 (t_{189} = 3.92, $P < 0.0001$), but no relation with *Nardus stricta* (either frequencies or cover) was found.

Discussion

Empirical results of the grazing effects on plants obtained from exclosure experiments in arctic and alpine habitats are complex; the effects appear to be dependent on the habitat characteristics as well as on the characteristics of herbivores (Oksanen & Moen, 1994; Austrheim & Eriksson, 2001; Olofsson *et al.,* 2004). This 5-y exclusion of sheep from a graminoid-dominated alpine habitat with long history of heavy grazing pressure had a significant impact on the plant community, although the effect varied among different plant groups. Vascular plant height increased, but only *Deschampsia flexuosa* increased in frequency within sheep exclosures. No evidence for the effects of sheep grazing on the graminoid community as a whole was found. Frequencies of bryophyte species both decreased and increased within sheep exclosures, but neither bryophyte community cover nor species-richness increased as predicted. Exclusion of sheep reduced the level of rodent grazing, suggesting that sheep grazing facilitates foraging by rodents. In addition to this experimental effect, rodent grazing was correlated with reduced vascular plant height, vascular plant and cryptogam cover, frequency and cover of *Nardus stricta,* and changed frequencies of 3 bryophyte species. We also examined the interactions between bryophytes and graminoids using bryophyte cover and vascular plant height and cover as explanatory variables, without detecting any significant correlations (results not shown).

Our results confirm the dynamic nature of bryophyte communities after cessation of grazing, as demonstrated in several other studies in arctic and alpine habitats (Virtanen, Henttonen & Laine, 1997; Virtanen, 2000; Olofsson *et al.,* 2004; van der Wal & Brooker, 2004). Four different mechanisms may be involved: Exclusion of sheep (1) reduces typical disturbance-favoured pleurocarpous species, such as *Brachythecium* coll. (mostly *B. reflexum*) and *Plagiothecium* coll., and (2) increases the frequencies of short-lived colonizers such as *Pohlia nutans* (marginally non-significant)
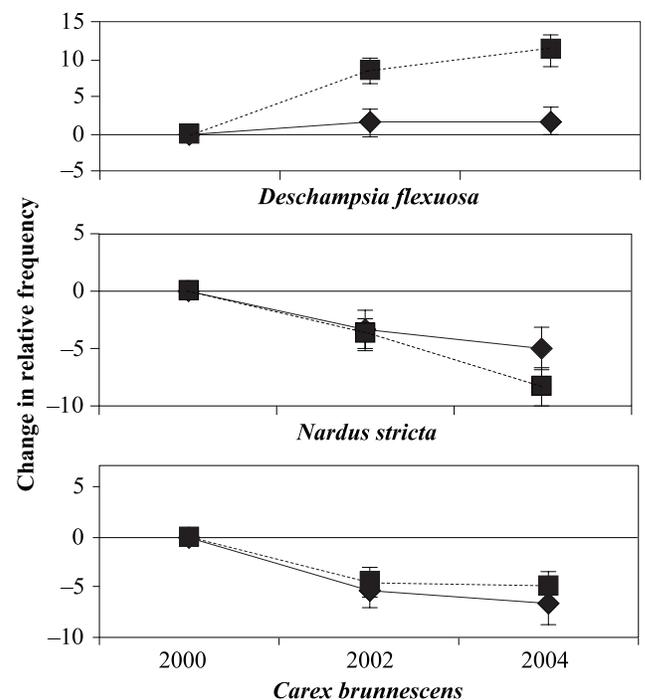

FIGURE 2. Change in relative frequency and SE for a) *Deschampsia flexuosa,* b) *Nardus stricta*, and c) *Carex brunnescens* at both grazed (solid line) and ungrazed plots (broken line) from 2000 to 2002 and from 2002 to 2004.

and *Cephalozia bicuspidata*. Sheep grazing (3) favours the grazing-resistant *Polytrichum* coll. (Helle & Aspi, 1983; Väre, Ohtonen & Mikkola, 1996; Virtanen, 2000; Olofsson *et al.,* 2004), and (4) herbivores bring about a decrease of frequency of hepatics like *Barbilophozia lycopodioides* (sheep and rodent) and *B. floerkei* (sheep), which are frequent in sub-alpine birch (*Betula pubescens*) forests. Other bryophytes typical of sub-alpine forests (*Pleurozium schreberi* and *Ptilidium ciliare*) tend to increase in exclosures (G. Austrheim, unpubl. data), thus supporting explanation (4). The strong compositional changes observed for bryophytes suggest that the predicted increase in cryptogam cover may be a secondary effect; *i.e.,* the increase in bryophyte biomass first takes place after establishment of early successional

TABLE IV. Linear mixed models (LME) on the effect of sheep (S) (exclosures), rodent (R) grazing, and possible interactions (S × R) on relative changes in bryophyte frequencies. DF refers to degrees of freedom used in *t*-tests.

Species	Variables	Coeff.	SE	DF	*t*	*P*
Brachythecium coll.	S	−0.42	0.20	189	−2.16	0.032
Plagiothecium coll.	S	−0.28	0.14	189	−2.07	0.040
Polytrichum coll.	S	−0.24	0.12	189	−2.04	0.042
Pohlia nutans	R	0.69	0.29	188	2.34	0.020
	S	0.32	0.19	188	1.68	0.094
Straminergon stramineum	S	0.33	0.13	188	2.58	0.011
	R	0.49	0.21	188	2.34	0.021
Cephalozia bicuspidata	R	0.73	0.26	187	2.70	0.008
	S	0.33	0.15	187	2.18	0.030
	S × R	−0.71	0.35	187	−2.02	0.045
Barbilophozia lycopodioides	S × R	0.56	0.28	189	2.00	0.047
Barbilophozia floerkei	S	0.44	0.20	189	2.18	0.030

bryophytes. The lack of an increase in cryptogam biomass in exclosures is most likely also an important explanation for the moderate effects on vascular plants following cessation of grazing.

Important for ecosystem functioning and possible trophic cascade effects of grazing is whether or not preferred forage plants of herbivores and grazing-resistant plants decrease or increase. A particularly important plant in this respect is the grazing-resistant and competitive plant *Nardus stricta* (Rawes & Welch, 1969; Grant *et al.,* 1996a) which made up nearly 50% of the total vascular plant cover in our study plots. We failed to find the predicted negative effect of exclosing plots on *Nardus stricta* (frequency and cover) and suggest that complex sheep–plant–rodent interactions may delay possible overall effects of the cessation of sheep grazing on *Nardus stricta* (*cf.* Hill, Evans & Bell, 1992). Nevertheless, the increase of *Deschampsia flexuosa* (Kausrud *et al.,* 2006) in sheep exclosures in our study corresponds with results of Scottish studies (Grant *et al.,* 1996a,b; Hulme *et al.,* 1999; Pakeman, 2004), and excluding sheep also caused an increase in fodder value index. This indicates that cessation of grazing leads to an increase of grazing-sensitive plants (*e.g.,* highly selected fodder plants) relative to grazing-resistant plants characteristic of heavily grazed habitats (Bråthen & Oksanen, 2001). In the short term, this is a change in frequency of species as vascular plant richness was not affected by the exclosure treatment.

The effects on plants of the cyclic behaviour of rodent populations may vary among years from dramatic to negligible, but a significant impact likely occurs over the long term (Moen & Oksanen, 1998; Olofsson *et al.,* 2004). Winter grazing can be particularly severe, with strong effects on both bryophytes and graminoids, while effects of summer grazing appear to be low, even during population peaks of rodents (Andersson & Jonasson, 1985; Moen, Lundberg & Oksanen, 1993; Virtanen, Henttonen & Laine, 1997; Grellmann, 2002). The effects of winter grazing were likely the dominating rodent effect also in our study; rodent grazing led to a significant decrease of *Nardus stricta*, and only litter remained in some plots. Nutrient-rich storage organs in graminoids and herbs provide the only winter food of moderate quality to the herbivore, which reduces

the plant's possibility of resprouting the following spring. Signs of stem base stores of *Nardus stricta* in rodent winter habitats (G. Austrheim, pers. observ.) suggest that the thick bulbs in dense turfs may be particularly vulnerable to rodent grazing during winter. However, the abundance of this grass cannot explain differences in rodent grazing between the sheep grazing treatments, and we suggest nutrient enrichment caused by sheep grazing as a facilitation mechanism, since rodents prefer fertilized habitats during winter (Grellmann, 2002). Seasonal differences in rodent forage imply that sheep effects on rodents during summer may differ from winter effects. Steen, Mysterud, and Austrheim (2005) found competitive effects on field vole during summer at high (80·km⁻²) compared to low (25·km⁻²) sheep densities, with values for controls without sheep having intermediate values. However, high rodent disturbance during winter (as shown in this study) is not necessarily directly related to rodent population growth rates. A positive interaction between sheep and rodents during a population peak does not indicate how sheep grazing will affect rodent population dynamics and ecosystem functioning. The long-term dynamics and the mechanisms behind the changes remain to be explored.

The sheep-facilitated rodent grazing pressure suggests complex interactions with plants as both additive and compensatory effects are indicated. First, the increase of rodent grazing with sheep fodder value index at the plot scale suggests a diet overlap among herbivores (and thus additive grazing *sensu* Ritchie and Olff, 1999). Indeed, both sheep and rodents significantly decreased vascular plant height and abundances of 2 bryophytes (*Straminergon stramineum, Cephalozia bicuspidata*), while *Barbilophozia lycopodioides* decreased with rodent grazing only in sheep grazed plots. Secondly, a major impact of rodent grazing was detected on a grazing resistant plant, *Nardus stricta*. This compensatory effect contributes to reducing the frequency of *Nardus stricta* in sheep pastures where it is normally the superior competitor. In addition, several plots grazed by rodents were totally cleared of biomass, and the effects on vegetation are thus mainly secondary: *i.e.,* the expected competitive advantage for graminoids will first appear in subsequent years if graminoid meristems are not destroyed.

Conclusion

This 5-y experimental study was conducted in a heavily grazed alpine region where previous studies (Austrheim, Evju & Mysterud, 2005; Austrheim, Hassel & Mysterud, 2005) suggest that grazing has reduced vegetation heterogeneity. Our study confirms significant effects of exclusion of sheep on several characteristics of the plant community, by inducing changes in frequency among species that promote herbivore-preferred vascular plants (*i.e., Deschampsia flexuosa*) and successional bryophytes, while grazing-favoured bryophytes decrease. Moreover, strong plant dynamics are expected to continue in exclosures as several grazing effects may be secondary. In the long term, a graminoid-dominated alpine–arctic system is expected to change into moss-rich heath tundra (Zimov *et al.,* 1995; Olofsson *et al.,* 2001), possibly with colonisation by trees (*Betula pubescens*).

Trees are presently restricted to lower altitudes, arguably due to grazing. The time scales for such shifts in response to cessation of grazing are largely unknown, although a positive sheep–rodent interaction suggests that the transition from grassland to tundra may accelerate due to a secondary reduction of rodent grazing intensity. However, plant–herbivore interactions are complex, indicating the need for an ecosystem perspective in the management of sheep grazing that includes not only sheep and their fodder plants, but also interactions with other plant groups and with rodents.

Acknowledgements

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APPENDIX I. Mean frequencies ± SE in the years 2000 and 2004 for vascular plants and bryophytes showing significant effects of sheep grazing cessation.

Species	2000		2004	
	Grazed	Ungrazed	Grazed	Ungrazed
Deschampsia flexuosa	79.20 ± 2.99	69.20 ± 3.52	79.89 ± 3.01	80.45 ± 3.14
Brachythecium coll.	6.26 ± 1.33	6.88 ± 1.05	6.51 ± 1.51	1.82 ± 0.87
Plagiothecium coll.	1.38 ± 0.49	5.88 ± 1.62	3.19 ± 0.98	4.44 ± 1.31
Polytrichum coll.	30.82 ± 3.80	39.45 ± 3.99	35.20 ± 3.93	39.95 ± 3.99
Pohlia nutans	4.70 ± 0.91	2.88 ± 0.70	4.19 ± 0.99	4.50 ± 0.85
Straminergon stramineum	0 ± 0	1.13 ± 0.71	0.88 ± 0.40	6.07 ± 1.62
Cephalozia bicuspidata	1.44 ± 0.65	0.44 ± 0.20	0.50 ± 0.21	1.50 ± 0.76
Barbilophozia floerkei	37.46 ± 3.67	**33.71 ± 3.45**	**31.14 ± 3.76**	**34.20 ± 3.71**