Response of the moss *Racomitrium lanuginosum* to changes in sheep grazing and snow-lie due to a snow-fence

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Abstract

Question: What are the responses of *Racomitrium lanuginosum* moss to altered snow-lie and sheep use?

Location: A *Carex bigelowii-Racomitrium lanuginosum* heath on a Scottish montane plateau affected since 1986 by a fenced ski corridor.

Methods: Permanent quadrats were set up along transects 45 m long perpendicular to the snow-fence. Cover was assessed over a 12-year period from 1990. Pellet-group clearance counts provided data on sheep usage between 1990 and 1996. Snow-lie was mapped in the springs of 1991-1996.

Results: The snow-fence created a gradient in sheep use and altered the duration of snow-lie. At the start of monitoring *Racomitrium* cover was lower immediately adjacent to the fence, and after 12 years its cover was significantly reduced within 10 m of the fence. Further away from the fence *Racomitrium* cover was relatively stable. The loss of *Racomitrium* was correlated both with increased snow-lie and heavier sheep usage. Grass cover increased near the fence and was related to sheep use. *Dicranum fuscescens* responded differently to *Racomitrium*, increasing significantly near the fence.

Conclusions: We found that changes in snow-lie and grazing pressure quickly brought about vegetation change in this montane ecosystem. *Racomitrium* was the most sensitive species to the changes in grazing and snow-lie caused by the fence, having the biggest initial changes. Loss of *Racomitrium* permitted increases of species more resistant to grazing including *Dicranum fuscescens* and grasses.

Keywords: Grazing; Montane plateau; Moss heath; Ski development; Snow; Vegetation dynamics.

Nomenclature: Stace (1997) for vascular plants; Smith (1978) for mosses.

Introduction

Large herbivores influence the composition and structure of plant communities worldwide (Augustine & McNaughton 1998). Their impact, however, is most apparent when grazing pressure increases in ecosystems that generally sustain only low densities of large herbivores (Zimov et al. 1995). Livestock grazing has intensified in many parts of the world leading to increased exploitation of natural and semi-natural ecosystems (Milchunas & Lauenroth 1993). Moss-dominated vegetation seemingly exemplifies a grazer-sensitive ecosystem component that is often transformed into grasslands (e.g. Zimov et al. 1995; Olofsson et al. 2001). Here, we report on the process of plant-species change in a grazer-sensitive European moss heath, dominated by *Racomitrium lanuginosum*, that was subjected to increasing grazing pressure.

Racomitrium lanuginosum has a wide world distribution but its altitudinal range lowers progressively as latitude increases, from mountains in the tropics to near sea level in the arctic (Tallis 1958; Kallio & Heinonen 1973). The community type studied with *Carex bigelowii* the main vascular plant – U10 in the British National Vegetation Classification (Rodwell 1992) – occurs in oceanic parts of Europe including Britain, Iceland and western Norway (Ratcliffe & Thompson 1988). It is the most extensive near-natural plant community in Britain, even though it is now mostly restricted to Scottish summit plateaux (Thompson & Brown 1992). Historically its distribution was probably much wider, but on many of the plateaux south of the Scottish Highlands *Racomitrium* moss heath has been replaced by grass-dominated heath or grassland (Ratcliffe & Thompson 1988). Several causes for this decline have been proposed, including the effects of increased nitrogen deposition and grazing (Thompson et al. 1987; Jones et al. 2002; Pearce & van der Wal 2002; van der Wal et al. 2003).

Racomitrium heaths have significant conservation value, being threatened by global warming due to the intolerance of *R. lanuginosum* to higher temperatures

(Kallio & Heinonen 1973), and containing several species themselves under threat. For instance, the dotterel (*Eudromias morinellus*), a rare bird in Britain listed under Annex 1 of the EC Birds Directive, much depends upon this habitat both for nesting and feeding (Galbraith et al. 1993). Changes in the composition of these heaths may impact on some of the preferred prey of dotterel, such as the crane fly (*Tipula montana*) whose larvae require dense bryophyte mats for shelter from predation (Smith et al. 2001). Reduced prey availability may affect nesting and breeding success of dotterel (Thompson & Whitfield 1993), as well as other montane birds such as snow bunting (*Plectrophenax nivalis*).

One such area of *Racomitrium* heath used for breeding by dotterel and grazed by sheep is the summit plateau of Glas Maol, a 1068 m mountain in the eastern Scottish Highlands. The vegetation of the plateau is principally *Carex bigelowii - Racomitrium lanuginosum* moss heath and is grazed by sheep between May and October (Welch & Scott 2001). Since 1986 the plateau has been affected by a ski corridor and uplift tow, which has changed sheep ranging behaviour; the snow-fencing acts as both a barrier to movement and a source of shelter (Welch & Scott 2001). The erection of this fencing triggered two main concerns, both predicted to drive changes in the vegetation: (1) grazing pressure would be altered and have a detrimental affect on the existing plant communities, and (2) increased duration of snow-lie would allow more snow-tolerant species such as mat grass (*Nardus stricta*) to establish.

This paper examines the response of *Racomitrium* to the changes in snow-lie and sheep grazing pressure observed on Glas Maol, while Welch et al. (2005) described the overall changes in the species composition of the vegetation, especially the increase of grasses in positions of prolonged snow-lie and heavy grazing. Distribution patterns for snow-lie and sheep grazing at the study site were presented in Welch et al. (2005), and detailed information on the sheep grazing was given in Welch & Scott (2001). Our aim in the present paper is to describe and explain the response of *Racomitrium*, the key species of this montane community.

Study site

The study was conducted on a 6 ha section of the summit plateau of Glas Maol (56°53'02'' N, 03°22'02'' W) affected by the skiing corridor. The climate of Glas Maol is wet and cold; it was assigned by Birse (1971) to his hemi-oceanic, extremely humid, lower oro-arctic type (defined as having 0 mm annual potential water deficit and receiving yearly 300-500 day degrees C). The plateau is an area of gently sloping ground partly surrounded by steep escarpments, cliffs and boulder scree. It

is well drained, with ranker soils and acidic rock types of graphitic schist or slate. The vegetation comprises *Carex bigelowii* and mosses, mainly *Racomitrium lanuginosum*, *Dicranum fuscescens* and *Polytrichum alpinum* and is of relatively short stature (height in 1990-1992 = 6 cm (overall mean) and 7 cm where *Racomitrium* had > 20% cover). The main herbivores using the site are Scottish Blackface sheep (*Ovis aries*), which graze the plateau during the summer months, mountain hares (*Lepus timidus*) and occasional red deer (*Cervus elaphus*). A mean density of ca. 1 sheep/ha from May to October has been estimated for the plateau (Welch & Scott 2001).

The ski corridor runs for 750 m along a ridge extending north from the plateau, starting at an altitude of just above 1020 m and falling gradually to 940 m. The snow-fencing consisted of vertical wooden palings standing about 1.3 m high. When in good condition this fencing formed an effective barrier to sheep but not to deer, which were capable of jumping the fences, or hares, that could pass easily between the gaps in the palings.

Methods

Vegetation recording

Transects spaced at random distances along the corridor (15 in total) were set out at right angles to its east fence, and permanently marked. Vegetation quadrats were set out along the south side of each transect at 0-1, 2-3, 5-6, 9-10, 19-20 and 39-40 m from the fence, giving a total of 90 quadrats. Each quadrat measured 1 m by 0.5 m with its long axis parallel to the transect. In the quadrats we recorded plant species cover, occurrence of dead material (including standing dead and litter) and amount of bare ground. Cover was assessed using a pin frame with five pins each 10 cm apart, the frame being placed at 10 cm intervals along the transect. All species hitting a pin were scored and bare ground was recorded only when no species or dead material hit a pin. Recording was first done in July 1990, four years after the erection of the ski corridor, and was repeated at the same time each year up to 1996, with one further recording in July 2002.

Sheep use and snow-lie

Sheep use was estimated using dung clearance counts. Because dung could introduce seeds and act as a fertiliser, and frequent trampling from counting and clearing of dung could impact on the vegetation, separate dung quadrats were located on the north side of transects, away from the vegetation quadrats at distances of up to 45 m from the fence. We used 10 m × 2 m quadrats, with

the long axis running parallel with the fence (Welch & Scott 2001). From 1990 to 1996 the dung quadrats were visited every three weeks from May to October each year. At each visit sheep and deer pellet groups were counted and then cleared from the quadrats; despite fears that dung clearance could over time result in decline in *Carex* growth and nutritive value, no differences between the quadrats and their surrounds were detected. Snow-lie was mapped during site visits in May and June between 1991 and 1996. Snow accumulated in the ski corridor and mostly within 5 m of the ski fences. Wind action on the plateau generally means that most snow gets blown away and does not lie for long.

Data analysis

To simplify analyses, some species were aggregated into the following groups: grasses – mainly *Agrostis capillaris*, *Deschampsia flexuosa*, *Festuca ovina*, *Nardus stricta* – and Other mosses – mainly *Dicranum fuscescens*, *Polytrichum alpinum*, *Pleurozium schreberi* but excluding *Racomitrium*. Also, as we were particularly interested in *Racomitrium*, and *Carex bigelowii* and *Dicranum fuscescens* had much cover, we examined these species individually. For each pin these individual species and the groups above were scored as either present or absent in 1990 and 2002, single scores being counted for group presence no matter how many constituent species were hit. Changes between 1990 and 2002 in the cover of *Racomitrium*, other selected species and species groups were analysed using paired *t*-tests on transect means for quadrats at three distance classes.

Dung data were used as an index to expose the relationship between species or species groups and sheep usage. Data from the dung quadrats were allocated to their equivalent vegetation quadrats.

The relationships of cover and of changes in cover as a function of sheep use, snow and distance from the fence were explored using generalised linear models with binomial errors and logit link functions (PROC GENMOD). In these regression models we included the distance covariate after fitting transect as a categorical variable, and we tested the mean square for distance against the mean square for the interaction between transect and distance. Other relationships, e.g. with sheep use, or multiple regressions with sheep use and snow lie, were estimated and assessed in a similar manner. Dung counts were log-transformed before inclusion as a covariate, similarly we used log(1+snow-days) rather than snow-days after May 1 as recorded. For illustrating the relationships, the quadrats were divided into nine groups according to sheep usage, and the pellet-group densities were converted to an annual sheep-stocking density by applying a mean deposition rate of 17 pellet-groups per day (Welch 1982).

Individual pin data were used to assess the associations of *Racomitrium* with other species or groups in 1990 and 2002. For both years we constructed a two-by-two table of counts of pin hits for each quadrat, with classifying factors the presence or absence of *Racomitrium* ($Pres_R$) and the presence or absence of another species or group ($Pres_O$). These counts were analysed by fitting generalised linear models (PROC GENMOD) with a Poisson distribution and a log link function, fitting a categorical variable for quadrat followed by $Pres_R$, $Pres_O$ and their interactions with quadrats. The two-way interaction of $Pres_R$ and $Pres_O$ was then added to the model, followed by the three-way interaction of $Pres_R$ and $Pres_O$ with a categorical variable for transect, and the ratio of their mean deviances was used for significance testing to avoid pseudo-replication.

To investigate if any species or group gained significantly where *Racomitrium* was lost, we used generalised linear models with binomial errors, but the tables of counts were constructed using only data from pins with no *Racomitrium* present in 2002 and with *Racomitrium* presence/absence in 1990 as a categorical variable. Additional explanatory variables were included to assess whether species and group changes depended on levels of sheep use, snow-lie and distance from the fence.

Individual pin data were also used to determine the fine-scale spatial distribution of *Racomitrium* and changes from 1990 to 2002. For all the pins that had eight neighbouring pins (24 = 8 rows of 3 pins per quadrat, each with four near neighbour pins 10 cm away and four diagonal neighbour pins 14.1 cm away) we created three covariates corresponding to: presence/absence at that pin in 1990 (C_{pin}); the number of near neighbours with *Racomitrium* in 1990 (C_{near}); and number of diagonal neighbouring pins with *Racomitrium* in 1990 (C_{diag}). We analysed presence/absence in 2002 using a binomial generalised linear model with a logit link function (PROC GENMOD). In this analysis, which estimated relationships entirely within quadrats, we fitted a categorical variable for quadrat, C_{pin}, C_{near}, C_{diag} and the interaction of one of these covariates with transect. Significance of covariates for previous occupancy was assessed by comparing mean deviance change on adding the covariate to the model with mean deviance change on adding its interaction with transect. All statistical analyses were done using the SAS statistical package v. 8.2.

Results

Cover trends in relation to the snow-fence

There were significant losses of *Racomitrium lanuginosum* within 10 m of the fence (Table 1). This reduction was most noticeable immediately adjacent to the fence where *Racomitrium* was absent in 12 of 15 quadrats in 2002, compared with only four in 1990. *Carex bigelowii* cover was significantly reduced across the whole study area whereas grasses increased significantly, most notably within 10 m of the fence (Fig. 1, Table 1). Other mosses also gained significantly within 10 m of the fence, most of the gain next to the fence being of *Dicranum* (Table 1).

The consistency of cover change over the 12 years of monitoring was much greater in *Racomitrium* and grasses than in *Dicranum* (Table 2). *Racomitrium* losses increased at 5-6 and 9-10 m in later years, but at 19–20 m and 39-40 m its cover was relatively stable. *Dicranum* increased abruptly in 1995 and 1996 at all distances but its cover had fallen by 2002, especially at 19-20 and 39-40 m (Table 2). Grass cover at 5-6 and 9-10 m increased quickly at first then stabilised, before increasing again by 2002; in comparison grass cover at 19-20 and 30-39 m was fairly stable (Table 2). There was a small but appreciable increase in bare ground close to the fence.

Racomitrium cover was already related to distance from the fence in 1990, four years after the erection of

Table 1. Changes in cover of main species and species groups between 1990 and 2002 at three pairs of combined distances from the snow-fence (N = 0-1 and 2-3 m, I = 5-6 and 9-10 m, D = 19-20 and 39-40 m) with significances from paired *t*-tests.

Species	Distance class	Mean % Cover 1990	Change in % Cover 1990-2002	*t*-value	*P*-value
Racomitrium lanuginosum	N	16.6	–12.0	–4.17	0.0010
	I	29.7	–8.1	–3.11	0.0076
	D	42.6	–3.8	–1.63	0.1259
Carex bigelowii	N	66.3	–27.4	–6.97	< 0.0001
	I	67.4	–19.5	–5.98	< 0.0001
	D	69.1	–10.9	–3.07	0.0082
Grasses	N	8.4	+13.7	4.71	0.0003
	I	7.5	+10.7	3.55	0.0032
	D	5.4	+4.7	2.40	0.0308
Other mosses	N	26.1	+12.0	2.85	0.0129
	I	32.9	+9.9	2.02	0.0630
	D	34.2	–7.1	–1.41	0.1793
Dicranum fuscescens	N	19.5	+11.3	2.83	0.0134
	I	26.8	+4.4	1.13	0.2794
	D	27.3	–13.5	–3.21	0.0063

the snow-fencing (linear regression: $F_{1,14}$ 16.34, P = 0.0012), with least cover at 0-1 m from the fence. This pattern was even more marked in 2002 (Fig. 1). The cover of other mosses was also much reduced at 0-1 m from the fence in 1990, and the cover of all mosses showed a similar reduction. By 2002 little further change occurred in the cover of all mosses, with gains in other mosses within 10 m of the fence largely cancelling out the losses
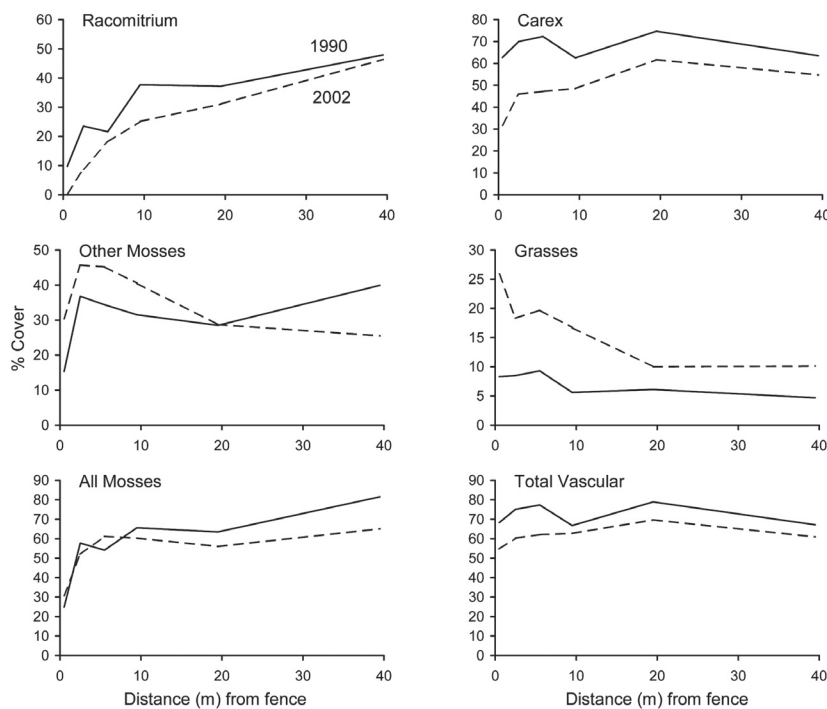

Fig. 1. Cover of main species and species groups in 1990 (solid line) and 2002 (dotted line) at six distances from a ski fence. Total Vascular cover is based on the presence of any *Carex*, grass or forb species at a pin and All Mosses, the presence of any moss species at a pin.

Table 2. Trends in % cover of *Racomitrium*, *Dicranum*, Grasses and Bare ground between 1990 and 2002 (distance from fence classes as in Table 1).

Species	Distance class	Year							
		1990	1991	1992	1993	1994	1995	1996	2002
Racomitrium	N	16.6	13.3	10.8	10.1	9.4	8.8	7.3	4.6
lanuginosum	I	29.7	28.9	29.0	27.4	25.6	21.7	23.4	21.6
	D	42.6	39.4	38.0	36.6	35.4	37.7	39.9	38.7
Grasses	N	8.4	10.5	12.7	14.0	14.4	16.5	18.5	22.1
	I	7.5	11.2	15.5	14.6	14.9	14.7	14.3	18.2
	D	5.4	6.3	7.1	6.9	7.1	6.3	6.1	10.1
Dicranum	N	19.5	22.6	21.6	22.3	21.7	30.3	35.0	30.7
fuscescens	I	26.8	30.2	29.9	28.4	28.0	35.1	41.2	31.2
	D	27.3	22.1	23.3	22.4	20.4	24.9	31.4	13.8
Bare	N	0.6	1.6	4.3	5.5	3.3	4.1	5.8	2.2
ground	I	0	0	0.3	0	0	0	0.1	0
	D	0	0	0	0	0	0	0	0

of *Racomitrium* (Fig. 1); the reduction at 39-40 m was due to the loss of mosses other than *Racomitrium*. The cover of *Carex* and grasses was not related to distance from the snow-fence in 1990. However, by 2002 clear patterns had emerged, with less *Carex* and greater grass cover near the fence (Fig. 1). Total Vascular cover fell slightly at all distances in 2002, more so within 10 m of the fence, reflecting the loss of *Carex*.

Sheep use, snow and Racomitrium cover

The distribution of sheep pellet groups across the plateau recorded between 1990 and 1996 showed a consistent spatial pattern (log linear regression: $F_{1,14} = 86.33$, $P < 0.0001$) with heavier usage nearer the fence. Snow-lie was also significantly more prolonged near the fence (log linear regression: $F_{1,14} = 33.84$, $P < 0.0001$) but had a rather different pattern. Only 11 quadrats had mean late snow-lie of 10 or more days; eight were situated within 6 m of the fence and the other three along one transect, this whole transect lying in a regular natural snow patch. Snow-lie and sheep use were positively correlated on both the scale recorded and after log-transformation of both variables ($r = 0.729$ and 0.750 respectively) and to both factors *Racomitrium* cover was significantly negatively related both in simple or multiple regression. The log transformation mostly raised F values but in multiple regression the variation explained by each variable was reduced by the presence of the other: for *Racomitrium* cover in 1996 $F_{1,14} = 51.36$, $P < 0.0001$ for log snow-lie fitted before log dung $F_{1,14} = 7.04$, $P = 0.0189$ whereas $F_{1,14} = 49.38$, $P < 0.0001$ for log dung fitted before log snow-lie $F_{1,14} = 8.40$ $P = 0.0117$. The negative relationships also held true for sub-sets of quadrats: for example for the 61 quadrats that had less than 4 days mean late snow-lie, *Racomitrium* cover in 1996 had a significant negative relationship to sheep use ($F_{1,13} = 13.3$, $P = 0.0026$).

Species replacement of Racomitrium

Where *Racomitrium* was lost there was potential for other species to gain. Overall, 46% of the pin-frame positions at which *Racomitrium* was lost between 1990 and 2002 did not gain another species, including 1% that became bare ground. Species appearing at positions of *Racomitrium* loss were, in descending order of importance: other mosses (at 56% of pins that had species gains), *Dicranum fuscescens* (43%), *Carex bigelowii* (32%), grasses (21%), all other species including liverworts and lichens (21%). The total of these percentages exceeded 100 due to more than one group or species appearing at some pin positions; the next most important moss after *Dicranum* contributing to the other mosses group was *Polytrichum alpinum*. Bare ground occurred mainly at 0-1 m distance from the snow-fence, and negligibly beyond the 2-3 m distance. On average 4.6% of pin positions at the 0-1 and 2-3 m distances were bare for the years from 1992 to 1996, while only 2.2% were bare in this zone in 2002; some of these positions have been
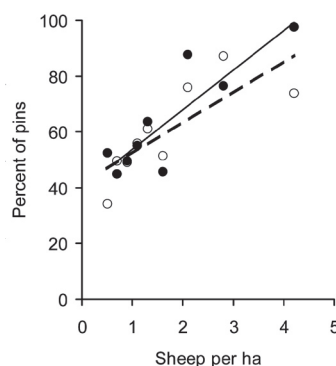

Fig. 2. Mean percentages of pins with *Racomitrium* in 1990 losing it by 2002 (filled circles) for nine classes of sheep usage with regression line (solid line), and the percentage of these points gaining other species (open circles) with regression line (dotted line).
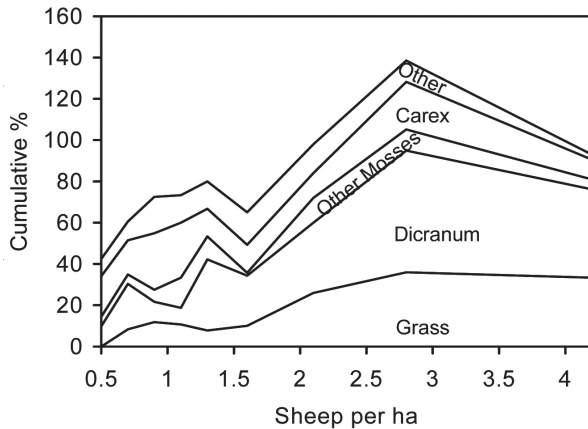
Fig. 3. The cumulative percentage of species/groups gaining at pin positions that lost *Racomitrium* between 1990 and 2002 against the nine classes of sheep usage. (Other = forbs, lichens and liverworts combined). The large gains in some usage classes are because more than one species/group could gain at a pin.

Fig. 4. Plots of log % Grass cover on log mean sheep per hectare in nine classes of sheep usage, for 1990 (filled circles) and 1996 (open circles).

colonised by *Dicranum*. The change from *Racomitrium* to *Dicranum* was however mostly direct.

Effects of sheep use and snow-lie on species replacement

With increasing sheep use, there was both greater *Racomitrium* loss at individual pins (log sheep in binomial model: $F_{1,14} = 14.27$, $P = 0.002$) and greater gains of other species at these pins ($F_{1,14} = 4.79$, $P = 0.0461$); for convenience nine dung classes are used to illustrate this (Fig. 2). The greatest gains in grasses and *Dicranum* were at higher sheep densities, but at the highest usage replacement fell, though only slightly in grasses (Fig. 3). Grass cover was positively related to log sheep dung, more so in 1996 than in 1990 (1996: $F_{1,14} = 49.20$, $P < 0.0001$; 1990: $F_{1,14} = 33.52$, $P < 0.0001$), and the greater gain of grass under heavier sheep usage is illustrated in Fig. 4 again with nine usage classes for convenience. For
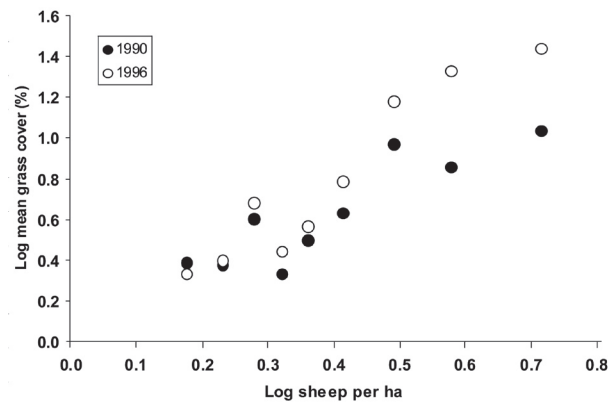
Dicranum, log sheep dung also explained a significant amount of the variance in cover in 2002 in individual quadrats ($F_{1,14} = 15.92$, $P = 0.0013$).

With increasing late snow-lie, there was much greater loss of *Racomitrium* (log snow-lie in binomial model: $F_{1,14} = 33.51$, $P < 0.0001$) but the combined gain of other species was non-significant at these pins. Grass cover was already significantly related to log snow-lie in 1990 ($F_{1,14} = 14.05$, $P = 0.0022$) and this relationship had strengthened in 1996 ($F_{1,14} = 26.98$, $P = 0.0001$) but weakened considerably by 2002 ($F_{1,14} = 6.56$, $P = 0.0226$). However *Dicranum* cover in 2002 was very closely related to log late snow-lie ($F_{1,14} = 31.75$, $P < 0.0001$).

Table 3. The proportion of quadrat pins with *Racomitrium* at which other species or species groups co-occurred, compared with the proportion of all pins at which these species or groups occurred in 1990 and 2002. Within-year comparisons are made using generalised linear models to show differences in species or group associations with *Racomitrium*.

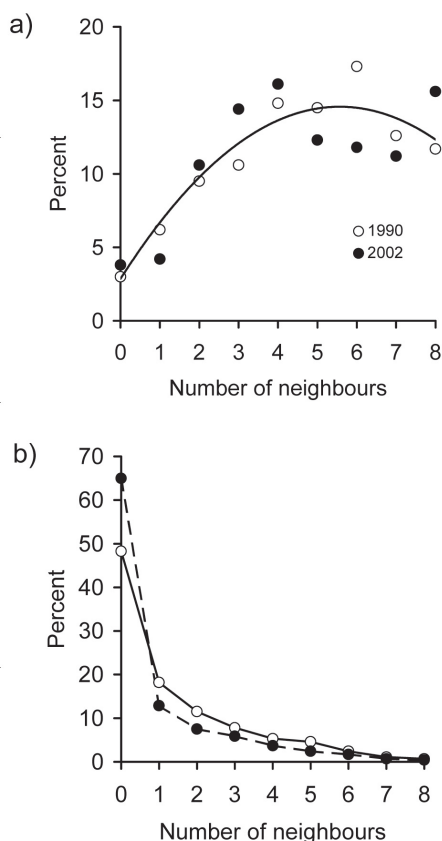| Species	Year	% Co-occurrence with *Racomitrium*	Overall cover %	Num df	Den df	F- value	P- value
Carex	1990	60.9	67.6	1	14	43.1	< 0.001
bigelowii	2002	41.8	48.3	1	14	28.9	< 0.001
Grasses	1990	2.6	7.1	1	9	12.4	0.002
	2002	7.1	16.8	1	12	7.8	0.016
Other mosses	1990	9.5	31.1	1	14	162.8	< 0.001
	2002	15.7	36.0	1	14	62.8	< 0.001
Dicranum	1990	5.7	24.4	1	14	159.2	< 0.001
fuscescens	2002	7.2	25.3	1	14	88.0	< 0.001

Fig. 5. a. Percentages of pin-frame points with *Racomitrium* present in 1990 (open circles) and 2002 (filled circles) belonging to nine classes of *Racomitrium* occurrence at neighbouring points. A polynomial curve is fitted as a visual aid to interpretation. **b.** Percentages of pin-frame points with *Racomitrium* absent in 1990 (solid line, open circles) and 2002 (dotted line, filled circles) belonging to these same classes.

Species associations with Racomitrium

Carex was the most frequently recorded species in the moss heath in both 1990 and 2002 and had the greatest co-occurrence of any species with *Racomitrium* (Table 3). Nevertheless, their co-occurrence was significantly less than expected, as was also the co-occurrence of *Racomitrium* with grasses. The co-occurrence of *Racomitrium* with *Dicranum*, the next most abundant moss, was also significantly less than predicted both in 1990 and 2002 (Table 3). This confirmed that the main moss species form relatively discrete mats. The greater co-occurrence observed in 2002 of *Racomitrium* with other mosses, *Dicranum* and grasses was in line with the increases that these groups/species experienced (Table 3).

Small-scale spatial relationship of Racomitrium

The occurrence of *Racomitrium* in 2002 was most strongly dependent on the species' occurrence at the same pin in 1990 ($F_{1,14} = 12.5$, $P = 0.0033$) followed by occurrence in 1990 at near-neighbour pins ($F_{1,14} = 12.1$, $P = 0.0037$) whereas former occurrence of diagonal neighbours was not significant ($F_{1,14} = 0.65$, $P = 0.4311$). Where *Racomitrium* occurred in the sward it had a clumped distribution, with most contacted pins having a high number of neighbouring hits (Fig. 5a). This pattern was the same in both 1990 and 2002, with at least 90% of hit pins having two or more neighbours and just over half having 5-8 neighbours. Similarly, pins at which there was no *Racomitrium* usually had few or no *Racomitrium* neighbours (Fig 5b). The increase in the proportion of pins with no neighbouring *Racomitrium* in 2002 suggests that some clumps had totally disappeared.

Discussion

Our study shows that the erection of a ski corridor on Glas Maol created gradients in sheep usage and altered the distribution of snow-lie. As a result, sheep use, as measured by pellet group counts, increased near the fence, being equivalent to a stocking rate of 3.9 sheep/ha at 0-1 m from it, and 1.0 sheep/ha at 39-40 m distance. Also, plots within 6 m of the fence had more prolonged snow-lie. When monitoring of the response of the *Carex bigelowii-Racomitrium* moss heath began, four years after the construction of the snow-fence, *Racomitrium* mean cover next to the fence was 10%, compared with 40-50% at the furthest sample distances. We find that over the next 12 years the main component species of the moss heath reacted differentially to the various imposed pressures (defoliation, trampling, enrichment from urine and faeces, increased snow-lie) reflecting their physiognomy, and although ideally baseline data would have helped in the interpretation of trends, nevertheless we have gained knowledge on the tolerance of *Racomitrium* to these factors and its interaction with other mosses and graminoids.

Dense moss cover produces nutrient-deficient soil conditions, limiting the potential establishment of vascular plants (Chapin & Shaver 1985), and thick moss carpets impede the growth of many higher plants. However, on Glas Maol the *Racomitrium* carpet is thin (mean vegetation height only 7 cm), more so than in many of its more northerly stands (e.g. Bjarnason 1991, and Jägerbrand 2004). Hence these Scottish *Racomitrium* stands are likely to be quite vulnerable to trampling damage and more susceptible to the spread of graminoids and other lower-growing mosses. Our Glas Maol moss heath

contains abundant *Carex bigelowii*, a species suited for soils with low nutrient availability (Brooker et al. 2001). However, due to this species' high palatability to deer and sheep, the plateau has long experienced substantial grazing pressure. During our study years many sheep were present on the plateau from June to September when the *Carex* shoots were green, while usage by red deer was negligible (just three pellet groups recorded on the plots), though large herds of deer grazed in the nearby valleys.

Racomitrium cover fell substantially within 10 m of the fence (Fig. 1, Table 2) but interestingly overall moss cover there changed negligibly from 1990 to 2002 due to other species, principally *Dicranum fuscescens*, increasing. *Racomitrium* is known to be sensitive to trampling from sheep (Jónsdóttir 1991; van der Wal et al. 2003) and also humans (Bayfield 1979; Gremmen et al. 2003). Thus, Jónsdóttir (1991) found a fourfold difference in *Racomitrium* biomass between grazed and ungrazed populations. She suggested that *Racomitrium* cover, followed by moss depth, probably increased quickly after protection from sheep trampling. Bayfield (1979) noted that the recovery he found after experimental trampling would have been much slower if damage had proceeded to the point where bare soil was exposed. *Dicranum* spp., however, seem able to withstand light trampling (Liddle 1997), and our present observations show that *D. fuscescens* increased substantially in cover (by ca. 10% in absolute amount, or ca. 50% of its initial cover) despite substantial sheep usage in this zone close to the snow-fence. In part *Dicranum* may have benefited from the decline in *Racomitrium,* and interactions between moss species have been demonstrated (Zamfir & Goldberg 2000), but our finding of direct replacement between these species is new.

Snow-lie also affects the balance between *Racomitrium* and *Dicranum fuscescens*. Rodwell (1992) describes the chionophobous behaviour of *Racomitrium lanuginosum* on British mountains, while *Dicranum fuscescens* and *Polytrichum alpinum* are reported to be common in vegetation types having longer snow-lie such as NVC U8 (*Carex bigelowii-Polytrichum alpinum* sedge heath). A segregation of *Racomitrium* and *Dicranum fuscescens* by snow-lie is supported by our finding that in 2002 *Dicranum* was more positively correlated with 1991-1996 snow-lie than with 1990-1996 sheep use.

Relationships between mosses and graminoids have been widely studied in cool environments, e.g. by Olofsson et al. (2001), Gremmen et al. (2003) and van der Wal & Brooker (2004), with a focus on herbivore impacts through trampling and the enrichment of soils from dung and urine. Trampling has been shown to reduce moss cover and depth, and certain mosses appear more sensitive to trampling damage than grasses and sedges (Liddle 1997; Gremmen et al. 2003). Reduced moss cover results in increased water loss from the soil and increased soil temperature, which makes conditions more suitable for colonisation by grasses (Zimov et al. 1995; Brooker & van der Wal 2003). A combination of these direct and indirect impacts together with the introduction of grass propagules in the sheep dung has doubtless led to the spread of grass near our Glas Maol snow-fence. We found that within 10 m of the fence the number of quadrats with grasses present increased from 25 in 1990 to 42 in 2002. A more grass-dominated vegetation attracts more herbivores whose grazing enhances the growth of old tillers and production of new ones (Chapin 1980), and whose faeces and urine enrich the soil, further stimulating grass growth (Van der Wal et al. 2003). Thus, we found that areas starting with highest grass cover attracted greater sheep use, and had greater increases in grass cover (Fig. 4). Similarly, in alpine areas of Europe local long-continued grazing and enrichment by urine and faeces may have been responsible for the reduction of some *Carex*-dominated communities and their subsequent development into *Poa alpina*-dominated communities (Erschbamer et al. 2003).

Sheltering by the sheep may have affected the width of the zone of grass spread and *Racomitrium* decline on Glas Maol. The sheltering effect of the snow-fencing is related to its height and extends about 15 m (Welch & Scott 2001) and animals were often observed lying in this zone, adding to the impacts from trampling and enrichment from urine and faeces.

Another indirect impact perhaps resulting from increased snow-lie could be prolonged contact with pollutants such as N. During snowmelt, high concentrations of pollutants are released in a process called 'acid flush' which has been shown to cause damage to underlying bryophytes (Woolgrove & Woodin 1996). Repeated snowfall and melt close to the fence could lead to flushes of high levels of N and contribute to *Racomitrium* loss. Increased N levels are known to rapidly suppress the growth and cover of *Racomitrium* (Pearce & van der Wal 2002); in comparison *Dicranum* and *Polytrichum* appear less affected (van der Wal et al. 2005). So in this way again snow and grazing animals can act in concert, due to the effects of soil enrichment on the vegetation (van der Wal et al. 2003) speeding up the rate of change in species composition.

Racomitrium tended to occur as distinct patches on Glas Maol, within which the cover of other bryophytes was sparse. Thus, when *Racomitrium* was recorded at a pin it was usually hit at several neighbouring pins. Where *Racomitrium* was recorded in 2002 was strongly related to its distribution in 1990, but generally there were fewer hits and neighbours than before. There was also a large increase in the number of pins with no *Racomitrium* and

no neighbouring hits (Fig 5b). So where *Racomitrium* cover was broken up at the start of the study it had disappeared almost completely in 2002, but where its cover was continuous then it remained reasonably intact. It could be argued that the fragmented distribution of *Racomitrium* is indicative of decline, and should signal the immediate need for the damaging impacts to be eased, otherwise extinction is likely.

Our observations over 12 years have shown that distant to the snow-fence *Racomitrium cover* has changed little, so there is not an immediate threat to the continued existence of this important community across the main Glas Maol plateau. But the significant decline of *Racomitrium* at intermediate distances from the fence suggests that at most an increase of 25% in sheep usage could be tolerated. We intend to continue the monitoring and check whether grasses further increase and attract greater usage from sheep or deer.

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