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Changes in the composition of *Carex bigelowii–Racomitrium lanuginosum* moss heath on Glas Maol, Scotland, in response to sheep grazing and snow fencing

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Abstract

Carex bigelowii–Racomitrium lanuginosum moss heath has high conservation value in Britain, being one of the most extensive near-natural habitats and also the preferred habitat of dotterel (*Eudromias morinellus*). This rare and attractive bird has declined in Britain in the past century, and loss of *Racomitrium* heath due to heavy sheep grazing and/or nitrogen deposition is probably responsible. Erection of snow fencing for a ski corridor across *Carex–Racomitrium* heath on Glas Maol, a mountain rising to 1068 m in the eastern Highlands, affected sheep (*Ovis aries*) usage, and so gave an opportunity to compare trends in botanical composition under different grazing intensities. We began monitoring in 1990, four years after the fence's erection, and report trends up to 2002/03.

Adjacent to the fencing (0–10 m away) sheep usage was much increased due to improved shelter, and *C. bigelowii* and *R. lanuginosum* declined, the latter sharply. *Racomitrium* cover was already reduced by a third in 1990, and fell by a further third over the next 12 years. Grass cover increased to nearly equal *Carex* cover 16 years after the fence erection. *Dicranum fuscescens* also spread but lichens declined. There was longer snow-lie near the fence, this being correlated with sheep usage despite somewhat different incidence, and logistic regression showed that for the 1990–1996/97 period *Racomitrium* loss was rather more closely related to snow-lie than to sheep pellet-group density, whereas *Agrostis* increase was highly significantly related to pellet-group density.

Distant to the fence the composition of the *Carex–Racomitrium* heath changed little over 12 years of monitoring. *Agrostis* increased and *C. bigelowii* declined, both changes being significant but much smaller than adjacent to the fence. Also *Polytrichum alpinum* increased significantly and some lichens declined. For *Racomitrium* there was a fall of only 2.5% from its initial cover of 40% in 1990. Since the dung counts showed only a negligible reduction in sheep usage between plots at 13–15 and 43–45 m from the fence, the trends in composition recorded at positions 19–20 and 39–40 m from the fence apply to the extensive moss heath used by the dotterel on Glas Maol. These birds still nest in the distant zone, and we judge that the condition of the *Carex–Racomitrium* heath will remain satisfactory for them unless sheep usage increases by 25% or more. However, the ongoing loss of lichens and the sparsity of *Vaccinium myrtillus* imply that the current level of sheep grazing has appreciably modified this community from its former pristine condition.

1. Introduction

Montane or alpine vegetation in the UK, defined as lying above the potential tree line at c. 750 m (lowering to 200 m in the far north) (Thompson and Brown, 1992), comprises many vegetation types whose relationships

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are not well understood (Thompson et al., 2001). Using the classification of Birks and Ratcliffe (1981), Thompson and Brown (1992) listed 38 communities as occurring in the montane zone, which equated to 32 main types in the National Vegetation Classification of Rodwell (1991, 1992a,b); allowing for NVC sub-types and also main types locally extending into the montane zone, there are at least 40 vegetation types present in the habitat despite its minor extent (3% of the GB land surface (Thompson and Brown, 1992).

The main factors responsible for the differentiation of British montane communities are snow-lie, exposure, drainage, soil wetness and fertility (Rodwell, 1992b; Averis et al., 2004). Grazing pressure is thought responsible for the broad divisions between fern-dominant, heath-dominant and grass/sedge or moss-dominant communities (McVean and Ratcliffe, 1962; Rodwell, 1992b; Averis et al., 2004); increases in pressure progressively cause succession from the first-listed to the latter communities. However, very few such successions have been adequately recorded, hence intuitive comments such as grazing "readily converting" NVC U10 *Carex bigelowii–Racomitrium lanuginosum* moss-heath to "some kind of" NVC H18 *V. myrtillus–Deschampsia flexuosa* heath (Rodwell, 1992b) are in much need of confirmation.

The montane heaths containing *R. lanuginosum* (NVC U9 and U10) are of special nature conservation value because they are the preferred habitat for dotterel (*Eudromias morinellus*) (Galbraith et al., 1993; Thompson and Whitfield, 1993; Thompson et al., 2003). This rare and attractive bird is listed in Annex 1 of the *EC Birds Directive* (EC Directive 79/409/EEC) and has decreased in numbers in Britain between 1987/88 and 1999 (Whitfield, 2002) and also across Europe (Stroud et al., 2004). The birds migrate to the Scottish Highlands for the spring and summer, and nest in the moss heaths; they find their invertebrate food species (e.g., tipulid larvae) within the *Racomitrium* carpets (Thompson and Brown, 1992; Smith et al., 2001). However, these heaths have declined in extent in Britain south of the Scottish Highlands over the past century probably due to heavy grazing by sheep (Thompson et al., 1987). Nitrogen deposition may also be damaging *Racomitrium* (Baddeley et al., 1994; Jones et al., 2002; Pearce and Van der Wal, 2002) since this moss is ectohydric, intercepting and absorbing all the solutes needed for growth from water contacting its leaves and stems. Hence the surviving *Racomitrium*-dominant communities of the Scottish Highlands appear vulnerable to decline because estimated deposition in the montane zone locally reaches levels that appreciably reduce *Racomitrium* shoot growth (Pearce et al., 2003) and quite heavy grazing by sheep occurs on some mountains. Moreover, it has been suggested recently that grazing interacts with nitrogen deposition to substantially increase overall impact, due to colonisation by graminoids, which then attract more herbivore usage and constrain *Racomitrium* by shading (Van der Wal et al., 2003). So to safeguard this valuable habitat and its associated fauna and flora, it is desirable to determine if *Racomitrium* heaths are actually changing in species composition on Highland mountains, and the cause of any changes.

Detailed studies of the composition of a *Racomitrium* heath began in 1990 on Glas Maol, a mountain rising to 1068 m in the eastern Highlands. These studies were triggered by the construction of a fenced skiing corridor and tow in 1986 which crossed ground known to support dotterel. Conservation organisations objected to the development, but the snow fencing was not removed. Instead funding was provided by the Scottish Development Department on behalf of a consortium of stakeholders to monitor the impact of the development. So permanent plots were set up in 1990 to record vegetation and also sheep usage and late snow-lie. The fencing was thought likely to modify the overall sheep usage of the Glas Maol plateau as well as having a more local impact due to the increased shelter and snow-lie immediately adjacent to it. Accordingly, monitoring positions were established at six fixed distances from the fencing in the expectation that the four positions nearest the fence would give an assessment of its direct impact, whereas the two outer positions would assess average sheep use on the plateau and act as controls against which to compare any vegetation trends close to the fence. This pattern of sheep usage was confirmed by six years of monitoring up to 1996, and was reported by Welch and Scott (2001), together with background information on the local sheep-grazing regime.

Now that we have observed successions on Glas Maol for up to 13 years, we judge it is opportune to report on the trends in composition. Our observations provide both a test on whether the declines in *Racomitrium* induced by experimental imposition of increased nitrogen levels (Pearce et al., 2003) are paralleled by declines under equivalent natural deposition in the Highlands montane zone, and also indicate the type of vegetation that develops when grazing pressures on *C. bigelowii–R. lanuginosum* heath are high.

2. Site description

Glas Maol is a flat-topped mountain surrounded almost entirely by steep escarpments and crags. Its summit plateau is extensive, comprising c. 80 ha above the 1000 m contour and a further 20 ha between the 1000 and 940 m contours on a broad ridge that extends NE. The skiing corridor monitored by us runs for 750 m along one side of this ridge, falling from 1020 m at the top of the uplift tow to 940 m at its lower end; a detailed map is provided in Welch and Scott (2001).

The vegetation of the plateau is mostly *C. bigelowii*–*R. lanuginosum* moss heath, and belongs to NVC U10b (Rodwell, 1992b). In some areas *Dicranum fuscescens* and *Polytrichum alpinum* have greater cover than *R. lanuginosum*, but *C. bigelowii* is the main vascular plant and the only other species to have appreciable cover are *V. myrtillus* (very locally) and the grasses *Agrostis capillaris*, *D. flexuosa* and *Festuca ovina*. The *Carex–Polytrichum* patches are more widespread on the higher parts of the plateau, which is consistent with their occurrence in the Cairngorms and central Highlands (Averis et al., 2004). A few patches of *Nardus–Carex* grass heath occur around snow beds and there are some small rock outcrops and areas of scree. Geologically the plateau is mapped as graphitic schist or slate, and all boulders and stones appear to be acidic. The soils are rankers, and are well-drained.

The climate of the Glas Maol plateau is wet and cold, being assigned by Birse (1971) to his hemioceanic, extremely humid, lower oroarctic type. The plateau is very exposed which much reduces snow-lie. The yearly deposition of total nitrogen has been estimated at 12 kg ha^{-1} (Pearce and Van der Wal, 2002).

Glas Maol is grazed by many sheep, small numbers of mountain hares (*Lepus timidus*) and very infrequently by red deer (*Cervus elaphus*). The sheep that pastured on Glas Maol during the study period could have come from three different flocks that grazed in the three main glens radiating from the plateau (Welch and Scott, 2001). However, because sheep access to the plateau is much easier from the north-west and encouraged by an area of grassy vegetation linking to Glen Clunie, the valley running north, it seems almost all the sheep came from that flock. The flock which grazed in Caenlochan Glen running south from Glas Maol was removed at the end of 1995, and the third sheep flock possibly utilising Glas Maol, which grazed in Glen Shee running south west, was removed at the end of 2001. The Glen Clunie flock was wintered on lower ground throughout the study and released into the glen at the end of April each year; it was then only gathered for shearing in July and to be taken off the hill in October. The Glen Shee flock was present throughout the year, but we found usage of the Glas Maol plateau to occur mainly from June to September, with sheep totally absent in winter (Welch and Scott, 2001). All the sheep encountered on Glas Maol belonged to the Scottish Blackface breed.

3. Methods

Monitoring took place on 18 transects extending at right angles from the snow fence. Botanical composition was estimated using point quadrats, and sheep and deer usage from pellet-group counts on fixed plots. For the latter we made visits at three-week intervals from May to September, and cleared counted groups from the plots (Welch and Scott, 2001). Because of fears that dung removal and regular trampling might modify vegetation composition, we kept the positions for botanical analysis separate from the dung plots; the latter were sized 10 × 2 m and had their long axes parallel to the snow fence. The point-quadrat positions were sized 1 × 0.5 m, and grids of 50 points were recorded in each using a frame with 5 vertical pins 10 cm apart placed in 10 positions at 10-cm intervals along the transect line. This gave estimates of cover that could be classified by main species for each position, and also allowed analyses of the spatial characteristics of species behaviour (Scott et al., in prep.). There were six positions on each transect, at 0–1, 2–3, 5–6, 9–10, 19–20 and 39–40 m from the fencing, giving a total of 300 points recorded per transect. At a point, each species touched was counted just once no matter the number of contacts.

Botanical recording was carried out in July yearly from 1990 to 1996 and then in 2002 on 15 transects (1–15) extending across the plateau from the snow fence, and in 1990, 1991, 1993, 1995, 1997 and 2003 on three transects (16–18) extending down from the snow fence towards the escarpment below. Most plant species showed gradual uni-directional changes in cover, so in this paper we use mainly the data collected in 1990, 1996/97 and 2002/03 and combine the plateau and escarpment quadrats; cover estimates for the intervening years were given in Welch and Scott (1995, 1996).

In the first few years after the ski corridor was built the fencing was an effective barrier to the sheep, hindering their grazing of the middle part of the plateau in comparison to the parts nearer the fence ends (Welch and Scott, 2001). Accordingly, botanical trends are reported in this paper for accessible (transects 1–6 and 13–15) and remote (transects 7–12) parts of the plateau and also for positions adjacent (within 10 m) and distant (19–20 and 39–40 m) to the fence. Significant changes over the six- and seven-year periods were assessed by *t* tests on the number of hits out of 50 in the 1 × 0.5 m quadrat positions; we bore in mind that with many species involved multiple testing made chance occurrence of the 0.05 *P* level more likely. Significant spatial differences in single years between plateau zones were found both by *t* tests and by regressions against distance from the fence, again using the 50-pin quadrat totals.

To expose any relationships between vegetation trends, sheep usage, late snow-lie, and altitude (range 940–1024 m) we used logistical regression analysis; although sheep usage and snow-lie were confounded their patterns of incidence differed allowing their impacts to be distinguished. We estimated days of snow-lie in the 1 × 0.5 m recording positions from maps of snow drifts made in May and June each spring from 1991 to 1996. The regression analysis was run primarily on the data set collected between July 1990 and July

1996/97, but because the patterns of sheep usage and snow-lie were believed to have continued similar after 1996, we did further runs of trends to 2002/03 against 1990–96 dung and snow-lie data. We also used the six-year means for dung deposition and snow-lie to create quadrat classes (six for dung, three for snow-lie), and calculated species trends for these classes.

4. Results

4.1. Overall trends in composition

Changes up to 2002/03 at the two distant positions considered to be unaffected by the fence were small (Table 1). In the first six/seven-year period the only significant change in this zone was a decline in *C. bigelowii*, though the sedge remained clearly dominant. By 2002/03 increases in *A. capillaris* and *P. alpinum* apparent in 1996/97 had become sufficiently large to be significant, likewise decreases of *Cetraria islandica* and *Cladonia uncialis* were now significant. The greatest change was a decline in *D. fuscescens* from 1996/97 to 2002/03; the behaviour of this acrocarpous moss is puzzling, and will be discussed later. *R. lanuginosum* although declining modestly and non-significantly to 1996/97 held steady in the next six years, and remained the chief bryophyte.

Adjacent to the snow fence there were highly significant increases of grasses (*A. capillaris*, *D. flexuosa* and *F. ovina*) and highly significant declines of *C. bigelowii* and

Table 1
Species trends (% mean cover) on Glas Maol from 1990 to 2002/03 on ground adjacent (within 15 m) and distant to the snow fencing

	Adjacent to fence			Distant from fence		
	1990	1996/97	2002/03	1990	1996/97	2002/03
Agrostis capillaris	4.0	11.2^{+++}	11.4^{+++}	1.6	2.6	4.7^{+}
Carex bigelowii	62.4	48.1−−−	41.4−−−	66.1	51.2−−−	55.8−−
Deschampsia cespitosa	0.1	0.1	0.0	0.0	0.0	0.0
Deschampsia flexuosa	4.5	6.9^{++}	8.5^{+++}	4.7	5.8	5.9
Festuca ovina	2.2	2.6	5.2^{++}	1.3	1.6	2.8
Galium saxatile	2.5	3.5	5.1^{+}	1.4	0.4	1.7
Luzula spicata	0.0	0.1	0.1	0.0	0.1	0.0
Nardus stricta	0.6	0.7	1.4^{+}	0.6	0.0	0.8
Poa pratensis	0.0	0.0	0.1	0.0	0.0	0.0
Salix herbacea	x	0.0	x	0.0	0.1	0.1
Vaccinium myrtillus	1.2	0.7	0.4	1.0	0.4	0.2
Barbilophozia floerkei	0.0	0.0	0.1	0.0	0.1	0.3
Barbilophozia hatcheri	0.0	0.0	0.2	0.0	0.0	0.0
Dicranum fuscescens	23.5	38.0^{+++}	32.3^{++}	29.9	33.9	17.0−
Dicranella subulata	0.0	0.1	0.1	0.0	0.0	0.0
Diplophyllum albicans	0.0	0.1	0.2	0.0	0.1	0.1
Lophozia ventricosa	0.3	0.4	0.6	0.0	0.1	0.1
Pleurozium schreberi	0.1	0.3	1.5^{+}	0.4	0.7	1.3
Pohlia nutans	0.0	0.0	x	0.0	0.0	0.0
Polytrichum alpinum	8.6	8.4	10.5	9.5	11.2	13.1^{+}
Ptilidium ciliare	0.3	0.8	0.7	1.0	1.1	1.3
Racomitrium lanuginosum	24.6	15.1−−−	13.6−−−	40.2	37.6	37.7
Rhytidiadelphus squarrosus	0.0	0.1	0.1	0.0	0.0	0.0
Scapania sp.	0.0	0.0	0.1	0.0	0.0	0.0
Splachnum sphaericum	x	0.0	0.0	0.0	0.0	0.0
Cetraria islandica	2.7	1.9	1.9	5.2	4.9	3.1−
Cladonia gracilis	0.1	0.2	0.3	0.0	0.9	0.2
Cladonia pyxidata	0.0	0.0	0.1	0.0	0.0	0.0
Cladonia rangiferina	1.9	1.1−	1.1	2.6	1.8	1.6
Cladonia squamosa	0.7	0.2	0.6	0.8	0.6	0.2
Cladonia uncialis	3.0	1.8−	2.1	6.1	4.8	3.1−−
Lecidea granulosa	0.0	0.0	x	0.0	0.0	0.0
Lecidea macrocarpa	x	x	0.1	0.0	0.0	0.1
Peltigera polydactyla	0.0	0.0	0.0	0.0	0.0	0.1
Rock	0.3	0.8	0.7	0.6	0.3	0.3
Late snow-lie (mean days yr^{-1})		6			2	
Sheep usage (pellet gr 100 m^{-2} yr^{-1})		71			36	

Significant changes (*t* tests) compared to 1990 are shown $^{+}$/− ($P < 0.05$), $^{++}$/−− ($P < 0.01$), $^{+++}$/−−− ($P < 0.001$)
x: 0 < mean cover < 0.05.

R. lanuginosum (Table 1). *C. bigelowii* remained the chief graminoid, but *Racomitrium* was overtaken by *D. fuscescens* in cover. *Dicranum* increased greatly up to 1996/97, but then declined appreciably in the next six years, the change being significant ($P < 0.01$). Smaller increases in cover significant at $P < 0.05$ were shown by *Galium saxatile*, *Nardus stricta* and *Pleurozium schreberi*. Most species both in this and the distant zone had very little cover (26 out of the total 34 species never exceeded 5% cover in any analysis), so they were unlikely to show major or significant changes. But by using the combined zones in the *t* tests we found a significant overall decline in *V. myrtillus* ($P < 0.05$), whilst *P. schreberi* had an overall increase significant at $P < 0.01$.

The recording positions adjacent to the fence experienced longer snow-lie and heavier sheep usage than the distant positions in the six years from 1990 to 1996 (Table 1). Late snow-lie and pellet-group totals were positively correlated (Pearson coefficient of r = 0.739), but the incidence patterns of snow-lie and dung deposition differed appreciably (Fig. 1): almost half the recording positions had no snow-lie after the start of May whilst 10 positions had on average 15 or more (maximum 19) days, whereas dung deposition was more evenly spread (Welch and Scott, 2001). For the classes of 36 quadrat positions receiving least, middle and heaviest usage, the mean deposition was, respectively, 24, 48 and 107 pellet groups 100 m^{-2} yr^{-1}.

4.2. Compositional trends for the three positional zones

For three key species we give mean values of % cover for nine sub-zones based on distance from the snow fencing and position (Table 2), and for all species we show significant differences between the plateau zones and also with respect to distance from the snow fencing (Table 3). *A. capillaris* had much greater cover in the accessible plateau zone and the escarpment than in the remote section of the plateau, and increased in both these areas (Table 2, Fig. 1). So throughout the study this grass showed highly significant differences between the plateau zones (Table 3). Significant preference for the accessible part of the plateau was also apparent in *D. flexuosa*, *F. ovina*, *G. saxatile* and the mosses *D. fuscescens* and *P. alpinum*. In contrast *C. bigelowii* had significantly greater cover in the remote than the accessible section of the plateau both in 1990 and 1996/97, but it declined in all sub-zones and especially in the remote zone (from 75% in 1990 to 53% in 2002/03) so the zonal difference was no longer significant in 2002/03.

The accessible plateau zone and the escarpment experienced more prolonged snow-lie and heavier sheep grazing than the remote plateau zone (Table 2). The difference in dung deposition was greatest during the first three summers of the study when the snow fencing was an almost totally effective barrier to the sheep (Welch and Scott, 2001). The difference then declined as the fence structure weakened and the sheep found gaps so they could reach all parts of the plateau from the escarpment without having to walk around the ends of the skiing corridor; the sheep appeared to use the plateau opportunistically since it was frequently less sheltered than the escarpment grasslands. In each of these zones the quadrat positions near the fencing were much more heavily utilised by sheep than the distant positions, the intermediate positions having intermediate usage (Table 2, Fig. 1); shelter was the likely main cause. Late snow-lie was also greater near the fence, but was negligible in the remote plateau zone, never being observed at 26 of its 36 recording positions in the six springs recorded.

Racomitrium lanuginosum declined sharply and significantly near the fencing in all three main zones (Table 2), with cover significantly related to distance from the fence except in 1990 in the remote plateau zone (Table 3). Four lichen species also had significantly less cover near the fencing in some analyses, and three of them lost cover both adjacent and distant to the fence up to 2002/03 (Table 1). *C. bigelowii* also declined near the fence, significantly so in both plateau zones (Table 2). Just two species had significantly greater cover near the fence, *A. capillaris* and *D. fuscescens*, these differences developing during the study.

4.3. Species trends in relation to site factors

Cover trends from 1990 to 1996/97 were positively related to dung deposition in *A. capillaris* ($P < 0.001$ in simple logistic regression) and *G. saxatile* ($P < 0.01$) (Table 4), these species showing greater gains in cover in the usage classes with greater deposition (Table 5). *R. lanuginosum* lost more cover in the heavier-usage classes and showed a highly significant negative relationship with dung density ($P < 0.001$) in simple regression. However *Racomitrium* was also negatively related to snow-lie ($P < 0.001$), and when both factors were included in multiple logistic regression only snow remained as a significant ($P < 0.05$) explanatory variable. With dung deposition and snow-lie being correlated, it would be expected that partitioning of variation between these factors would sometimes much reduce significances in multiple regression. Other species showing significant relationships were *C. bigelowii* (negative $P < 0.05$ to altitude), and *F. ovina* and *C. uncialis* (both negative $P < 0.05$ to snow-lie).

Cover trends from 1996/97 to 2002/03 (Table 1) showed different relationships to the site factors, as would be expected from the general slowing down of changes in this period compared with the first six- or seven-year period. The most clear-cut significant relationship was for *D. fuscescens* (positive $P < 0.01$ with both dung and snow-lie). For *C. islandica* and *C. uncialis* there were apparent positive effects of dung ($P < 0.01$

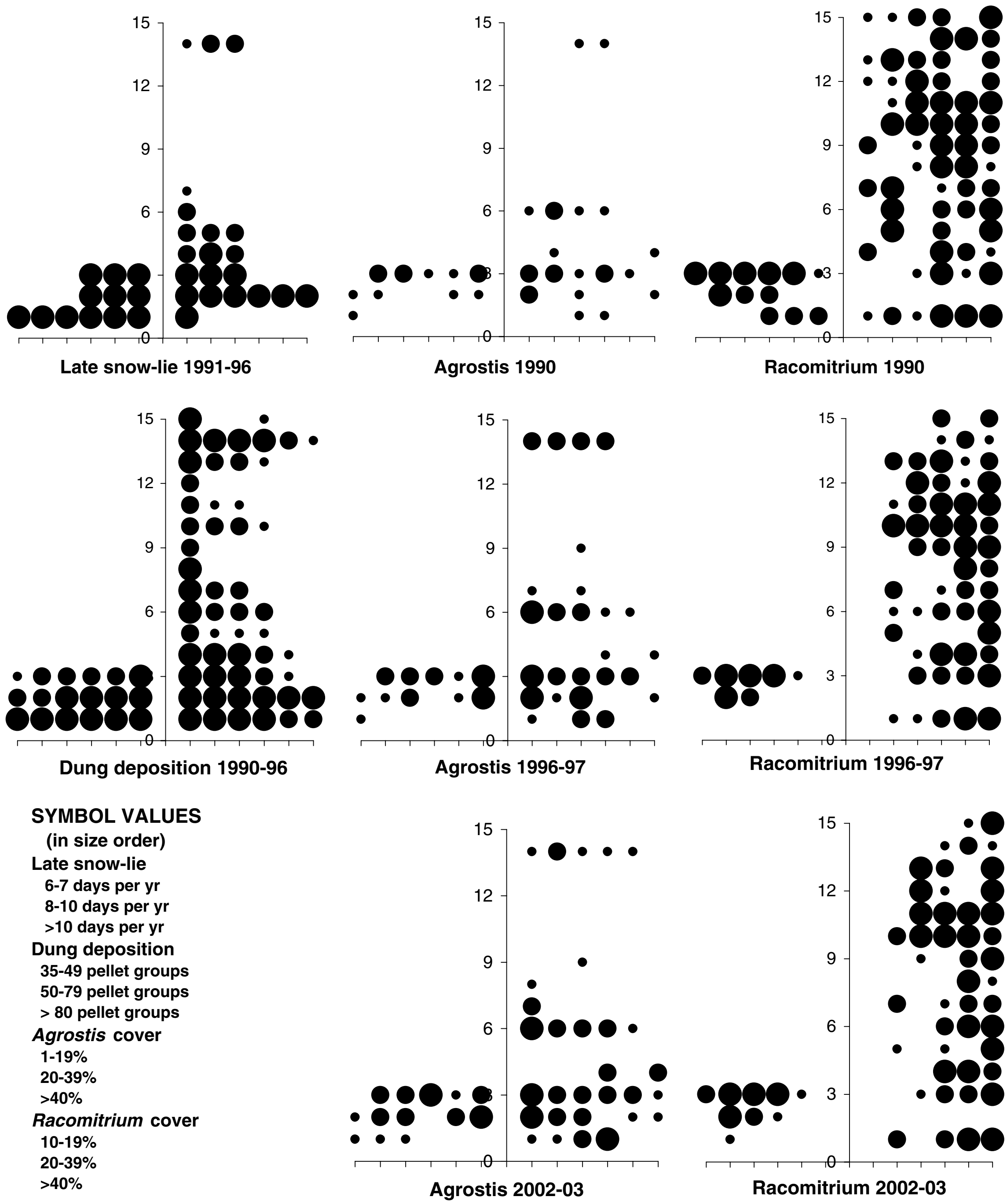

Fig. 1. Spatial pattern in the incidence of late snow-lie and dung deposition and in the cover of *Agrostis capillaris* and *Racomitrium lanuginosum* in the Glas Maol study area. The central vertical line represents the ski corridor, and the symbols to each side give means for plots lying at progressively greater distances (0–1, 2–3, 5–6, 9–10, 19–20 and 39–40 m) from the corridor. The transect numbers run from 1 to 15 (top of figure, right-hand side, plateau plots) and 16 to 18 (top of figure, left-hand side, escarpment plots). Dung deposition units are pellet groups 100 m^{-2} yr^{-1}.

and 0.05, respectively); both resulted from the declines of these species in the distant zone from 1996/97 to 2002/03 not being parallelled by declines in the more heavily grazed adjacent zone (Table 1). Likewise *A. capillaris* had an apparent negative relation to dung for this latter period ($P < 0.01$) due to a greater increase distant to the fence than adjacent to it.

The cover changes for the usage class with heaviest sheep grazing (Table 6) indicate that a state of near-equilibrium was reached by 1996/97, only negligible changes occurring in the next six years. However *C. bigelowii* continued to lose dominance to grasses in this second period since all five grass species increased, albeit modestly: in 2002/03 the combined cover of the five

Table 2
Trends in the mean cover of key species in the three main zones at three distances from the snow fencing (Nr = 0–1 and 2–3 m, Int = 5–6 and 9–10 m, Dist = 19–20 and 39–40 m)

Species	Year	Accessible plateau			Remote plateau			Escarpment		
		Nr	Int	Dist	Nr	Int	Dist	Nr	Int	Dist
Agrostis	1990	6	5	1	0	0	0	8	6	7
	1993	14^{+}	16^{++}	3	0	1	0	13	10	10
	1996/97	17^{+}	15^{++}	2	1	x	0	21	14	9
	2002/03	15^{+}	15^{++}	6^{+}	3	1	0	19	19	12
Carex	1990	62	63	63	72	74	79	45	36	51
	1993	37−−−	47−−	43−−−	54−−−	61−	58−−−	25−	18	41
	1996/97	44−−	53−	46−−−	56−−	61−−	63−−	34	20−	44
	2002/03	40−−−	44−−−	52−	37−−−	53−−−	68−	42	22	44
Racomitrium	1990	16	22	40	17	41	46	20	43	28
	1993	9−	20	37	12−	38	36	12	35	26
	1996/97	6−−	18	38	9−	31−	43	4−	24−−	26
	2002/03	4−	15−	39	6−−	31	39	3−	29−−	32
Late snow-lie (days yr^{-1})	1991–96	9	5	2	2	1	0	12	9	6
Sheep usage (gr 100 m^{-2} yr^{-1})	1990–92	77	50	35	31	17	13	117	88	67
	1993–94	112	70	37	65	42	21	102	71	63
	1995–96	87	62	32	62	48	22	130	100	82

Significant changes compared to 1990 are indicated as in Table 1.

Table 3
Preferences of species as shown by significantly greater cover (a) in the accessible (a/A) or remote (r/R) plateau zones, and (b) near (n/N) or distant (d/D) to the snow fencing

	Zonal preferences on plateau			Distance-from-snow-fence preferences								
				Accessible zone			Remote zone			All zones		
	1990	1996/97	2002/03	1990	1996	2002	1990	1996	2002	1990	1996/97	2002/03
Agrostis capillaris	**A**	**A**	**A**		N						N	n
Carex bigelowii	**R**	R							D			D
Deschampsia flexuosa	a	A	A									
Festuca ovina	a											
Galium saxatile	a											
Dicranum fuscescens		**A**	**A**		N	N	D		N			N
Polytrichum alpinum	**A**	**A**	**A**									
Racomitrium lanuginosum				**D**	**D**	**D**		D	D	**D**	**D**	**D**
Cetraria islandica				D	D			D	d	D	D	D
Cladonia gracilis					**D**						**D**	
Cladonia rangiferina							d	D	d			D
ladonia uncialis					D		D	D		D	**D**	

Significances are shown: $P < 0.05$ lower case; $P < 0.01$ upper case, $P < 0.001$ upper case bold.

grasses (44.2%) exceeded *Carex* cover by 6.3% compared to 1.7% in 1996/97. *D. fuscescens* was the main lower plant, with cover surpassing 60% in four of the 18 quadrats and being less than 20% in only six quadrats.

4.4. Species trends in *Polytrichum alpinum* patches

Quadrats with substantial cover of *P. alpinum* differed negligibly from the remainder in the abundance of other species (Table 7). For no species were there significant differences between *Polytrichum*-rich quadrats and all quadrats, although *R. lanuginosum* was slightly less abundant in the former. Likewise, cover changes from 1990 to 1996/97 were very similar in *Polytrichum*-rich quadrats to all quadrats (Table 7). *Polytrichum* abundance was not related to dung deposition or snow-lie (Table 7); some quadrats with much *Polytrichum* did have long snow-lie but they were balanced by most having no late snow.

5. Discussion

The changes in composition of the *C. bigelowii*–*Racomitrium* heath near the Glas Maol ski corridor occurred rapidly, and there were highly significant spatial

Table 4
Factors significantly accounting for species trends between 1990 and 1996/97 in simple and multiple logistic regression (Dg = dung, Sn = late snow-lie, Alt = altitude)

	Simple regression	Multiple regression
Agrostis capillaris	Dg^{+++}, Sn^{+}	Dg^{+++}
Carex bigelowii	Alt^{-}	
Deschampsia flexuosa		
Festuca ovina	Sn^{-}	Dg^{+}, Sn^{--}
Galium saxatile	Dg^{++}, Sn^{+++}	Alt^{-}, Sn^{++}
Dicranum fuscescens		
Polytrichum alpinum		
Racomitrium lanuginosum	Dg^{---}, Sn^{---}	Sn^{-}
Cetraria islandica		
Cladonia rangiferina		
Cladonia uncialis	Sn^{-}	Sn^{-}

differences in the cover of *A. capillaris*, *C. bigelowii*, *R. lanuginosum* and some lichens by the fourth summer after the erection of the fencing (Table 3, Fig. 1). We presume that in this initial unmonitored period the fencing gave rise to similar patterns of sheep grazing and late snow-lie as we recorded from 1990 to 1992 (Table 2), but we cannot distinguish which factor was most responsible for these early individual changes. For the 1990–96 period of full monitoring we were able to show that *Agrostis* cover was significantly positively related to sheep usage and *Racomitrium* was significantly negatively related to snow-lie (Table 4). These relationships could be expected: *Agrostis* may well be being introduced into the *C. bigelowii–Racomitrium* heath by endozoochoric dispersal (Welch, 1985), the sheep having earlier grazed lower-altitude *Agrostis* grasslands, and the chionophobous behaviour of *R. lanuginosum* is very evident in its distribution within the montane zone (McVean and Ratcliffe, 1962; Rodwell, 1992b; Thompson and Brown, 1992; Averis et al., 2004).

For *Racomitrium*, changes induced by the fencing occurred especially quickly, there being substantial reductions in cover at the two quadrat positions nearest the fence by 1990 in all three main zones (Table 2, Fig. 1), and the relationship with distance was highly significant, much more so than for any other species (Table 3). In the next six years decline continued in the four positions within 10 m of the fencing (Table 2) but the overall rate was slower than before 1990; decline after 1996/97 was slower still, but little cover remained to be lost. Some quadrats in the zone adjacent to the fence experienced negligible late snow-lie, and it is clear that sheep grazing was also causing *Racomitrium* decline (Table 4). For quadrats having 0–1 days yr^{-1} late snow-lie, cover in the adjacent zone (28 plots) was already significantly lower in 1990 ($P < 0.05$) than in the distant zone (31.4% cf. 44.9%) and declined significantly to 24.9% and 20.6% in 1996/97 and 2002/03, respectively, whereas cover fell only to 41.9% in the distant zone (32 plots); dung deposition was significantly greater ($P < 0.01$) for these adjacent plots than the distant ones (43 cf. 28 groups 100 m^{-2} yr^{-1}). Previously, Van der Wal et al. (2003) showed with our data a highly significant negative relationship ($P < 0.001$) between *Racomitrium* cover and sheep usage, but cover trend was regressed only on dung using nine plot classes. Our present findings of a significant negative relationship to snow but not dung when both factors are included in the regressions (Table 4) probably resulted from the pre-1990 *Racomitrium* decline being greater in plots with heavy sheep usage than in plots with prolonged snow-lie, so reducing the scope for further decline (1990 cover 16.8% in the 40 adja-

Table 5
Mean trends in % cover for main species in six usage classes of quadrat, obtained by ranking total pellet-group deposition in the 108 quadrats from 1990 to 1996

	Mean change in % cover in usage classes					
	1	2	3	4	5	6
Agrostis capillaris		*0.0*	0.8	3.9	11.7	14.6
Carex bigelowii	−15.7	−10.8	−9.3	−16.4	−17.3	−17.4
Deschampsia flexuosa	*−0.6*	*0.0*	*−0.1*	*1.6*	5.1	6.1
Festuca ovina	*0.3*	0.2	−0.1	1.6	−0.3	0.6
Galium saxatile		−1.2	−1.2	−0.4	*0.0*	4.8
Dicranum fuscescens	4.0	5.1	17.4	15.7	14.4	9.3
Polytrichum alpinum	*−0.9*	2.4	3.8	−2.1	1.1	−1.7
Racomitrium lanuginosum	−6.3	−1.3	−8.1	−13.1	*−4.0*	*−10.1*
Cetraria islandica	0.0	−0.3	−2.0	−0.7	−1.1	*0.2*
Cladonia rangiferina	−1.3	−1.0	−0.9	*−0.1*	−1.0	*−0.4*
Cladonia uncialis	−2.3	−0.3	−1.1	0.2	−3.1	−0.7
Late snow-lie (days yr^{-1})	0	0.4	2	3	9	12
Sheep usage (pellet gr 100 m^{-2} yr^{-1})	18	29	41	54	82	131

Trends are italicised when 1990 cover means for classes were small, being less than half the overall cover mean for the species, and hence liable to obscure the species reaction pattern.

Table 6
Changes in mean cover (1990 to 1996/97 and 1996/97 to 2002/03) in the usage class having heaviest sheep grazing from 1990 to 1996

Species	Changes in % cover for periods		% Cover in 1996/97
	1990–1996/97	1996/97–2002/03	
Agrostis capillaris	14.6^{++}	0.1	19.6
Carex bigelowii	-17.4^{--}	−0.4	38.3
Deschampsia flexuosa	6.1^{+}	2.0	17.1
Festuca ovina	0.6	2.1	2.7
Galium saxatile	4.8	−0.6	9.3
Nardus stricta	0.4	1.0	0.6
Poa pratensis		0.6	0.0
Vaccinium myrtillus	−1.3	−0.9	1.6
Dicranum fuscescens	9.3	1.3	36.6
Diplophyllum albicans	0.3	0.4	0.3
Lophozia ventricosa	0.6	−0.6	0.8
Pleurozium schreberi		0.4	0.0
Polytrichum alpinum	−1.7	−1.1	9.9
Racomitrium lanuginosum	-10.1^{--}	0.8	2.2
Cetraria islandica	0.2	0.5	1.3
Cladonia rangiferina	−0.4	0.2	0.4
Cladonia uncialis	−0.7	0.8	0.6

Significances are given as in Table 1.
Includes only species with cover >0.4% in an analysis in the usage class.

Table 7
Mean species % cover in 1996/97, and change since 1990, for quadrats (n = 23) with *Polytrichum alpinum* cover >20% in a recording, compared to overall cover and change on Glas Maol

	% Cover in 1996/97		Change since 1990	
	Polytrichum quadrats	All quadrats	*Polytrichum* quadrats	All quadrats
Agrostis capillaris	6.4	8.3	4.3	5.1
Carex bigelowii	50.7	49.2	−14.4	−14.5
Deschampsia flexuosa	7.6	6.6	3.0	2.0
Festuca ovina	2.7	2.3	0.8	0.4
Galium saxatile	2.9	2.5	1.1	0.3
Vaccinium myrtillus		0.6	−1.3	−0.5
Dicranum fuscescens	42.8	36.7	9.7	11.0
Pleurozium schreberi	1.1	0.4	1.0	0.2
Polytrichum alpinum	27.7	9.4	3.6	0.4
Racomitrium lanuginosum	18.8	22.6	−4.2	−7.2
Cetraria islandica	3.1	2.9	0.3	−0.6
Cladonia rangiferina	1.7	1.3	−1.3	−0.8
Cladonia uncialis	3.2	2.8	−1.6	−1.2
Late snow-lie (mean days yr^{-1})	5	4		
Sheep usage (pellet gr 100 $m^{-2}yr^{-1}$)	55	59		

Omits species whose cover did not exceed 1% either in *Polytrichum* quadrats or overall.

cent-zone plots with heaviest dung deposition and 19.1% in the 40 adjacent-zone plots with longest snow-lie). The behaviour of *Racomitrium* is further discussed in Scott et al. (in prep.).

The nature of the vegetation which will develop from montane *C. bigelowii–Racomitrium* heath (NVC U10b) under heavy grazing is indicated by the composition of the 18 quadrats in the heaviest usage class (Table 6). Clearly snow-lie also affected these positions, but with only a mean of 12 days yr^{-1} after the start of May (Table 5) it is unlikely to have much impaired the growth of graminoids. *C. bigelowii* fell sharply in cover up to 1996/97 but then stabilised at 38% (Table 6), so it remained the most prominent species despite being surpassed by the combined cover of grasses. *D. fuscescens* gained in cover (Table 6) whereas *P. alpinum* decreased; *Dicranum* is by far the main lower plant in these *Carex*-grass stands having 38% cover in 2002/03, the only other species with appreciable cover being *P. alpinum*. The prominence of *D. fuscescens* and *P. alpinum* could suggest that these *Carex*-grass stands belong to NVC U8 *C. bigelowii–P. alpinum* sedge-heath (Rodwell, 1992b), but this community occurs in late snow beds with *Deschampsia cespitosa* and *Salix herbacea* prominent, and until a more-detailed classification of montane vegetation is developed these stands are best placed in NVC U10a; Thompson and Baddeley (1991) described similar stands as NVC U10a (some grasses) and U10a (mostly grasses).

The *P. alpinum* stands (Table 7) are also distinct from NVC U8, and lacked its species characteristic of wet ground. Although overall the quadrats only had an average incidence of late snow-lie (Table 7), they comprised some with no late snow and some with much late snow. It seems that other site factors as well as snow promote the growth of *P. alpinum*, since the cover increases which led to its significant change from 1990 to 2002/03 (Table 1) occurred mostly in quadrats with no observed late snow-lie. Similarly the behaviour of *D. fuscescens* is hard to explain beyond recognising that it benefits when competition from *R. lanuginosum* is reduced. Some of its increase in the zone adjacent the fencing from 1990 to 1996/97 (Table 1) was into ground made bare by the trampling and lying of sheep, but subsequently other species including grasses appeared and overgrew it. The big decline of *Dicranum* in the distant zone from 1996/97 to 2002/03 was not caused by increased competition from *Racomitrium* which throughout the study overtopped *Dicranum* here; the *Racomitrium* carpet seemed no deeper in 2002/03 than 1996/97, and perhaps warmer, drier summers affected *Dicranum*. Rodwell (1992b) commented that the patchy abundance of *D. fuscescens* and, to a lesser extent, *P. alpinum* within stands of NVC U10 occurred "often where there are slight depressions... which catch and hold a little snow in winter"; we concur with this opinion.

Compositional trends in the distant zone not evidently influenced by the ski fence are important in judging whether *C. bigelowii–Racomitrium* moss heath is currently being modified by nitrogen deposition or grazing pressures, with the implications that any loss of the *Racomitrium* carpet would have for the dotterel. Changes from 1990 to 2002/03 were appreciable (Table 1) particularly in lichens, which lost almost half their cover. This decrease and the significant decline of *C. bigelowii* is more likely a response to sheep grazing than to nitrogen deposition. But *Carex* still remained the main dominant and *Racomitrium* lost only 2.5% cover from its initial 40.2% in 1990. Essentially the slightly-modified community still provides the features necessary for dotterel (Nethersole-Thompson, 1973; Thompson and Whitfield, 1993; Thompson et al., 2003). Grasses did increase somewhat up to 2002/03 (Table 1), but their total cover is similar to levels previously reported in the community (McVean and Ratcliffe, 1962; Rodwell, 1992b). But compared to these earlier descriptions, the Glas Maol *C. bigelowii–Racomitrium* was very lacking in *V. myrtillus*, and further loss occurred during the study period, whereas protection in cages allowed strong growth (Van der Wal, pers. comm.). Hence we regard *V. myrtillus* as being very sensitive to grazing at high altitudes, and reject Rodwell's hypothesis (1992b) that grazing readily converts NVC U10 to NVC H18 *Vaccinium–Deschampsia flexuosa* heath.

From the behaviour of *R. lanuginosum* at the intermediate distance to the snow fence (Table 2), we can make judgements on the threshold levels of sheep grazing that would cause serious loss of cover and threaten the dotterel. Dung deposition of 45 groups 100 m^{-2} yr^{-1} was associated with *Racomitrium* cover falling to 31%, whereas distant to the fence where cover held steady there was 36 m^{-2} yr^{-1} deposition. Hence, at most an increase of 25% in sheep usage could be tolerated under present conditions on Glas Maol. To date, dotterel have continued to nest on Glas Maol in this zone distant to the fence, but if the spread of grasses leads to greater grazing and then decline of *Racomitrium*, it will be interesting to see if dotterel abandon this zone in line with our predictions.

Future work to disentangle the impacts of sheep grazing, snow-lie and nitrogen deposition is desirable but partly dependent on the state of the snow fence. Despite repairs in summer 2003, the palings and posts are now fragile, and some lengths collapsed in early 2004. With renewal of the fence doubtful due to cost, the extra impact from sheltering sheep may end; whether botanical trends then reverse will give more insight on the importance of grazing and snow-lie in controlling composition. Sheep usage along the fence was recorded in summer 2004, and has been monitored at plots given nitrogen treatments (Pearce and Van der Wal, 2002). For amenity, conservation and logistic reasons the latter plots are small, and if skiing use ceased a larger-scale experiment could be set up along the corridor with grazing/no grazing and nitrogen treatments imposed on selected plant communities.

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