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Red deer impacts on the montane *Racomitrium lanuginosum* moss-heath community in north-west Scotland

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Background: The effect of sheep grazing on the internationally important moss-heath community of the British uplands has been well studied but less is known about the impact of red deer (*Cervus elaphus*).
Aim: To compare the impact of different densities of red deer on bryophytes and lichens associated with moss-heath vegetation at Beinn Eighe National Nature Reserve (low deer density) and a traditional sporting estate at Letterewe (with higher deer density), Scotland.
Methods: Suitable pairs of summit study sites were selected at random, and species cover data were collected from thirty 1-m^2 quadrats at each location. The dung pellet group count method was used to estimate red deer usage. Generalised linear models were fitted to the data.
Results: Mean graminoid cover was significantly higher in two of the Letterewe study sites compared with their Beinn Eighe counterparts. Bryophyte cover and height in general matched the pattern for *Racomitrium lanuginosum* in that they were not significantly different between any of the study site pairings.
Conclusions: Despite differences in mean deer density between the Beinn Eighe and Letterewe properties as a whole, red deer numbers actually using the exposed summit moss-heath vegetation were estimated to be very low. Therefore, bryophyte cover within the Letterewe summit study sites was not significantly different from that at Beinn Eighe.

Keywords: Beinn Eighe; bryophyte; *Cervus elaphus*; graminoid; lichen; sheep grazing; summit vegetation

Introduction

Carex bigelowii–Racomitrium lanuginosum moss-heath community (U10, as described in the National Vegetation Classification after Rodwell 1992) is of international importance (Averis et al. 2004). This climax vegetation occurs on high and exposed summits throughout Britain, most frequently and extensively in Scotland (Averis et al. 2004), but is threatened in some areas by high densities of herbivores (Thompson et al. 1987, 2001; Ratcliffe and Thompson 1988; Rodwell 1992; Thompson and Brown 1992; Thompson et al. 2001; Averis et al. 2004). Previous research on the impacts of grazing on the U10 moss-heath vegetation of summits has largely focused on the effects of sheep grazing (Van der Wal et al. 2003; Britton et al. 2005; Welch et al. 2005; Scott et al. 2007; Pearce et al. 2010). In a study quantifying the grazing impacts associated with different herbivores on open-hill habitats in upland Scotland, deer population density was not linked to any impact on alpine grassland (Albon et al. 2007). Albon et al. (2007) scored impacts on a 5-point scale based on a range of field indicators, such as presence of dung, physical damage, sward height and structure, biomass removal and selectivity of grazing. However, no consideration was given to the implications for plant diversity/species richness, habitat condition and the consequences for biodiversity in general (Albon et al. 2007) and to bryophytes and lichens in particular.

This study assessed the impact of red deer (*Cervus elaphus*) on the bryophytes and terricolous lichens associated with the U10 moss-heath community on two neighbouring estates near Loch Maree in the north-west Highlands, Scotland. Letterewe is a private estate managed primarily for sporting interests, while Beinn Eighe National Nature Reserve (NNR) is managed for conservation by Scottish Natural Heritage. Differences in culling regimes have resulted in mean deer density being three times higher at Letterewe (ca. 9 red deer km^{-2}) compared with Beinn Eighe (ca. ≤3 red deer km^{-2}). This study comes at a time when numbers of red deer in Scotland have reached an estimated 360,000–400,000 (Edwards and Kenyon 2013) and knowledge of their impact on summit vegetation is required to assist with management decisions.

Graminoids and grazing-resistant dicotyledons are favoured at the expense of bryophytes and lichens as a result of heavy grazing on the U10 moss-heath community (Rodwell 1992; Averis et al. 2004). Van der Wal (2006) cited evidence for three mechanisms by which herbivores might promote graminoid growth in moss-dominated ecosystems: (1) graminoids are tolerant to grazing since they grow back quickly from a basal meristem; (2) urine and

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faecal deposition increase soil nutrient status that favours the growth of grasses; and (3) disturbance through trampling of the moss layer allows soils to warm up more quickly, enabling more efficient nutrient uptake by grasses. It is argued that moss-dominated ecosystems are driven towards those dominated by graminoids through all three mechanisms operating collectively (Van der Wal and Brooker 2004). Degradation of the U10 moss-heath community was compounded by an interaction between sheep grazing and atmospheric nitrogen deposition in a Scottish alpine ecosystem (Van der Wal et al. 2003). Nitrogen deposition has a direct toxic effect on *R. lanuginosum* and a fertilisation effect on graminoid growth whereby graminoids shade out the moss layer and attract herbivores, resulting in further damage to the moss layer by trampling (Van der Wal et al. 2003). Britton et al. (2005) presented evidence from the Carneddau plateau in North Wales that matched the decline in *Racomitrium* heaths to an increase in atmospheric nitrogen deposition and an increase in sheep numbers over a period of 40 years. The improved shelter provided by the lee side of a 20-year-old snow fence in U10 vegetation at Glas Maol, Scotland, encouraged a greater usage by sheep which has been linked to an increase in grass cover and subsequent reduction in *R. lanuginosum* (Welch et al. 2005; Scott et al. 2007). However, contact with pollutants was prolonged at this site by the increased snow-lie and this has resulted in high levels of nitrogen deposition during snow melt which may have exacerbated the loss of *R. lanuginosum* (Scott et al. 2007). Britton et al. (2009) recognised that change in species composition of these communities was the result of interaction among many driving forces.

Loch Maree is within an area of low nitrogen-loading according to figures cited in Mitchell et al. (2005), and there has been no grazing by sheep at Letterewe or Beinn Eighe for over 30 years (Averis and Averis 1998; Milner et al. 2002). Therefore, the main driver of change that has differed between the two estates is red deer density (assuming that there is little difference in climate on either side of Loch Maree). It was hypothesised that higher numbers of red deer on the Letterewe estate would be affecting bryophyte and lichen communities, associated with the U10 moss-heath community, to a greater extent than in comparable habitats in the Beinn Eighe NNR, through their grazing, trampling and dunging activity.

Materials and methods

Site description

Beinn Eighe NNR is located south of Loch Maree, Wester Ross, Scotland (Latitude 57° N 36' and Longitude 5° W 22'), and is managed by Scottish Natural Heritage for its conservation interest. A sustained programme of intensive culling at Beinn Eighe since the early 1990s has reduced numbers of red deer to a level that is encouraging natural regeneration of native pine woodland (E. Maclean, personal communication 2013). For this to occur, red deer density must be ca. ≤3 km^{-2} (similar to the numbers reported for the beginning of the twenty-first century) according to Johnston and Balharry (2001). Letterewe estate is located north of Loch Maree, and there has been a mean annual density of ca. 8–14.5 red deer km^{-2} since 2001 (Milner et al. 2002; S. Miller, personal communication 2011). Caution is advised regarding these estimates of deer density since obtaining an accurate count of red deer in rugged terrain is difficult (Daniels 2006).

The Loch Maree area is subject to an oceanic climate with temperatures in the range 3–4°C (mean winter) and 11–12°C (mean summer) and receives ≥1 mm rain for >220 wet days per year based on figures for the 30-year period 1981–2010 (Meteorological Office 2013). Mean nitrogen deposition on the summits in Beinn Eighe NNR was higher at 8.0 kg ha^{-1} $year^{-1}$ compared with values between 5.2 and 6.3 kg ha^{-1} $year^{-1}$ given for the Letterewe summits (Air Pollution Information System 2013). These figures are based on averages for the 3-year period 2009–2011. They contain large uncertainties and have only a 5-km resolution (Air Pollution Information System 2013). The siliceous rock known as hornblende schist (British Geological Survey 1962) comprises the bedrock of the main summits of the Letterewe Forest study area (Beinn Airigh Charr, British Grid Reference NG9376; Beinn Lair, NG9873; and Sgùrr Dubh, NG9872). Of the comparable field sites at Beinn Eighe, the summit of Meall a' Ghiuthais (NG9763) is made up of Torridonian sandstone, and Còinneach Mhòr (NG9560) is underlain by quartzite.

The gently sloping and north-west face of the Beinn Lair (859 m) study site was compared to similar terrain on Meall a' Ghiuthais (887 m). The summit plateau study sites of Sgùrr Dubh (808 m) and Meall a' Ghiuthais were also paired. The U10 moss-heath community is very exposed at these locations and the vegetation is sparse, amid wind-blasted ground littered with rocks. The species-poor variant of the U10c *Silene acaulis* sub-community (Rodwell 1992) describes this vegetation although the characteristic lichens suggestive of the U10b typical sub-community were frequent. The U10b typical sub-community (Rodwell 1992) was well represented on the south-east-facing slopes of Beinn Airigh Charr (792 m) and Còinneach Mhòr (956 m), which comprise another pair of study sites. The vegetation on these summits was dominated by a thick blanket of *R. lanuginosum*, and characteristic lichens such as *Cladonia uncialis* ssp. *biuncialis* and *Cetraria islandica* were frequent.

Sampling procedure

Five potential alpine study sites of 20,000 m^2 area were identified at Letterewe and Beinn Eighe. These were paired as far as possible on the basis of similar gradient, aspect, altitude and sub-community of the U10 *C. bigelowii–R. lanuginosum* moss-heath (following a site visit). Three pairs of study sites were then selected at random from the five potential pairings. Thirty 1-m^2

quadrats were placed by means of random grid references at each study site. A GARMIN eTrex Legend GPS device was used to locate quadrat positions. A 7 m × 7 m sample plot was marked out with tape measures, taking each of the 180 1-m^2 quadrat positions as the centre. The red deer dung pellet groups inside each of these 7 m × 7 m sample plots were counted, to gain an index of mean red deer usage within each of the six summit study sites, in line with a similar method described by Mayle et al. (1999). An estimate of red deer density could then be calculated. Fieldwork was carried out in early summer 2012.

A grid with squares of 0.01 m^2 in area was used to determine visually the percentage cover of each bryophyte and lichen taxon within each 1-m^2 quadrat. Total graminoid cover and the percentage rock/bare ground cover within each 1-m^2 quadrat were also estimated. Mean vegetation height inside each quadrat was determined from 10 measurements with a metre rule at regular intervals along a predetermined diagonal. Mean bryophyte height was established in a similar fashion.

Nomenclature follows Hill et al. (2008) for bryophytes, Macdonald and Barrett (1993) for mammals, Smith et al. (2009) for lichens and Stace (2010) for vascular plants.

Data analysis

Deer density for each 7 m × 7 m sample plot was determined using the dung pellet group count–deer density graph shown in De Nahlik (1992). Defaecation rate was assumed to be 25 dung pellet groups per day, and a decay rate of between 6 and 12 months (based on observations of dung on the summit of Beinn Lair) gave an estimate of deer numbers using each summit. Bryophyte and lichen dominance was calculated by dividing the cover of the bryophyte or lichen with the greatest cover within a quadrat by the total bryophyte or lichen cover for that quadrat. The Shannon diversity index was used to calculate species diversity for each quadrat, because this takes into account the abundance of each species present and provides information concerning the evenness of species composition rather than just reporting species richness alone. Arcsine transformation of the percentage cover data was carried out prior to fitting a simple linear model to the data (units in radians) in R version 2.11.1 (R Development Team 2010) using location as the explanatory variable. Each summit pairing was analysed separately (making use of all 30 pseudo-replicates within each study site, on the understanding that conclusions are only relevant to that pair of study sites) and genuine replication came only from carrying out the procedure at three pairs of study sites. For each summit pairing, the null hypothesis under test was for no significant difference in mean bryophyte cover, lichen cover and graminoid cover between Letterewe and Beinn Eighe. Bryophyte and lichen dominance and Shannon diversity, deer density and bryophyte and sward height were also analysed using a simple linear model for each summit pairing. A generalised linear model was used to analyse bryophyte and lichen species richness for each summit pairing. The non-constant variance associated with count data was dealt with by specifying a Poisson error structure, and the log-link function was used to transform the response variable.

Results

Mean red deer density was not consistently higher at each of the Letterewe summit study sites compared with those on Beinn Eighe as might have been expected. There was a significantly higher red deer density (P = 0.009) in the summit study site at Sgùrr Dubh, Letterewe (0.6 km^{-2}), compared with the plateau study site at Meall a' Ghiuthais, Beinn Eighe (none), and the standard error (SE) of the difference between means was ± 0.2. However, mean red deer density was not significantly different (P = 1.000) between the north-west-facing summit study sites of Beinn Lair, Letterewe (0.1 km^{-2}), and Meall a' Ghiuthais, Beinn Eighe (0.1 km^{-2}), with SE ±0.1. There was an estimated mean of 1.4 red deer km^{-2} at Beinn Airigh Charr (Letterewe) compared with 2.8 red deer km^{-2} in the study site at Còinneach Mhòr (Beinn Eighe). This was not statistically significant (P = 0.060) because the SE ±0.73 was high. These estimates of red deer density have poor precision since far fewer than 100 faecal pellet groups were counted in total from plots within each study site (Mayle et al. 1999).

Mean graminoid cover was generally higher at Letterewe compared with Beinn Eighe – significantly so for the Beinn Lair (P < 0.001) and Sgùrr Dubh (P = 0.025) summits of the Letterewe study area compared with their Meall a' Ghiuthais (Beinn Eighe) counterparts (Figure 1a). Mean sward height was significantly higher in the Beinn Eighe study sites on the north-west face of Meall a' Ghiuthais (P < 0.001) and the south-east face of Còinneach Mhòr (P = 0.001) compared with the corresponding Letterewe study sites (Figure 1b). There was an enforced delay of 1 week in surveying the north-west-facing study site of Meall a' Ghiuthais (Beinn Eighe) after Beinn Lair (Letterewe). The Còinneach Mhòr (Beinn Eighe) study site was also visited 1 week after its counterpart at Beinn Airigh Charr (Letterewe) had been sampled. Therefore, the increased growing time also confounds these data. There was no significant difference in mean sward height between the Sgùrr Dubh (Letterewe) and Meall a' Ghiuthais (Beinn Eighe) plateau study sites where it had been possible to carry out fieldwork on consecutive days.

There was a significantly greater mean lichen cover for two of the Letterewe summits – Beinn Lair (P = 0.014) and Sgùrr Dubh (P < 0.001) – compared with their Beinn Eighe counterparts, but there was no significant difference between the Beinn Airigh Charr (Letterewe) and Còinneach Mhòr (Beinn Eighe) study sites (Figure 1c). No general pattern for Beinn Eighe and Letterewe was seen in the mean log lichen species richness data (Figure 1d). There was a significantly higher (P = 0.002)

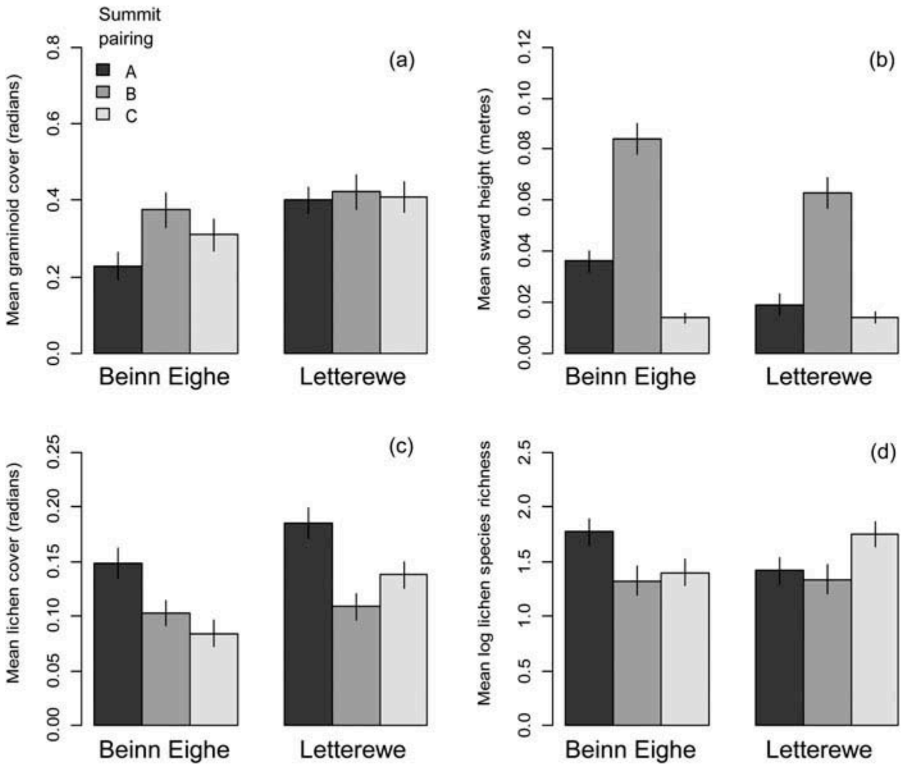

Figure 1. A comparison of the mean arcsine graminoid cover (a), mean sward height (b), mean lichen cover (c) and mean log lichen species richness (d) between pairs of summit study sites at Beinn Eighe (low red deer density site) and Letterewe (high deer density site), western Scottish Highlands, following analysis of data in a linear model (n = 60). The standard error is for the difference between means.

Notes: Summit pairing A – Meall a' Ghiuthais and Beinn Lair (north-west-facing aspect).
Summit pairing B – Còinneach Mhòr and Beinn Airigh Charr (south-east-facing aspect).
Summit pairing C – Meall a' Ghiuthais and Sgùrr Dubh (summit plateau).

mean log lichen species richness for the north-west-facing summit study site of Meall a' Ghiuthais (Beinn Eighe) compared with Beinn Lair (Letterewe). However, mean log lichen species richness was significantly higher (P = 0.004) at Sgùrr Dubh (Letterewe) compared with the plateau study site at Meall a' Ghiuthais (Beinn Eighe). The Beinn Airigh Charr (Letterewe) and Còinneach Mhòr (Beinn Eighe) study sites shared almost identical mean log lichen species richness values, with no significant difference. Other than a significantly higher mean lichen diversity (P < 0.001) and lower mean lichen dominance (P < 0.001) in the north-west-facing summit study site of Meall a' Ghiuthais (Beinn Eighe) compared with Beinn Lair (Letterewe), there were no other significant differences in these response variables between the Beinn Eighe and Letterewe summit pairings (Table 1).

Table 1. Mean values of lichen diversity and dominance between comparable summit study sites at Beinn Eighe (low deer density site) and Letterewe (high deer density site), western Scottish Highlands, following analysis of data in a linear model (n = 60).

	Mean values				
Response variables	Difference	Beinn Eighe	Letterewe	Standard error	*P*-value
Summit pairing A					
Lichen diversity	−	1.438	0.921	0.096	**<0.001**
Lichen dominance	+	0.413	0.648	0.039	**<0.001**
Summit pairing B					
Lichen diversity	+	0.966	0.978	0.139	0.930
Lichen dominance	−	0.603	0.571	0.071	0.651
Summit pairing C					
Lichen diversity	+	1.106	1.303	0.133	0.145
Lichen dominance	+	0.456	0.504	0.057	0.401

Notes: Summit pairing A – Meall a' Ghiuthais and Beinn Lair (north-west-facing aspect).
Summit pairing B – Còinneach Mhòr and Beinn Airigh Charr (south-east-facing aspect).
Summit pairing C – Meall a' Ghiuthais and Sgùrr Dubh (summit plateau).
The standard error is for the difference between means. Significant P-values are given in boldface.

Table 2. Mean values of bryophyte variables between comparable summit study sites at Beinn Eighe (low deer density site) and Letterewe (high deer density site), western Scottish Highlands, following analysis of data in a linear model (n = 60).

	Mean values				
Response variables	Difference	Beinn Eighe	Letterewe	Standard error	*P*-value
Summit pairing A					
Bryophyte cover (radians)	−	0.594	0.491	0.075	0.172
Bryophyte diversity	+	0.328	0.360	0.071	0.661
Bryophyte dominance	−	0.914	0.908	0.025	0.802
Log bryophyte species richness	−	1.60	1.548	0.483	0.629
Bryophyte height (metres)	−	0.014	0.011	0.003	0.327
Summit pairing B					
Bryophyte cover (radians)	−	1.053	1.026	0.064	0.671
Bryophyte diversity	−	0.332	0.131	0.062	**0.002**
Bryophyte dominance	+	0.919	0.969	0.018	**0.009**
Log bryophyte species richness	−	1.787	1.378	0.118	**<0.001**
Bryophyte height (metres)	−	0.040	0.037	0.004	0.452
Summit pairing C					
Bryophyte cover (radians)	−	0.471	0.418	0.059	0.369
Bryophyte diversity	−	0.279	0.250	0.058	0.613
Bryophyte dominance	−	0.926	0.934	0.019	0.641
Log bryophyte species richness	−	1.184	1.289	0.139	0.445
Bryophyte height (metres)	−	0.007	0.006	0.001	0.718

Notes: Summit pairing A – Meall a' Ghiuthais and Beinn Lair (north-west-facing aspect).
Summit pairing B – Còinneach Mhòr and Beinn Airigh Charr (south-east-facing aspect).
Summit pairing C – Meall a' Ghiuthais and Sgùrr Dubh (summit plateau).
The standard error is for the difference between means. Significant *P*-values are given in boldface.

There was no significant difference in mean bryophyte height or cover between any of the Beinn Eighe and Letterewe study sites (Table 2). Differences in geology and elevation might account for the significantly greater bryophyte diversity and species richness (but lower bryophyte dominance) within the Còinneach Mhòr (Beinn Eighe) study site compared with that at Letterewe in the Beinn Airigh Charr study site (Table 2). The rock has weathered on the summit of Còinneach Mhòr (Beinn Eighe) to a particle size better suited for moisture retention and the higher elevation is likely to receive increased precipitation. This may have been beneficial to moss species such as *Hypnum callichroum, Rhytidiadelphus loreus* and *Hylocomium splendens* (see Appendix), which are less tolerant of desiccation compared with *R. lanuginosum*. There was no significant difference in bryophyte diversity, dominance or species richness between the other two summit pairs (Table 2). Rock/bare ground cover was also not significantly different between any of the summit pairings.

Racomitrium lanuginosum was the dominant bryophyte within quadrats at all six locations and there was no significant difference in the cover of this moss between any pairs of the two study sites (Table 3). The mean cover of *C. islandica* was not significantly different between any of the Beinn Eighe and Letterewe summit pairings. Some lichen species such as *Ochrolechia tartarea* and *Stereocaulon vesuvianum* were much more abundant within the Letterewe summit study sites at Beinn Lair and Sgùrr Dubh compared with those at Beinn Eighe (Table 3). However, this is more likely a response to differences in geology rather than anything to do with red deer numbers. For example, *S. vesuvianum* favours siliceous rock with a high metal content (Dobson 2011). Other lichens associated with moss-heath vegetation, such as *Alectoria nigricans* and *Thamnolia vermicularis*, were too uncommon to permit analysis.

Discussion

The estimated mean red deer density for the whole property was three times higher at Letterewe than at Beinn Eighe, but there appeared to be twice as many deer using the Còinneach Mhòr (Beinn Eighe) study site compared with the numbers on Beinn Airigh Charr (Letterewe). This demonstrates the difficulty in managing numbers of red deer since favoured sites will have a high localised density of this herbivore, almost independent of the overall average density. The cover and depth of *R. lanuginosum* in the summit moss-heath vegetation were not affected by these differences in deer usage. However, estimates of mean red deer density (based on the standing crop of dung pellet groups) were found to be very low within the study sites. Dung counts carried out in early summer (to avoid disruption to stalking later in the season) are likely to underestimate the numbers of red deer using the summit, because these herbivores will have been absent throughout the winter period and dung from the summer may have already disintegrated. Milner et al. (2002) described patterns of habitat use by red deer at Letterewe by counting dung in different habitats throughout the seasons. Red deer were found to generally avoid north-west-facing slopes

Table 3. Mean arcsine cover values of selected bryophyte and lichen species between comparable summit study sites at Beinn Eighe (low deer density site) and Letterewe (high deer density site), western Scottish Highlands, following analysis of data in a linear model (n = 60).

	Mean arcsine cover (radians)				
Species	Difference	Beinn Eighe	Letterewe	Standard error	*P*-value
Summit pairing A					
Cetraria islandica	−	0.030	0.022	0.009	0.335
Cladonia uncialis ssp. *biuncialis*	−	0.052 (0.3%)	0.029 (0.1%)	0.009	**0.009**
Ochrolechia tartarea	+	0.026 (<0.1%)	0.071 (0.5%)	0.013	**0.001**
Racomitrium lanuginosum	−	0.652	0.543	0.078	0.167
Stereocaulon vesuvianum	+	0.013 (<0.1%)	0.134 (1.7%)	0.012	**<0.001**
Summit pairing B					
C. islandica	−	0.048	0.047	0.008	0.910
C. uncialis ssp. *biuncialis*	−	0.040	0.033	0.006	0.223
R. lanuginosum	+	1.179	1.205	0.066	0.691
Summit pairing C					
C. islandica	−	0.007	0.004	0.003	0.321
C. uncialis ssp. *biuncialis*	−	0.025	0.023	0.006	0.711
O. tartarea	+	0.008 (<0.1%)	0.073 (0.5%)	0.007	<**0.001**
R. lanuginosum	−	0.466	0.414	0.058	0.378
S. vesuvianum	+	0.000 (0%)	0.062 (0.4%)	0.009	**<0.001**

Notes: Summit pairing A – Meall a' Ghiuthais and Beinn Lair (north-west-facing aspect).
Summit pairing B – Còinneach Mhòr and Beinn Airigh Charr (south-east-facing aspect).
Summit pairing C – Meall a' Ghiuthais and Sgùrr Dubh (summit plateau).
The standard error is for the difference between means. Significant *p*-values are given in boldface (percentage cover values are in parenthesis).

and open summits despite heavily using other high-altitude habitats at Letterewe in the summer and autumn (Milner et al. 2002). Therefore, impacts were unsurprisingly minimal on the exposed summit heath vegetation compared with the effects of very high densities of sheep seen elsewhere where grazing and nitrogen deposition have compounded the degradation of the U10 moss-heath community (Van der Wal et al. 2003; Britton et al. 2005). The stocking ratio of sheep was much higher in these studies; for example, numbers of sheep peaked at the equivalent of 500–600 km^{-2} on the Carneddau early in the twenty-first century (personal observation by B. Jones cited in Pearce et al. 2010). Nonetheless, the Beinn Lair and Sgùrr Dubh study sites had a significantly greater graminoid cover than their Beinn Eighe counterparts, which is consistent with the mechanisms described in Van der Wal and Brooker (2004) and Van der Wal (2006).

Jones et al. (2002) showed that growth of *R. lanuginosum* generally benefitted from the presence of *Festuca ovina* in laboratory experiments looking at the interaction with different nitrogen loads. The increased humidity around the grass was thought to increase the amount of time available for photosynthesis in this moss (Jones et al. 2002). This could explain why *R. lanuginosum* cover had not diminished within the summit study sites at Letterewe despite the significantly higher graminoid cover. However, Jones et al. (2002) cautioned that their study was short term and only dealt with small quantities of moss in a laboratory situation. Other studies have shown that graminoids outcompete *R. lanuginosum* within moss-heath vegetation as a result of grazing and nitrogen enrichment (Pearce and Van der Wal 2002; Van der Wal et al. 2003). The high wind speeds associated with some open summits are thought to suppress the colonisation of these areas by higher plants but are not disadvantageous to bryophytes, which exist in an altogether different microclimate (Britton et al. 2009). This is another possible explanation for why *R. lanuginosum* has not been replaced by graminoids in the most exposed study sites at Letterewe.

Degraded areas of summit moss-heath are characterised by a low and fragmentary cover of *R. lanuginosum* and plenty of bare ground brought about by trampling (Britton et al. 2005; Pearce et al. 2010). The U10b vegetation at Còinneach Mhòr (Beinn Eighe) and Beinn Airigh Charr (Letterewe) was dominated by a thick blanket of *R. lanuginosum*, and there was no evidence of trampling damage in the study sites. This is encouraging since *R. lanuginosum* is thought to have a positive density dependence for growth (Pearce et al. 2010). Photosynthesis can only occur when the moss is wet, so being part of a continuous moss carpet reduces desiccation and permits a longer growing period (Pearce et al. 2010). The vegetation at Beinn Lair, Meall a' Ghiuthais and Sgùrr Dubh was of the open, stonier U10c *Silene* sub-community with scattered and thin cover of *R. lanuginosum*. This is a result of wind exposure, freeze–thaw weathering and solifluction rather than red deer usage. Rodwell (1992) described how the moss-heath community was particularly diminished where exposure was the most extreme, over the high plateaux in the north-west Highlands. Damage to fruticose lichens such as *S. vesuvianum* would have been expected had there been regular trampling, but this was not observed.

Stereocaulon vesuvianum, O. tartarea and *Sphaerophorus globosus* contributed to the greater total lichen cover at the Letterewe study sites Beinn Lair and Sgùrr Dubh. The presence of these species may have reduced the available space for other terricolous lichens. This might account for the reduced lichen species richness and significantly lower cover of *C. uncialis* ssp. *biuncialis* at Beinn Lair. The difference in estimated density of red deer at Letterewe and Beinn Eighe was not thought to be responsible for these findings. This is supported by the lack of significant difference in any of the measures of lichen diversity between the Còinneach Mhòr (Beinn Eighe) and Beinn Airigh Charr (Letterewe) study sites.

Britton et al. (2005) and Pearce et al. (2010) made use of natural obstacles on the Carneddau plateau, such as an area of blocky scree that deterred sheep from grazing areas of moss-heath, to compare similar habitat in the same proximity that was accessible to sheep. This was not possible at Beinn Eighe and Letterewe. Therefore, despite efforts to match up comparable sites in terms of their aspect, gradient and vegetation, it is accepted that confounding factors, such as differences in geology, latitude, elevation, nitrogen loading and climate, between the Beinn Eighe and Letterewe summits remain. Suitable sites with similar characteristics were limited and conclusions are drawn from just three summit pairings. Any extrapolation is restricted to summits in the study area. Comparison of vegetation inside and outside randomly located exclosures (encompassing an area ≥10 × 10 m of moss-heath vegetation) on a number of randomly selected exposed summits throughout the Highlands for which red deer are the only large herbivore would take this research further and provide firmer conclusions.

Pollution can have a direct negative effect on lichen growth (Nash and Gries 1995; Jones et al. 2002). It also reduces terricolous lichen cover indirectly by encouraging competition from higher plants in response to nitrogen enrichment, for example (Britton et al. 2009). Loss of *R. lanuginosum* is likely to result from even low increments in nitrogen deposition (Pearce and Van der Wal 2002). The critical load for nitrogen deposition on alpine summits is 5–10 kg ha^{-1} $year^{-1}$ (Bobbink et al. 2011). Bowman et al. - (2012) go further and recommend that critical loads for nitrogen should be 3 kg ha^{-1} $year^{-1}$ in the Rocky Mountain National Park if alpine plant communities are to be protected. This is already a concern for summits in the Loch Maree area, and Beinn Eighe in particular. Lichen diversity is also sensitive to changes in climate (Britton et al. 2009) which will be influenced by latitude and elevation. Despite these confounding affects, red deer impact on exposed summit heath vegetation within the study sites at Letterewe should still have been manifested through evidence of trampling, dunging and breaking up of the moss carpet. One explanation why the exposed summit vegetation in the study sites at Letterewe did not show any obvious signs of deer impact (relative to comparable study sites at Beinn Eighe) could be that red deer were concentrating their grazing activity at another alpine habitat. High-altitude 'greens' (or *F. ovina–Agrostis capillaris–Galium saxatile* grassland, U4, according to the NVC after Rodwell 1992) were particularly favoured by red deer at Letterewe throughout the year (Milner et al. 2002). This observational study has presented data to suggest that red deer impact on bryophyte cover associated with exposed areas of summit moss-heath vegetation at Letterewe is very low, and this is consistent with the findings of Albon et al. (2007).

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References

Air Pollution Information System [Internet]. 2013. Nitrogen deposition data. [cited 2013 July 8]. Available from: http://www.apis.ac.uk/

Albon SD, Brewer MJ, O'Brien SO, Nolan AJ, Cope D. 2007. Quantifying the grazing impacts associated with different herbivores on rangelands. Journal of Applied Ecology 44:1176–1187.

Averis ABG, Averis AM. 1998. Vegetation Survey of Beinn Eighe 1997. Wester Ross. Unpublished Report for Scottish Natural Heritage.

Averis ABG, Averis AM, Birks HJB, Horsfield D, Thompson DBA, Yeo MJM. 2004. An illustrated guide to British upland vegetation. Peterborough (UK): Joint Nature Conservation Committee.

Bobbink R, Braun S, Nordin A, Power S, Schütz K, Strengbom J, Weitjers M, Tomassen H. 2011. Review and revision of empirical critical loads and dose-response relationships. Proceedings of an expert workshop; 2010 June 23–25; Noordwijkerhout. RIVPM Report: 680359002.

Bowman WD, Murgel J, Blett T, Porter E. 2012. Nitrogen critical loads for alpine vegetation and soils in Rocky Mountain National Park. Journal of Environmental Management 103:165–171.

Britton AJ, Beale CM, Towers W, Hewison RL. 2009. Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. Biological Conservation 142:1728–1739.

Britton AJ, Pearce ISK, Jones B. 2005. Impacts of grazing on montane heath vegetation in Wales and implications for the restoration of montane areas. Biological Conservation 125:515–524.

Daniels MJ. 2006. Estimating red deer *Cervus elaphus* populations: an analysis of variation and cost effectiveness of counting methods. Mammal Review 36:235–247.

De Nahlik AJ. 1992. Management of deer and their habitat – principles and methods. Gillingham. Dorset (UK): Wilson Hunt.

Dobson FS. 2011. Lichens: an illustrated guide to the British and Irish species. 6th ed. Slough (UK): The Richmond Publishing Co. Ltd.

Edwards T, Kenyon W [Internet]. 2013. Scottish parliament information centre: wild deer in Scotland. [cited 2014 January 8]. Available from: http://www.scottish.parliament.uk/ResearchBriefingsAndFactsheets/S4/SB_13-74

Hill MO, Blackstock TH, Long D, Rothero G. 2008. A checklist and census catalogue of British and Irish bryophytes. Cheshire (UK): British Bryological Society.

Jones MLM, Oxley ERB, Ashenden TW. 2002. The influence of nitrogen deposition, competition and desiccation on growth and regeneration of *Racomitrium lanuginosum* (Hedw.) Brid. Environmental Pollution 120:371–378.

Laughton Johnston J, Balharry D. 2001. Beinn Eighe: the mountain above the wood. Edinburgh (UK): Birlinn Ltd.

Macdonald D, Barrett P. 1993. Mammals of Britain & Europe. London (UK): HarperCollins Publishers.

Mayle BA, Pearce AJ, Gill RMA 1999. How many deer? A field guide to estimating deer population size. Forestry Commission Field Book 18. Edinburgh (UK): Forestry Commission

Meteorological Office [Internet]. 2013. UK mapped climate averages. [cited 2013 July 8]. Available from: http://www.metoffice.gov.uk/climate/uk/averages/ukmapavge.html

Milner J, Alexander J, Griffin C. 2002. A highland deer herd and its habitat. London (UK): Red Lion House.

Mitchell RJ, Truscot AM, Leith ID, Cape JN, Vandijk N, Tang YS, Fowler D, Sutton MA. 2005. A study of the epiphytic communities of Atlantic oak woods along an atmospheric nitrogen deposition gradient. Journal of Ecology 93:482–492.

Nash III TH, Gries C. 1995. The response of lichens to atmospheric deposition with an emphasis on the Arctic. The Science of the Total Environment 160–161:737–747.

Pearce ISK, Britton AJ, Armitage HF, Jones B. 2010. Additive impacts of nitrogen deposition and grazing on a mountain moss-sedge heath Botanica Helvetica 120:129–137.

Pearce ISK, Van der Wal R. 2002. Effects of nitrogen deposition on growth and survival of montane *Racomitrium lanuginosum* heath. Biological Conservation 104:83–89.

R Development Core Team. 2010. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Ratcliffe DA, Thompson DBA. 1988. The British uplands: their ecological character and international significance. In: Usher MB, Thompson DBA, editors. Ecological change in the uplands. Oxford (UK): Blackwell Scientific Publications; p. 9–36.

Rodwell JS. 1992. British plant communities, volume 3: grasslands and montane communities. Cambridge (UK): Cambridge University Press.

Scott D, Welch D, Van der Wal R, Elston D. 2007. Response of the moss *Racomitrium lanuginosum* to changes in sheep grazing and snow-lie due to a snow-fence. Applied Vegetation Science 10:229–238.

Smith CW, Aptroot A, Coppins BJ, Fletcher A, Gilbert OL, James PW, Wolseley PA. 2009. The lichens of Britain and Ireland. London (UK): British Lichen Society.

Stace CA. 2010. New flora of the British Isles. 3rd ed. Cambridge (UK): Cambridge University Press.

Survey BG. 1962. Inverbroom – Sheet 92. Southampton (UK): Ordnance Survey.

Thompson DBA, Brown A. 1992. Biodiversity in montane Britain: habitat variation, vegetation diversity and some objectives for conservation. Biodiversity and Conservation 1:179–208.

Thompson DBA, Galbraith H, Horsfield D. 1987. Ecology and resources of Britain's mountain plateaux: conflicts and land-use issues. In: Bell M, Bruce RGH, editors. Agriculture and conservation in the hills and uplands. Merlewood (UK): Institute of Terrestrial Ecology; p. 21–31.

Thompson DBA, Gordon JE, Horsfield D. 2001. Montane landscapes in Scotland: are these natural artefacts or complex relics? In: Gordon JE, Leys KF, editors. Earth science and the natural heritage: interactions and integrated management. Edinburgh (UK): The Stationery Office; p. 105–119.

Van der Wal R. 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114:177–186.

Van der Wal R, Brooker RW. 2004. Mosses mediate grazer impacts on grass abundance in arctic ecosystems. Functional Ecology 18:77–86.

Van der Wal R, Pearce I, Brooker R, Scott D, Welch D, Woodin S. 2003. Interplay between nitrogen deposition and grazing causes habitat degradation. Ecology Letters 6:141–146.

Welch D, Scott D, Thompson DBA. 2005. Changes in the composition of *Carex bigelowii* – *Racomitrium lanuginosum* moss heath on Glas Maol, Scotland, in response to sheep grazing and snow fencing. Biological Conservation 122:621–631.

Appendix. Bryophyte and lichen species list and frequency in thirty 1 m × 1 m quadrats on moss-heath vegetation at each of the six summit locations

Species	Beinn Lair	Meall a' Ghiuthais (NW)	Beinn Airigh Charr	Còinneach Mhòr	Sgùrr Dubh	Meall a' Ghiuthais (plateaux)
Allantoparmelia alpicola	0	3	0	0	0	0
Alectoria nigricans	0	5	0	0	0	6
Anastrepta orcadensis	1	3	1	3	0	0
Andreaea rothii	2	0	1	0	2	0
Andreaea rupestris	16	1	10	1	7	0
Anthelia julacea	2	0	0	0	0	0
Aulacomnium turgidum	0	1	0	0	0	0
Baeomyces rufus	0	0	0	0	1	0
Barbilophozia floerkei	0	3	0	6	1	1
Campylopus atrovirens	1	0	0	0	1	0
Campylopus brevipilus	0	1	0	0	0	0
Campylopus flexuosus	0	1	1	0	9	18
Cephaloziella divaricata	1	1	0	0	0	0
Cetraria aculeata	5	11	2	1	13	3
Cetraria islandica	15	15	27	25	3	6
Cladonia arbuscula	1	9	3	2	1	4
Cladonia bellidiflora	2	1	2	5	0	3
Cladonia chlorophaea	1	1	0	0	0	0
Cladonia ciliata	0	1	0	0	0	0
Cladonia crispata	0	0	1	0	0	0
Cladonia diversa	4	10	4	12	18	22
Cladonia furcata	0	10	4	7	3	7
Cladonia gracilis	3	4	0	0	2	0
Cladonia portentosa	0	1	2	0	0	0
Cladonia pyxidata	0	0	0	1	0	0
Cladonia squamosa	0	0	2	1	1	0
Cladonia sp.	7	11	9	8	0	0
Cladonia subcervicornis	8	20	8	5	24	16
Cladonia uncialis ssp. *biuncialis*	15	27	23	26	20	18
Dibaeis baeomyces	1	1	3	0	0	0
Dicranella heteromalla	0	0	0	2	0	0
Dicranum fuscescens	0	7	3	4	0	0
Dicranum scoparium	3	5	6	6	1	0
Diplophyllum albicans	25	24	2	7	11	23
Frullania tamarisci	0	0	1	0	2	0
Frutidella caesioatra	0	0	0	0	0	5
Hylocomium splendens	0	2	8	14	0	0
Hypnum callichroum	0	0	7	13	0	0
Hypnum cupressiforme	0	2	3	0	0	0
Hypnum jutlandicum	0	3	1	1	1	0
Isothecium myosuroides var. *brachythecioides*	0	0	1	0	0	0
Isothecium myosuroides var. *myosuroides*	0	1	0	0	0	0
Kiaeria starkei	0	0	0	1	0	0
Lecidoma demissum	0	0	0	0	0	1
Lichenomphalia alpina	0	0	0	3	0	4
Lichenomphalia hudsoniana	0	6	0	2	0	8
Lophozia sudetica	0	5	0	1	1	3
Lophozia ventricosa	0	1	1	1	0	0
Marsupella sp.	0	0	0	1	0	0
Micarea turfosa	1	0	0	0	0	0
Micarea lignaria var. lignaria	0	0	0	0	1	0
Mnium hornum	0	2	0	0	0	0
Mylia taylorii	0	7	0	0	0	0
Nardia scalaris	4	0	1	5	2	0
Ochrolechia androgyna	0	2	0	5	0	0
Ochrolechia frigida	0	14	1	0	9	8
Ochrolechia tartarea	23	9	6	0	30	5
Oligotrichum hercynicum	1	0	0	0	1	0
Parmelia omphalodes	0	2	0	1	2	0
Peltigera hymenina	0	0	0	6	0	0

(*Continued*)

Appendix. (*Continued*).

Species	Beinn Lair	Meall a' Ghiuthais (NW)	Beinn Airigh Charr	Còinneach Mhòr	Sgùrr Dubh	Meall a' Ghiuthais (plateaux)
Pertusaria dactylina	0	0	0	0	1	1
Pertusaria glomerata	0	0	1	0	0	0
Plagiothecium undulatum	0	0	0	1	0	0
Pleurozium schreberi	2	2	2	7	0	0
Pogonatum urnigerum	0	0	0	1	0	0
Pohlia nutans	1	4	1	2	1	2
Polytrichum alpinum	6	16	14	21	7	17
Polytrichum commune	0	0	0	2	0	0
Polytrichum juniperinum	7	0	0	0	0	0
Polytrichum piliferum	14	3	6	2	13	1
Ptilium ciliare	2	1	0	0	0	0
Racomitrium heterostichum	16	4	5	3	0	0
Racomitrium fasciculare	4	0	4	4	0	0
Racomitrium lanuginosum	30	30	30	30	30	30
Racomitrium sudeticum	0	0	0	0	0	2
Rhytidiadelphus loreus	1	3	8	22	0	0
Rhytidiadelphus squarrosus	0	0	1	1	0	0
Scapania scandica	0	0	1	3	0	0
Sphaerophorus globosus	0	5	4	5	19	0
Stereocaulon condensata	0	0	2	1	0	0
Stereocaulon vesuvianum	29	5	8	1	23	0
Tetralophozia setiformis	6	3	0	0	1	0
Thamnolia vermicularis	0	0	2	0	1	1
Tritomaria quinquedentata	0	0	0	1	0	0