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The natural exclusion of red deer from large boulder grazing refugia and the consequences for saxicolous bryophyte and lichen ecology

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Abstract   Large boulder grazing refugia permitted comparison of saxicolous bryophyte and lichen assemblages with those boulder tops accessible to red deer (*Cervus elaphus*) on a sporting estate in northwest Scotland. Plant succession was predicted to occur unchecked by grazing on the tops of these large boulders with cascading effects on bryophytes and lichens – assuming boulders had been in place over the same time period. Fifty pairs of boulders (one ≥ 2 m and the other accessible to red deer) were selected at random from various locations below north-facing crags. Percentage cover of each bryophyte and lichen species was estimated from three randomly placed quadrats on each boulder top. Due consideration was given to the influence of island biogeography theory in subsequent model simplification. Mean shrub cover and height, leaf-litter, bryophyte cover and bryophyte species richness were significantly higher within quadrats on large boulder tops that naturally excluded red deer. Lichen cover and lichen species richness were significantly higher on boulder tops accessible to red deer. Lichen cover was in a significant negative relationship with bryophyte cover, shrub cover and litter cover. Bryophyte cover showed a significant positive relationship with shrub height but there was an optimum shrub cover. Natural exclusion of red deer from the tops of large boulders has facilitated plant succession. The results suggest that grazing arrests the lithosere on boulder tops accessible to red deer at an early plagioclimax favouring saxicolous lichens. The results are relevant to situations where red deer might be excluded from boulder fields that hold lichen assemblages of conservation value.

Key-words: *Cervus elaphus*, conservation, lichens, species richness, succession

Introduction

Bryophytes and lichens contribute considerably to overall Scottish biodiversity (Church et al. 1996, 2001; Hodgetts 1997). Siliceous rock is a very important substrate for lichen species diversity in particular (Gilbert 2000; Porley and Hodgetts 2005) and boulders lying within a matrix of otherwise unsuitable wet heath vegetation represent valuable habitat islands. There have been few studies that have examined the impact of grazing by large herbivores on bryophyte and lichen assemblages associated with siliceous boulders. With red deer (*Cervus elaphus*) numbers on the open hill in Scotland almost doubling since the 1960s to estimates of 360 000–400 000 individuals (Edwards and Kenyon 2013), it is important to understand the impact of this large herbivore and its management on saxicolous bryophytes and lichens.

Fryday (2001) found reduced saxicolous lichen species richness on small stones inside upland sheep exclosures at scattered localities in upland Britain. Moore and Crawley (2014) also used exclosures to show that saxicolous lichen diversity and cover were reduced on low-lying boulders in the absence of red deer. These studies demonstrate how saxicolous bryophytes and lichens respond to successional changes in the matrix vegetation over a relatively short period inside exclosures. However, grazing pressure is artificially increased outside of the deer fence if there is no compensatory culling (Thomson et al. 2006). Large boulders that are inaccessible to red deer have the advantage over exclosures of being natural features in the environment. These ungulate-free refugia enabled us to investigate the response of saxicolous bryophyte and lichen assemblages to a long and natural absence of red deer and concentrated on changes directly related to the lithosere rather than with the surrounding matrix vegetation. The response of bryophytes and lichens associated with siliceous boulders to a natural exclusion of large herbivores has not previously been investigated.

Physical features of the environment such as boulder tops, up-turned tree root-plates and inaccessible cliffs have long been recognised as ungulate-free refuges for plants to flower without being predated and woodland to regenerate (Rooney 1997; Long et al. 1998; Banta et al. 2005). Milchunas and Noy-Meir (2002) noted the importance of small geologic refugia from herbivores for the maintenance of higher plant diversity, citing many studies from around the world. However, Crawley et al. (2004) observed a monoculture of *Festuca rubra* and greatly reduced plant diversity in the absence of sheep grazing on the inaccessible turf roofs of cleits on Hirta, St. Kilda, compared to adjacent grassland. In this example, the action of the herbivore has reduced the dominance of the competitive grass species to the advantage of other plants in the grassland. Comisky et al. (2005) demonstrated greater woody and herbaceous plant species richness and abundance on tall boulders compared to those accessible to white-tailed deer (*Odocopileus virginianus*) in the Allegheny National Forest, Pennsylvania. Deer browsing in this study was also implicated in preventing an increase in higher plant species richness with an increase in area of the smaller boulders.

Our investigation set out to determine how the natural exclusion of red deer was affecting bryophyte and lichen assemblages associated with inaccessible siliceous boulder tops by comparison with those boulders accessible to this large herbivore. Arnesto and Contreras (1981) recognised that plant succession on rocks was likely to affect local saxicolous lichen populations, through modification of the microclimate, long before any kind of competitive exclusion became manifest in the development of these communities. Increasing shrub cover and leaf litter on the tops of boulders that naturally exclude red deer, is likely to shade out and smother saxicolous lichens but the increased humidity and shelter would benefit bryophyte cover. Therefore, it was hypothesised that lichen species richness and cover would be reduced due to plant succession on those boulder tops inaccessible to red deer and that

bryophyte cover would be increased. Aspects of island biogeography theory were taken into account in the design of this investigation.

The results presented here enable contrast with studies focused on higher plant-herbivore systems associated with boulder top grazing refugia. Herbaceous plants are susceptible to direct predation whereas bryophytes and lichens are more likely to be influenced by the cascading effects that result from changes to their microhabitat. Comparison of boulder tops that naturally exclude red deer with those that do not provides an insight into how this large herbivore might be affecting bryophyte and lichen assemblages on these habitat islands. This is important in order to inform those concerned with managing red deer numbers in the Highlands and elsewhere.

Method

Site description

This natural experiment was conducted at Letterewe, Wester Ross (57° 42' N, 5° 25' W), where there are many large boulders for which the uppermost surface is inaccessible to red deer (*Cervus elaphus*). Letterewe Estate is a privately-owned tract of land in the Scottish Highlands comprising ca. 20,000 ha and is primarily managed for its deer-stalking interest. There has been no sheep grazing for > 30 years and the only other large herbivore is a small population of goats that frequent the woodland along the edge of Loch Maree (Milner et al. 2002). Red deer density at Letterewe has been estimated at 14.5 km^{-2} (Milner et al. 2002) but annual counts from a helicopter have been lower in recent years at 8–10 km^{-2} (Stephen Miller pers. comm. 2012). However, caution is advised concerning these estimates of red deer density without repeat counts during the year (Daniels 2006).

The study area is subject to mild winters and cool summers and receives ≥ 1 mm rain on > 220 days per year (Meteorological Office 2013). Nitrogen loading is low in the Loch Maree area (Mitchell et al. 2005) ranging from 5.18 – 6.30 kg N ha^{-1} $year^{-1}$ based on the latest three-year averages (Air Pollution Information System 2013). Lewisian gneiss underlies much of the estate with outcrops of Torridonian sandstone in the higher summits (British Geological Survey 1962). Several suitable boulder fields exist, at different locations, below an impressive series of north-facing cliffs that extend for approximately 10 km in a southeast to northwest direction. These are comprised of the siliceous rock known as horneblende schist (British Geological Survey 1962).

The boulders in the study area rest in a matrix of the slow-growing and unproductive M15 *Trichophorum germanicum–Erica tetralix* wet heath community (Rodwell 1991). This

community accounts for 54% of the total land cover of the Letterewe estate (Milner et al. 2002) and occupies ground that would once have held woodland (Averis et al. 2004). Remnant birch and rowan woodland grows from inaccessible parts of the cliffs from which the boulders originate. One or two trees have colonised a few of the larger boulders that are inaccessible to red deer. Some (but not all) of these boulders are covered in a deep layer of humus, pleurocarpous bryophytes and ericoid vegetation. The vegetation on these inaccessible habitat islands is best described by the H12 *Calluna vulgaris–Vaccinium myrtillus* heath (Rodwell 1991) owing to the frequency of these dwarf-shrub species and *Empetrum nigrum* and only occasional *Erica cinerea* (Elkington et al. 2001). A few large boulders supported the H21b *Mastigophora woodsii–Herbertus aduncus* ssp. *hutchinsiae* sub-community of the *Calluna vulgaris–Vaccinium myrtillus–Sphagnum capillifolium* heath (Rodwell 1991). Those boulders sampled from drier parts of the slope where the heath had been grazed down to a U4 *Festuca ovina–Agrostis capillaris–Galium saxatile* grassland community (Rodwell 1992) showed a stark contrast between boulder top and surrounding vegetation. *Racomitrium lanuginosum* was a feature of many of the rocks in the wet heath vegetation at Letterewe sometimes completely covering the topmost surface. Wet heath vegetation also occurred on top of several of the lower rocks.

The main lichen community of the upper surfaces of siliceous rocks within the study area is best described by the *Pamelietum omphalodis* association of the *Umbilicarion cylindricae* alliance (James et al. 1977) or the SS F2 *Parmelia saxatilis–Parmelia omphalodes* community (Orange 2009). *Parmelia omphalodes* is abundant on several boulders and other lichens were frequent such as *Hypogymnia physodes*, *Ochrolechia androgyna*, *O. tartarea*, *Ophioparma ventosum*, *Parmelia saxatilis*, *Pertusaria corallina* and *Sphaerophorous globosus* that characterise this association. *Hypnum andoi* and other bryophytes, such as those belonging to the genus *Racomitrium*, are common in this community (Orange 2009). Other

lichens encountered on un-vegetated and well-drained rock surfaces of hard siliceous rocks in the study area belonged to the *Umbilicarietum cylindricae* association (James et al. 1977). This included the SS A1 *Rhizocarpon geographicum–Fuscidea lygaea*, SS B3 *Fuscidea lygaea–Porpidia tuberculosa* and SS F1 *Rhizocarpon geographicum–Umbilicaria cylindrica* communities as described by Orange (2009). The species-poor SS D4 *Lecidea lithophila* community (Orange 2009) was also encountered but infrequently.

Procedure

Boulders were assumed to be of similar age in this study. However, the data might still be confounded by effects associated with spatial dynamics. According to island biogeographic theory (MacArthur and Wilson 1967), species richness of any particular taxon found on oceanic islands depends on extinction and immigration rates and these are functions of island area and distance from the mainland respectively (Arnesto and Contreras 1981). The probability of colonisation is also increased with greater connectivity among habitat islands and so less isolated patches of habitat should have a greater number of species (Virtanen and Oksanen 2007). Since boulder area and connectivity cannot be controlled in this natural experiment the necessary measurements were recorded during fieldwork and included in the maximal models.

Potential locations within the study area that held boulders large enough to exclude red deer were identified on a 1:50,000 Ordnance Survey map and then eight were selected at random. All potential sites were on north-facing slopes below cliffs and crags to control for climate and insolation. Boulder tops deemed inaccessible to red deer, such as those ≥ 2 m above the ground or of prohibitive shape if slightly lower than this, were sampled at these locations. Five accessible boulders of the same geology in the vicinity of each large boulder were identified then one was selected at random for comparison. The height and upper-most

surface area of each boulder was established using a tape measure. In order to ascertain the connectivity of each boulder, boulder density m^{-2} was calculated based on a count of rocks within a 5 m radius.

Three 0.2 m x 0.2 m quadrats were placed at random on top of each boulder selected for sampling. Hence, the sampling design was of a hierarchical nature with three pseudoreplicates per boulder. One boulder was accessible to red deer and the other was inaccessible so the pair of boulders constituted a 'block'. The most suitable quadrat size, shape and number had been determined in a pilot study. Making use of an acetate overlay with 100 circles of 20 mm diameter (described in Bates 1992) the percentage cover of each bryophyte and lichen species was estimated visually. Most taxa were identified in the field but small specimens of lichens were collected when identification with a microscope and keys were necessary. Occasional specimens required the assistance of a referee for identification. There were some lichen specimens for which identification was impossible owing to their condition or lack of fertility for example. These unknowns were recorded on the data sheet separately if there were more than one in a quadrat. The percentage cover of vascular plant species and leaf-litter was also recorded from each quadrat. The altitude of each boulder was determined using a GARMIN eTrex Legend GPS device and these elevations ranged from 185–445 m above sea level. For quickness, micro-gradient was scored on a five-point scale from the horizontal (1) to vertical (5) based on the angle of the quadrat. Roughness of the rock was allocated a score of 1 (smooth), 2 (intermediate) or 3 (very rough) and aspect of the rock beneath each quadrat was also noted. Mean height of vascular plant vegetation (metres) within each quadrat was determined with a metre rule based on five measurements on a randomly selected diagonal. Bryophyte and lichen height was measured in a similar fashion but with a smaller rule. Bryophyte and lichen species richness was recorded for the entire top surface of each boulder sampled. Data were collected from 50

pairs of boulders giving 150 quadrats in total from each treatment – as directed by the power analysis to ensure a suitable number of samples for statistical analysis.

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

Analysis

A linear mixed effects model (lmer) was used to analyse the species cover data within quadrats due to the hierarchical nature of the experimental design and the pseudoreplication on each boulder top. The fixed effect was presence or absence of red deer and the random effects took account of quadrats within boulders, within pairs of boulders, within locations. Variance components analysis (VCA) revealed what percentage of the unexplained variance in the data was attributed to each of the random effects after that explained by the fixed effect had been removed.

The percentage cover data were arcsine transformed (units in radians) before an lmer was fitted in R version 2.11.1 (R Development Core Team 2010) to test the null hypothesis that a natural exclusion of red deer, from the top surfaces of large boulders, in a matrix of wet heath vegetation, had no effect on the cover of selected species of bryophyte and lichen. Total bryophyte, total lichen and total dwarf-shrub species cover within quadrats were analysed in the same manner. Differences in mean bryophyte and lichen height and mean vegetation height between deer accessible and inaccessible boulder tops were also analysed in an lmer.

Division of the most abundant species' cover by the total cover of all species belonging to a particular taxonomic group, within each quadrat, gave us a value for dominance. These data were then analysed in an lmer to test the null hypothesis that there was no difference in mean

bryophyte and lichen dominance between boulder tops that were accessible to red deer and those that were not.

A Poisson error structure was specified in the generalised lmer used to analyse bryophyte and lichen species richness within quadrats. This dealt with the non-constant variance associated with count data and a log-link function constrained the predicted counts to the non-negative.

Model simplification in an ANCOVA was performed to determine which of the explanatory variables influencing total bryophyte cover and total lichen cover within quadrats were most important. The relevant quadrat data from each boulder were first averaged to remove the pseudoreplication before model simplification. Tree models, box plots and scatter graphs were generated to assist with the initial parameterisation of the maximum models. Parameters considered for inclusion in the maximum models were categorical variables such as treatment (accessibility of the boulder to red deer or not), aspect, micro-gradient, roughness of the rock and continuous variables including surface area of the boulder-top, height of the boulder, connectivity, mean shrub cover, mean shrub height, mean bryophyte cover (where relevant), mean litter cover and altitude at which the boulder rests.

Model simplification for bryophyte and lichen species richness of the entire boulder top (count data) was performed in a generalised linear model (glm) with a quasipoisson error structure due to over-dispersion in the response. Explanatory variables such as treatment, boulder top area, height of boulder, connectivity and altitude were included in the initial parameterisation of the maximum models. This analysis of boulder top bryophyte and lichen species richness gave an indication about how much of an influence island biogeography was having on the data.

Maximum models were constructed following the guidelines given in Crawley (2005, 2013) on how to avoid over-parameterisation. During the model simplification process, ANOVA

was used to justify the removal or retention of variables from successive models (specifying the F test to compare models with a quasipoisson error structure). The minimum adequate models (MAMs) produced in this way were each tested for goodness of fit and attempts were made to repeat the model simplification with transformed variables when goodness of fit was poor.

Results

Mean shrub cover (t = 9.126), litter cover (t = 6.093), dwarf-shrub height (t = 8.084) and bryophyte and lichen height (t = 7.799) were all significantly greater on boulders that were inaccessible to red deer (Figure 1). The most common shrubs on the boulder tops were *Calluna vulgaris*, *Vaccinium myrtillus*, *Erica cinerea* and *Empetrum nigrum* (in order of frequency within quadrats – see Online Resource 1) but the rare occurrences of *Arctostaphylos uva-ursi*, *Erica tetralix*, *Juniperus communis*, *Salix herbacea* and *Sorbus aucuparia* were also included in the determination of mean shrub cover.

Mean bryophyte cover (radians) was significantly greater (t = 11.14) within quadrats on the top of boulders that naturally excluded red deer at 1.059 compared to those that were accessible at 0.567 with standard error for the difference between means (SE) ±0.044. However, mean lichen cover (radians) was significantly lower (t = 6.382) within quadrats on boulder tops that naturally excluded red deer at 0.456 compared to 0.754 (SE ±0.047) for those that could be accessed. Mean dominance by any one bryophyte or lichen was significantly higher (t = 3.748) on the tops of boulders that naturally excluded red deer at 0.667 compared to 0.553 (SE ±0.031) for accessible boulder tops. Differences between quadrats accounted for most of the unexplained variation in these data (ca ≥50%) after the variance explained by the fixed effect had been removed. This suggests that more quadrats on each boulder would have been useful to account for this variability. There is also a case for sampling from additional pairs of boulders owing to the high amount of unexplained variance attributed to this random effect for bryophyte cover (39%) and lichen cover (20%).

A total of 142 bryophyte and lichen taxa were recorded from the 300 quadrats on boulder tops in the study area (Online Resource 1). The abundance of those species present in > 20 quadrats were fitted with an lmer (Table 1). Lichens that were significantly lower in cover on

the top of large boulders were those that grew directly on siliceous rock – such as *Fuscidea cyathoides* and *Pertusaria corallina*. Pleurocarpous mosses such as *Hylocomium splendens* and *Rhytidiadelphus loreus* that thrive below a dwarf-shrub canopy were significantly more abundant in quadrats on the top of large boulders. Differences between quadrats accounted for most of the unexplained variance (mean 64%) in the data after that explained by the fixed effect had been removed. This is because bryophytes and lichens are very sensitive to small-scale differences in their microhabitat.

Mean bryophyte and lichen (combined) species richness and mean lichen species richness were significantly lower in quadrats on boulder tops that were inaccessible to red deer but there was a significantly higher number of bryophyte species in the same situation (Table 2). Most of the unexplained variance (mean 47.8%) in these models was attributed to differences between boulders or at the level of pairs of boulders (mean 40.3%). Several factors beyond the fixed effect of red deer presence/absence are influencing species richness in this instance.

Explanatory terms associated with island biogeography theory were among the factors remaining in the MAMs for total bryophyte and lichen species richness of boulder tops (Tables 3 and 4). There was a significant positive relationship between bryophyte species richness and boulder top surface area and also with increasing connectivity with other boulders. Bryophyte species richness significantly decreased with altitude but the reverse was true for lichen species richness. This is apparent in the scatter plots (see Online Resources 2 and 3). There was a significant quadratic function for boulder connectivity remaining in the MAM for lichen species richness which described a minimum in the data. Very little variation in the data was explained by the MAMs for bryophyte species richness ($r^2 = 0.297$) and lichen species richness ($r^2 = 0.129$). There was little heteroscedasticity in the residuals of these MAMs but curvature occurred in the normal errors. Influential factors such as bryophyte cover, shrub height, shrub cover, litter cover and so forth were not included in the

foregoing maximum models as this data was specific to the quadrats and could not be applied to the whole boulder top. A full list of bryophytes and lichens recorded from boulder tops in this investigation is given in Online Resource 4.

Over two thirds of the quadrats were on the horizontal or of shallow micro-gradient and most quadrats were facing directly upwards. Nearly two-thirds of the quadrats were assigned the intermediate roughness of rock category and no discernible differences were seen in the data for the other roughness scores. Therefore, these variables were not included in the maximal models of averaged quadrat data. Tree diagrams showed that other explanatory variables such as ericoid height, shrub and litter cover were far more important terms to include at the initial parameterisation.

The MAM for mean bryophyte cover within quadrats on each boulder accounted for 68.4% of the variation in the data (Table 5). There was a significant positive relationship between bryophyte cover and shrub height but there was an optimum shrub cover in the model as suggested by the significant quadratic function for this explanatory variable. Increased litter cover on rock accessible to red deer appeared to benefit bryophyte cover but higher litter levels on the larger boulder tops generally resulted in an optimum. There was a reasonable goodness of fit for this model. Scatter graphs that support the statistics here are provided in Online Resource 5.

Table 6 describes the MAM for mean lichen cover within quadrats on each boulder which accounts for 82.5% of the variation in the data. Figure 2 shows the distribution of the data around the fitted model. The local abundance of terricolous lichens *Cladonia portentosa* and *C. uncialis* ssp. *biuncialis* in quadrats below a heather canopy explains the anomalous high mean lichen cover at higher values of mean shrub cover. Three significant interaction terms remained in this MAM. Increasing area of boulder tops that naturally excluded red deer saw a

decrease in lichen cover where no pattern was apparent for those rocks accessible to the herbivore in question. Increasing shrub cover on rocks at higher altitudes ($> 250 < 450$ m) was causing a decrease in lichen cover but at lower altitudes there was no such pattern. There was also an interaction between altitude and litter cover. This seems to have been influenced by higher than expected lichen cover at moderate litter levels – again caused by the local abundance of the *Cladonia* lichens and altitude was coincidental. There was evidence of heteroscedasticity in the residuals versus fitted plot of this MAM but the normal errors showed good linearity.

Despite the likely correlation between the main explanatory terms of shrub height/cover, litter cover and bryophyte cover in the MAM for lichen cover they remain in the models because of their individual influences. Increasing shrub cover does not necessarily correspond to increasing shrub height. The former can lead to competition for space whereas shrub height causes a reduction in incident light and changed moisture regime. Although bryophyte cover responded positively to shrub height and cover (to an optimum) bryophytes may also be abundant in the absence of a shrub cover. This information would be lost if only shrub cover was used in the model to explain lichen diversity for example.

Transformation of the explanatory variables (where possible) did not result in any improvement in the MAM when there was a poor goodness of fit. However, the high significance of the explanatory variables in the MAMs outweighed concerns and the interpretations made scientific sense.

Discussion

The data suggest that red deer browsing on accessible boulder tops continues to arrest succession to the advantage of saxicolous bryophytes and lichens which persist in an early plagioclimax community. Modification of the habitat through plant succession on boulder tops that naturally exclude red deer has affected local saxicolous lichen populations as expected (Arnesto and Contreras 1981). The increased shelter and humidity below a canopy of dwarf-shrubs (mostly H12 heath vegetation) and the build-up of leaf-litter and humus has resulted in conditions conducive to the growth of bryophytes. The favourable conditions on the top of large boulders have also allowed more bryophyte species to coexist. The saxicolous bryophyte and lichen species of this lithosere have been replaced by bulky pleurocarpous mosses and ericoid shrubs on those boulder tops inaccessible to red deer. This might be symptomatic of lithoseres on boulder tops elsewhere where succession is not arrested. This could be a cause for concern if rare lichens are being ousted by common bryophytes and ericoid shrubs on deer-accessible boulders inside exclosures for example (Moore and Crawley 2014).

The results indicate that red deer are not preventing bryophyte species richness from continuing to increase with boulder top surface area at Letterewe. This contrasts with the impacts of white-tailed deer on plant species richness on boulder tops in the Allegheny National Forest, Pennsylvania (Comisky et al. 2005). However, bryophyte species richness was significantly higher on those boulders that were inaccessible to red deer for the reasons discussed above. Combined bryophyte and lichen species richness as a whole was significantly lower on boulders that naturally excluded red deer. This is because of the significantly lower number of lichens on large boulder refugia which is not consistent with the pattern observed for higher plants in similar studies (Banta et al. 2005; Comisky et al.

2005). Therefore, it was justified to separate bryophyte and lichen species richness patterns in this investigation. Virtanen and Crawley (2010) have previously argued the case for organism-specific adjustments to general species richness models for similar reasons. Boulder top surface area did not remain in the MAM for lichen species richness but lichen cover within quadrats became significantly reduced with increasing boulder area. Much of the available area on the bigger boulder tops has become unsuitable for saxicolous lichen species, increasing the probability that a randomly placed quadrat would land on heath vegetation with a ground layer dominated by bryophytes.

There is an argument that boulder area itself is facilitating succession rather than an absence of red deer. The greater topmost surface areas associated with the biggest boulders would have more microhabitats available compared to smaller rocks. This in turn would provide more opportunities for dwarf shrub species to establish and enable succession to proceed more quickly. Accessibility to red deer might only be coincidental with this effect. In order to tackle this question, the data-frame was restricted to those rocks with a boulder top surface area < 15.7 m^2 to include all deer accessible rocks and a reduced number of boulders that naturally exclude red deer with comparable boulder top surface area. In the event, only nine boulders were removed from the data set. Examination of scatter graphs and box plots generated with this limited dataset showed that variables such as mean shrub cover, mean shrub height and mean litter cover remained consistently higher on the boulders that were not accessible to red deer. There was no apparent difference between the scatter plots presented here and those produced with the restricted data set. This is consistent with Moore and Crawley (2014) who demonstrated significantly increased vascular plant cover on small low-lying rocks inside deer exclosures compared to those outside. This had similar consequences for saxicolous lichen cover and diversity on the top of rocks but the matrix vegetation had also undergone succession in this observational study.

Boulder size and connectivity have had a significant effect on the bryophyte and lichen species richness of boulders in some studies (Weibull and Rydin 2005; Virtanen and Oksanen 2007) but not in others (Kimmerer and Driscoll 2000). Island biogeographic effects were influential in terms of the connectivity of the boulders in our investigation. Bryophyte species richness of the whole boulder top did increase with enhanced connectivity which is consistent with previous studies (Virtanen and Oksanen 2007). The initial decrease in lichen species richness of the entire boulder top with increasing connectivity could be attributed to the influence of the matrix around the habitat islands. Lichens associated with the wet heath are able to colonise those isolated boulder tops that have suitable microhabitats. The importance of the matrix vegetation may also explain the negative relationship between bryophyte cover within quadrats and connectivity. The bryophyte community on boulder tops was strongly influenced by pleurocarpous species colonising from the surrounding matrix vegetation. The wet heath habitat around more isolated boulders would also have conferred greater humidity to the advantage of bryophyte growth. Boulder tops sampled within a boulder field are further away from the matrix. Hence, the slightly drier conditions and proximity to propagule sources are advantageous for saxicolous lichens and less competitive bryophytes such as *Gymnomitrion* spp., *Hedwigia stellata* and *Andreaea* spp. to colonise, without being overgrown by the larger pleurocarpous mosses. Therefore, bryophyte cover was reduced within quadrats in these situations but overall bryophyte species richness increased.

Unlike studies involving bryophyte and lichen communities on glacial erratics (Kimmerer and Driscoll 2000; Virtanen and Oksanen 2007) there will inevitably be differences in the period of time a boulder has been in a certain position below the north-facing crags at Letterewe. However, it was assumed that many of the 50 boulders accessible to red deer will have been in place long enough for succession to have occurred to a similar extent as that for the larger boulders. Not knowing how the boulders came to rest in their current positions is

another confounding factor. Their place of origin is known but whether the rock slid down the slope with ledge vegetation intact or whether the boulder rolled and vegetation has developed since that event is open to question. The latter was assumed since most of the boulders are a substantial distance from the crags (> 50 m). Altitude was a measurable factor that would lead to microclimatic differences experienced by boulder top communities. Succession occurs more slowly under harsher conditions at higher altitudes (which are better tolerated by lichen communities) and a climax of woodland is unlikely on boulders above the present-day tree line. These factors might go some way to accounting for the unexplained variation between boulders and pairs of boulders in the linear mixed effects models.

After consideration of potential confounding small-scale biogeographic factors, this observational study presents evidence to suggest that boulder-tops inaccessible to red deer in the study area serve as refugia, primarily for a H12 *Calluna vulgaris–Vaccinium myrtillus* heath community (Rodwell 1991) in slow transition to woodland. This has had cascading effects on bryophytes and lichens. Bryophyte cover and bryophyte species richness have increased below a canopy of dwarf shrubs, on top of those boulders which naturally exclude red deer, to the detriment of saxicolous lichen communities. Estimated densities of 8–14.5 red deer km^{-2} in the landscape have arrested succession on similar boulders that are accessible to these herbivores. Therefore, saxicolous lichen species on deer–accessible boulders remain unaffected by the next seral stage in this lithosere. There was no evidence to suggest a negative effect of red deer on the lichens growing on deer-accessible siliceous boulders (such as presence of species assemblages associated with nutrient enrichment from dung and urine). The findings of this study are consistent with Moore and Crawley (2014) and become relevant to situations where red deer might be excluded (for the purposes of woodland regeneration) from boulder fields that hold lichen communities of high conservation value.

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Table 1 Mean arcsine cover values of the most frequent bryophyte and lichen species in 300 0.04 m^2 quadrats, on 100 boulders, that differ in their accessibility to red deer, following analysis in an lmer. The Standard Error (SE) is for the difference between means. Significant t values are in bold type

Species	Effect of no deer	Mean arcsine cover (radians)			
		Deer access	No deer access	SE	t value
Andreaea rupestris	−	0.039	0.023	0.008	**2.033**
Cladonia diversa	+	0.022	0.027	0.009	0.581
Cladonia portentosa	+	0.009	0.037	0.016	1.766
Cladonia subcervicornis	−	0.046	0.027	0.011	1.821
Dicranum scoparium	+	0.012	0.038	0.009	**2.693**
Diplophyllum albicans	+	0.024	0.024	0.007	0.044
Fuscidea cyathoides	−	0.073	0.033	0.019	**2.155**
Hylocomium splendens	+	0.002	0.106	0.034	**3.099**
Hypnum andoi	+	0.080	0.167	0.032	**2.747**
Hypnum jutlandicum	+	0.020	0.059	0.013	**2.900**
Lecanora polytropa	−	0.057	0.053	0.010	0.396
Lecidea lithophylla	−	0.111	0.054	0.016	**3.552**
Parmelia omphalodes	+	0.159	0.167	0.025	0.333
Pertusaria corallina	−	0.141	0.034	0.021	**5.131**
Pleurozium schreberi	+	0.002	0.026	0.009	**2.776**
Porpidia melinodes	−	0.064	0.013	0.015	**3.532**
Porpidia tuberculosa	−	0.046	0.013	0/013	**2.540**
Racomitrium fasciculare	−	0.034	0.017	0.009	1.887
Racomitrium heterostichum	−	0.067	0.030	0.014	**2.569**
Racomitrium lanuginosum	+	0.358	0.555	0.071	**2.776**
Rhizocarpon geographicum	−	0.077	0.029	0.013	**3.664**
Rhizocarpon reductum	−	0.039	0.003	0.009	**3.904**
Rhytidiadelphus loreus	+	0.004	0.093	0.020	**4.321**
Scapania gracilis	+	0.024	0.039	0.011	1.426
Stereocaulon vesuvianum	−	0.059	0.015	0.013	**3.354**

Table 2 Mean values of species richness (SR) following lmer analysis with a Poisson error structure fitted to the data from 300 0.04 m^2 quadrats shared between boulders that differ in their accessibility to red deer. The Standard Error (SE) is for the difference between means. Significant p values are in bold type

Response variable	Effect of no deer access	Log species richness		SE	*P* value
		Deer access	No deer access		
Combined bryophyte and lichen SR	–	1.969	1.687	0.081	**< 0.001**
Bryophyte SR	+	0.759	1.029	0.080	**< 0.001**
Lichen SR	–	1.416	0.505	0.146	**< 0.001**

Table 3 The MAM for bryophyte species richness of 100 boulder tops after model

simplification in ANCOVA. Significant *P* values in bold type.

Explanatory variable	Effect	Estimate	Standard error	*P* value
Intercept		2.287		
Treatment (absence of red deer)	+	0.200	0.086	**0.023**
Boulder top area	+	0.019	0.005	**< 0.001**
Altitude	−	0.001	< 0.001	**0.006**
Boulder density in 5 m radius	+	0.997	0.405	**0.016**

Table 4 The MAM for lichen species richness of 100 boulder tops after model simplification in ANCOVA. Significant *P* values in bold type.

Explanatory variable	Effect	Estimate	Standard error	*P* value
Intercept		2.697		
Treatment (absence of red deer)	−	0.510	0.167	**0.003**
Altitude	+	0.001	< 0.001	**0.046**
Boulder height	+	0.163	0.066	**0.016**
Boulder density in 5 m radius	−	3.624	1.352	**0.009**
Quadratic function for boulder density	+	8.845	3.750	**0.021**
Interactions				
Treatment/Boulder density	−	1.734	0.805	**0.034**

Table 5 The MAM for total bryophyte cover after simplification in ANCOVA using mean data from 3 x 0.04 m^2 quadrats on each of 100 boulder tops. Significant *P* values in bold type.

Explanatory variable	Effect	Estimate	Standard error	*P* value
Intercept		0.552		
Treatment (absence of red deer)	+	0.370	0.088	**< 0.001**
Shrub height	+	2.835	0.511	**< 0.001**
Boulder density in 5 m radius	−	1.075	0.300	**< 0.001**
Shrub cover	+	0.461	0.243	0.061
Litter cover	+	0.536	0.343	0.121
Quadratic function for shrub cover	−	0.355	0.135	**0.010**
Interactions				
Treatment/Litter cover	−	1.100	0.364	**0.003**

Table 6 The MAM for total lichen cover after simplification in ANCOVA using mean data from 3 x 0.04 m^2 quadrats on each of 100 boulder tops. Significant P values in bold type.

Explanatory variable	Effect	Estimate	Standard error	P value
Intercept		0.386		
Treatment (absence of red deer)	+	0.055	0.053	0.307
Bryophyte cover	−	0.515	0.005	**< 0.001**
Shrub cover	−	0.489	0.201	**0.017**
Litter cover	−	1.913	0.458	**< 0.001**
Boulder top area	−	0.014	0.006	**0.016**
Altitude	+	0.005	0.002	**0.020**
Quadratic function for altitude	−	< 0.001	< 0.001	**0.010**
Interactions				
Treatment/Boulder top area	+	0.014	0.006	**0.024**
Shrub cover/Altitude	−	0.002	0.001	**0.003**
Litter cover/Altitude	+	0.005	0.002	**0.001**

Fig. 1 Mean values of (a) total arcsine shrub cover, (b) arcsine litter cover, (c) shrub height and (d) bryophyte and lichen height from quadrats on boulders in wet heath vegetation at Letterewe, Wester Ross, that were either accessible to red deer (D) or not (ND). The Standard Error is for the difference between means

Fig. 2 The MAM for total lichen cover within quadrats on each boulder top is fitted to selected scatter graphs. There was a significant negative relationship with arcsine bryophyte cover (top left), shrub cover (top right) and litter cover (bottom left). Triangles indicate data points from boulder tops that were accessible to red deer and dots for those that were not

Online Resource 1 Bryophyte, lichen and plant species list and frequency from 300 0.2 m x 0.2 m quadrats on boulder tops that were accessible or not to red deer in wet heath vegetation at Letterewe, Wester Ross

Online Resource 2 The MAM for bryophyte species richness of the entire boulder top fitted to the relevant scatter graphs. Bryophyte species richness was significantly higher on boulder tops that were inaccessible to red deer (upper line in each graph). There was a significant positive relationship with boulder top area (top left). Bryophyte species richness significantly decreased with increasing altitude (top right) and there was a significant positive relationship with connectivity (bottom left). Triangles indicate data points from boulder tops that were accessible to red deer and dots for those that were not

Online Resource 3 The MAM for lichen species richness of the entire boulder top fitted to the relevant scatter graphs. Lichen species richness was significantly higher on boulder tops that were inaccessible to red deer (upper line in each graph). There was a significant positive relationship with altitude (top left) and boulder height (top right). There was a significant quadratic function remaining in the model for connectivity (bottom left). Triangles indicate data points from boulder tops that were accessible to red deer and dots for those that were not

Online Resource 4 Bryophyte and lichen species list from 100 boulder tops at Letterewe, Wester Ross

Online Resource 5 The MAM for total bryophyte cover within quadrats on each boulder top is fitted to the relevant scatter graphs. There was significantly greater bryophyte cover on boulder tops that were inaccessible to red deer (represented by the upper line in each graph). There was a highly significant positive relationship between arcsine bryophyte cover and mean shrub height (top left). A significant negative quadratic function remained in the model for mean arcsine shrub cover (top right). There was a significant negative relationship with

connectivity (bottom left). Triangles indicate data points from boulder tops that were

accessible to red deer and dots for those that were not