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# **Effects of removing sheep grazing on soil chemistry, plant nutrition and forage digestibility: lessons for rewilding the British uplands**

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## **Running head**

Removal of sheep grazing: lessons for Rewilding

## **Keywords**

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## **Abstract**

Rewilding is currently being proposed as a means of enhancing the conservation value of marginal land in many parts of the world. This is especially true in the British uplands where rewilding will almost certainly involve either a reduction in livestock grazing, or its complete removal. The aim of reducing stock numbers would be to reverse the degradation of these ecosystems that has been caused by past over-grazing. However, little is known about the likely outcomes, or the time-scales over which such ecosystem recovery might occur. Here, we report preliminary results from a recent study of eight sites at Moor House NNR in the north-Pennines, where permanent plots with- and without-sheep grazing were established between 1954–67 on a range of typical upland plant communities. Soils and vegetation were sampled, and their chemical properties analysed; for vegetation an assessment of the herbage quality for animal nutrition was also made. No significant differences in soil properties, above-ground biomass and nutritional status of the vegetation was detected that could be attributed to sheep grazing removal. The only significant effect associated with grazing removal was a reduced digestibility of the vegetation (greater Acid Detergent Fibre concentration) where sheep were removed. These results show that a rewilding strategy that relies only on reducing sheep numbers will have very little impact on ecosystem recovery in terms of soil or herbage chemistry over short- to medium-term time-scales. Rewilding policies, therefore, attempting to restore ecosystems degraded by over-grazing must, therefore, be viewed as long-term (> 50 years).

## Introduction

Rewilding means different things to different people. Ideally, it should be focussed on the conservation at the big scale and the restoration of natural process with the introduction of wide-ranging large animals, especially top carnivores (Soulé & Noss, 1998). In practice, rewilding has included re-introductions of keystone species, for example the European beaver (Law *et al.*, 2017), of top-carnivores, black bears (Malaney *et al.*, 2018), lynx, (Gaston *et al.*, 2016), wolves (Ripple *et al.*, 2015; Beschta & Ripple, 2016), and of macro-herbivores (Baker *et al.*, 2016; van Klink *et al.* 2016). In addition, the abandonment of land has also been described as rewilding and here land that has been managed usually for agriculture has had the management intensity reduced or stopped completely (Merckx & Pereira, 2015; Corlett, 2016). In the foreseeable future (by 2040) the amount of land potentially available for abandonment in Europe has been estimated at 71,277-211,814 km<sup>2</sup> (van der Zandena, *et al.*, 2017) with suggestions that policies should concentrate on this marginal land where benefits to ecosystem services and ecological restoration might outweigh those derived from agriculture (Merckx & Pereira, 2015).

The British uplands have been central to this debate with suggestions of, amongst other measures, a policy of reducing deer numbers in Scotland (Dreary & Warren, 2017) and that grazing livestock should be more or less eliminated in upland ecosystems (Monbiot, 2013). Unfortunately, we know relatively little about the effects of reducing stock grazing pressures, especially to zero, and specifically how long it will take for any change to take effect. Removal of stock-grazing would be expected to impact on successional processes, promoting a move to woodland if below the natural tree-line, a change in species composition and a change in nutrient dynamics. For stock grazing there are two predicted impacts depending on the time-scale considered (Marrs *et al.*, 1989). In the short-term, grazing could enhance nutrient cycling and hence make nutrients more available, but in the longer-term result in an overall decline as some nutrients are exported off the site (Perkins, 1978). Grazing removal should, therefore, result in an overall increase in nutrients held on site, but much of the above-ground material might reside in accumulating litter where it could be considered out of short-term circulation.

One way of starting to gain an understanding of the processes involved is to measure change in long-term enclosure experiments, set up to assess the impacts of removing stock grazing altogether. This approach should provide an insight into what might happen. However, because enclosures are usually relatively small-scale (<1000 m<sup>2</sup>) in comparison to the scale of rewilded areas, they only give a first approximation of likely impacts and timescales.

One good example of a series of such enclosure studies are those set up on Moor House NNR in the North of England between 1953 and 1967. These experimental sites, each with a sheep-grazed

plot and an ungrazed comparator were distributed across the reserve to assess the effects of grazing removal on a range of plant community types that encompass a large proportion of British upland plant communities. The plant communities included vegetation dominated by dwarf-shrubs, grasses and sedges, growing on soils ranging from deep blanket peat through to brown-earth soils, and subject to very different, and indeed changing, sheep grazing pressures which are related to forage quality (Eddy *et al.*, 1968; Rawes & Welch, 1969). These vegetation types, in common with those elsewhere in upland Britain, would be described as degraded by over-grazing with sheep (Fraser Darling, 1955; McGovern *et al.*, 2011).

However, in common with many parts of upland Britain, there has been a reduction in sheep grazing pressure since the 1960s (McGovern *et al.*, 2011). At the time that these studies were set up there were estimated to be ca. 15,400 sheep on the Reserve in the summer months; assuming a grazing area of 3500 ha, this equates to 4.4 sheep ha<sup>-1</sup>. Numbers were then more than halved to 7000 sheep (2 sheep ha<sup>-1</sup>) in 1972, after formalization of grazing rights under the Commons Registration Act (1965). Thereafter, the statutory Conservation Agency bought up some of the common grazing rights following the outbreak of Foot and Mouth disease in 2001, and grazing pressure was reduced again to ca. 3500 sheep (1 sheep ha<sup>-1</sup>). It was hoped that this reduction would lead to an improvement in vegetation quality for conservation outcomes. However, for the purposes of this paper no sheep grazing is being compared to the “Business-as-usual” scenario for upland Britain, i.e. sheep grazing. Any change brought about by reducing the grazing pressure in upland grasslands must also be set against changes in species composition brought about through climate change (Mitchell *et al.*, 2018) and changing atmospheric pollutant loads – elevated N (Mitchell *et al.* 2017; Pakeman *et al.*, 2016) and elevated, and then reducing, S (Mitchell *et al.*, 2018).

The experimental sites were originally set up to measure changes in plant community composition through time (Rawes, 1981; Rawes, 1983; Marrs *et al.*, 1988). An holistic analysis of change in all experiments up to the year 2000 (Milligan *et al.*, 2016) concluded that where sheep continued to graze there was a reduction in species diversity in abundance of vascular plants, grasses, lichens, liverworts and mosses; whereas herbs, sedges and shrubs increased. Removal of sheep grazing had some positive benefits; with herbs, mosses, sedges and shrubs increasing, but with reductions in grasses and liverworts compared to their grazed counterparts. There was no evidence of species invasion such as tree encroachment. However, these sites also provide an opportunity to assess how the reduction in sheep grazing has changed other aspects of these grazed ecosystems, in particular soil processes. A comparative study was carried out in the mid-1980s between 18-31 years after sheep were excluded. Although at that time there was an increase in both dry matter content and nutrient content in the litter at most sites, there were no consistent

differences in soil properties in the ungrazed treatment, some sites become slightly more acidic and some less so (Marrs *et al.*, 1989). The reduction in litter in grazed sites is a common phenomenon in ecological restoration (Lindenmayer *et al.*, 2018).

Given that these sites have been degraded by extensive sheep grazing, we hypothesise that removal of the sheep grazing pressure will allow them to recover. We test this hypothesis here by assessing the effects of no sheep grazing versus the “business-as-usual” sheep grazing pressure on both soil properties and the nutritional properties of the vegetation after between 48-62 years free of grazing. The information collected allowed assessments of forage quality across a range of common upland ecosystems.

## Methods

This study compared the chemical properties of soils and vegetation in an ungrazed enclosure and a comparator plot subject to free-range sheep grazing at eight sites on the Moor House reserve (Table S1; Fig. S1). The sites were located across a range of upland vegetation types that collectively cover ca. 80% of this reserve (Table S1) and are representative of many ecosystems found in much of upland Britain with six different National Vegetation Classification plant communities identified (Table S1). Vegetation change has been described previously (Rawes, 1981; Rawes, 1983; Marrs *et al.*, 1988; Milligan *et al.*, 2016). The sheep grazing pressure across these plant communities is, however, not random, with up to 23.2 times greater densities on the most-grazed grassland communities compared to the least-grazed blanket bog ones (Table S1; Rawes & Welch, 1969).

### Vegetation and soil sampling and processing

In late May 2015, at the start of the growing season, four random positions were located in both the enclosed and grazed plots at each site. At each position, the surface vegetation was harvested with secateurs to ground level within a 0.25 m<sup>2</sup> quadrat and two soil cores taken (1 cm diameter, 21 cm depth) and pooled. A random sub-sample was removed for sorting to species level. Both the sorted fractions and the residual fraction were dried at 80°C for three days, dry weight measured and then converted to g m<sup>-2</sup>. Species nomenclature follows Stace (2010).

The chemical properties of vegetation and soil samples were determined the methods of Allen (1989). Vegetation was ground to pass a 1mm sieve and the concentrations of C, N, P, K, Ca, Mg and Na measured after dry-ashing (Allen, 1989). For soils the following properties were measured: soil pH, soil available N nitrogen (NH<sub>4</sub>-N and NO<sub>3</sub>-N) and P, and exchangeable K, Ca, Mg and Na. These were assessed on fresh soils using 2M KCL as the extractant for available N and 2.5% vol:vol acetic acid for both available P and the cations. Thereafter, the soil was oven-dried and ground to pass a

1mm mesh. Total N and C determinations were made using a Thermo Scientific Flash 2000 Organic Elemental Analyser; NH<sub>4</sub>-N and NO<sub>3</sub>-N and P were analysed by colorimetry (P) on a Seal Analytical AA3 HR AutoAnalyser and cations by both absorption (Ca and Mg) and emission spectrophotometry (K and Na) on a Thermo Electron Corporation Solaar S4 AAS. Element concentrations were expressed as either % (C, N) or  $\mu\text{g g}^{-1}$  (all others) for soils and as  $\mu\text{mol g}^{-1}$  for vegetation.

For determinations of dietary fibre, larger samples were required, and accordingly individual plot samples were combined to produce four replicates of each of three plant community groups; Bog, Grass and the intermediate *Juncus squarrosus*/*Nardus stricta* grasslands (following Milligan *et al.* 2016, Table S1). Dry matter, Acid Detergent Fibre (ADF), Neutral Detergent Fibre (NDF) were determined by the Analytical Services Department, Central Analytical Services, SAC Commercial Ltd using standard procedures outlined in Allen (1989). Estimates of cell contents, and hemicellulose were determined using the protocol of Goering and Van Soest (1970). These were all expressed as  $\text{g kg}^{-1}$ . Crude protein (%) was estimated by multiplying the herbage nitrogen concentration  $\times 6.25$  (Allen, 1989).

#### Statistical analysis

All analyses were performed in the R statistical environment (R Core Team, 2017); the 'vegan' package was used for all multivariate analyses (Oksanen *et al.*, 2017).

The main problem in analyzing data from these individual experiments is that they are replicated with only one sheep-grazed plot and an equivalent ungrazed enclosure at each site (Marrs *et al.*, 1986; Milligan *et al.* 2016). Here, we have analyzed the eight experiments together as a randomized block experiment with the sites as blocks and the grazed/ungrazed plots as treatments; the analysis was performed on the mean data per plot to avoid pseudo-replication issues. A secondary issue is that experiments have been run for different periods of time, but any temporal effect will be site-specific and will be included within the site effect. Here, analysis of variance and its interpretation was performed using the 'aov' function in R. Model reduction *sensu* Crawley (2013) was performed using the 'anova' function and differences assessed using the 'TukeyHSD' function. QQ-plots were inspected to assess normality and transformations used as necessary ( $\log_e$  and arcsin for percentages). Rank correlation coefficients (Kendall's tau) were calculated between herbage and soil chemical variables using the 'cor.test' function.

Principle Components Analysis (PCA) of both vegetation and soil chemical data was performed using the 'rda' function on data standardized using the 'decostand' function. Site data were visualized by 2-dimensional standard-deviational ellipses fitted using the 'ordiellipse' function. Finally, plant and soil ordinations were compared using the 'procrustes' and 'protest' functions (Lisboa *et al.*, 2014).

Comparable historic data on some soil properties (pH and total N) were available for seven sites in the Centre for Ecology and Hydrology's archive based on samples collected in 1985/6 (here denoted 1985). An assessment of temporal differences between sites, treatments and time was made using Generalized Linear Modelling ('glm' function).

## Results

### Effects on soil properties

Removal of sheep grazing had no significant effect on any of the soil properties measured ( $P > 0.05$ ). There were, however, highly significant site differences for all soil variables; these are detailed in Fig. S.2. The PCA results provide a summary; this analysis produced eigenvalues of 3.66 and 2.75 respectively accounting for 62% of the variation explained by the PCA. The sites were separated on axis 1 from those with large total C and N concentrations at the negative end, and high pH and available concentrations of  $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$ , K and Ca at the positive end (Fig. 1a). Separation on the second axis reflected a gradient of nutrient availability, low at the negative end to and high at the positive end (Fig. 1a). The sites showed a clear gradient from the Bog sites (Bog Hill, Silverband, Troutbeck Head) and the *Juncus*-dominated grassland at the negative end of axis 1 with high total C and N concentrations and the other grasslands placed nearer the positive end (Fig. 1b). The *Nardus* and *Festuca*-grasslands are positioned around the middle of axis 1 but at the positive end of axis 2, i.e. with greater concentrations of most available nutrients. The *Agrostis-Festuca* grassland at Knock Fell is situated furthest along axis 1 (high pH and available Ca concentrations) but has a low position on axis 2 reflecting its low available element concentrations.



### Temporal effects on soil properties

There were significant differences between years for pH at seven of the eight sites; there was a slight reduction at the Bog sites and *Festuca*-grasslands (Hard Hill and Little Dun Fell), and slight increases at the *Juncus squarrosus* grassland and the calcareous grassland at Knock Fell (Fig. 2a). There was no significant change at the *Nardus*-grassland. There was only one significant interaction between grazing treatments and time; this was at the *Agrostis-Festuca* grassland at Knock Fell, where there was a significantly greater pH in the ungrazed treatment through time compared to the sheep-grazed one (Fig. 2b). Total N also increased through time at Little Dun Fell, there was no effect at other sites (Fig. 2c). No other significant temporal effects were detected.

### Effects of herbage

Like the soils, removal of sheep grazing produced no significant differences in either the herbage biomass or the elemental composition ( $P > 0.05$ ). The herbage biomass showed marginally significant differences between sites ( $F_{7,8} = 4.18$ ,  $P < 0.03$ ) with low values in Silverband (recovering bog) and the *Festuca*- and *Agrostis*-dominated grasslands at Little Dun Fell and Knock Fell respectively (Fig. 3a). There was, however, a significant negative relationship with elevation (Fig. 3b, regression equation: Herbage yield ( $\text{g m}^{-2}$ ) =  $6113.396 - 6.526 \times \text{Elevation (m)}$ ;  $F_{1,6} = 20.88$ ,  $r^2_{\text{adj}} = 0.74$ ,  $p = 0.0038$ ). The herbage biomass at the lowest elevations was ca.  $3000 \text{ g m}^{-2}$  reducing to ca.  $1000 \text{ g m}^{-2}$  at the higher elevations. No significant relationship with sheep grazing density was detected ( $F_{1,6} = 3.61$ ,  $r^2_{\text{adj}} = 0.30$ ,  $p = 0.30$ ).

The elemental composition of the herbage is detailed by element (Fig. S3) and summarized by the PCA which produced eigenvalues of 3.705 and 1.309 that accounted for 62.7% of the variation explained by the PCA. The chemical constituents were clearly separated along axis 1 from high C and C:N ratio at the negative end, Ca and Na were intermediate and N, P, K and Mg at the positive end (Fig. 4a); on axis 2 the cations and C:N ratio were plotted at the negative end and N and C were at the positive end. The sites showed a very clear sequence along axis 1 with the three bog sites at the negative end (high C) moving through to the grasslands at the positive end (high N, P, K, Mg, Fig. 4b).

### Links between soil and herbage plant composition

There were significant positive rank correlations ( $P < 0.0003$ ) between herbage chemical properties and some soil variables total C, C:N ratio, exchangeable K and available as  $\text{NO}_3\text{-N}$ ,  $\text{NH}_4\text{-N}$  and the summed total of available N; no significant correlation was detected with soil total N, available P and exchangeable Ca, Mg or Na. The Procrustes rotation test of the two multivariate analyses of the chemical composition of soils (Fig. 1) and herbage (Fig. 4) produced a significant correlation ( $r = 0.35$ ,

P=0.0020). Inspection of the residuals (Fig. S4) indicated that the greatest deviations were at Little Dun Fell and Knock Fell, *Festuca*- and *Agrostis-Festuca*-dominated grasslands respectively.

#### Effects on dietary components

The only significant effect of removal of sheep grazing was an increased ADF concentration in the ungrazed treatment compared to the sheep-grazed one ( $592 \pm 10$  versus  $542 \pm 20$  g kg<sup>-1</sup> DM;  $F_{2,3} = 39.24$ ,  $P = 0.0245592$ ). There were, however, significant differences between the site groups for NDF ( $F_{2,3} = 36.91$ ,  $P = 0.0077$ ), ADF ( $F_{2,3} = 34.42$ ,  $P = 0.0282$ ), cell contents ( $F_{2,3} = 48.50$ ,  $P = 0.0052$ ), and crude protein ( $F_{2,3} = 20.55$ ,  $P = 0.0177$ ), but not for hemicellulose ( $P > 0.05$ ). The NDF values were greater in the *Nardus/Juncus* grassland  $719 \pm 11$  g kg<sup>-1</sup> DM compared to bog or grass communities ( $635 \pm 11$  and  $664 \pm 8$  g kg<sup>-1</sup> DM) whereas cell contents were lower (*Nardus/Juncus* =  $195 \pm 11$ , Bog =  $290 \pm 11$ , Grass =  $256 \pm 9$  g kg<sup>-1</sup> DM) (Fig. 5a,c). Crude protein showed an increasing trend from the Bog through *Nardus/Juncus* to the Grass communities, with the Bog communities ( $7.2 \pm 0.6\%$ ) being significantly lower than the *Juncus/Nardus* ( $8.9 \pm 0.4\%$ ) and Grass communities ( $9.45 \pm 0.5\%$ ) (Fig. 5d). ADF concentrations were lower in the grass community  $522 \pm 13$  g kg<sup>-1</sup> DM than both the *Juncus/Nardus* ones and bog,  $578 \pm 18$  and  $601 \pm 34$  g kg<sup>-1</sup> DM respectively (Fig. 5b).

#### Effects on herbage species composition

There were no significant differences between the proportion of litter in the herbage, with an overall mean value of  $53 \pm 0.02\%$  (mean  $\pm$  SE) or indeed most fractions of the vegetation. Dwarf shrubs were greatest in the bog communities (Bog Hill =  $34 \pm 0.05\%$ , Silverband =  $8 \pm 0.06\%$ , Troutbeck Head ( $14 \pm 0.06\%$ ) and the *Agrostis*-grassland at Knock Fell ( $8.7 \pm 0.07\%$ , *Vaccinium myrtillus*) with much less in the other communities ( $<0.1\%$ ). Lichens were greatest in one of the bog communities (Bog Hill,  $6.3 \pm 3.1\%$ ) and Hard Hill *Festuca*-grassland ( $7.4 \pm 3.0\%$ ) compared to all other sites ( $<0.1\%$ ). The graminoids were the only fraction to show a grazing treatment effect being greater in the grazed compared to the ungrazed treatments,  $12.7 \pm 1.5$  and  $5.3 \pm 0.7$  respectively.

#### Discussion

Current predictions of future land use suggest that marginal land use in Northern Europe will change over the next few decades through abandonment (van der Zandena, *et al.*, 2017) or by massive reductions in numbers of grazing livestock in free-range grazing systems in some cases to zero (Dreary & Warren, 2017; Monbiot, 2013). This latter approach is a simple approach to rewilding. It assumes that over-grazing by livestock has degraded the ecosystem relative to its previous state over a long period and that by removing the cause of degradation, the ecosystems will recover to an

approximation of their former state. This should involve a change in species composition and both herbage and soils quality. Here, this hypothesis was tested by measuring change in soils and herbage quality in long-term sheep enclosure studies on a range of common British upland plant communities.

We have already demonstrated that removal of sheep grazing has degraded the vegetation on these sites. In a holistic analysis of species change up to the year 2000 (Milligan *et al.*, 2016), showed a reduction in overall species diversity where sheep grazing was continued, and that removal of sheep grazing benefitted some herbs, mosses, sedges and shrubs, but reduced grasses and liverworts. The reduction in overall diversity with continued sheep grazing is consistent with the views from elsewhere in the British uplands (Fraser Darling, 1955; McGovern *et al.*, 2011). At most sites, the dominant species has remained in place but there was a changed hierarchy.

The results reported here rejects the hypothesis that there will be a rapid recovery in herbage biomass, plant nutrient content and herbage dietary components. The only variable that showed a significant difference between grazed and ungrazed treatments was the ADF concentration in the herbage, which was greater in ungrazed plots, suggesting reduced digestibility. All other herbage and soil variables measured showed no treatment effects. Therefore, removal of sheep has had very little impact on soil fertility or vegetation nutrition over the timescales of these relatively long-term experiments (48-62 years) and lag behind observed changes in species composition (Milligan *et al.*, 2016). It is possible that more subtle effects may be picked up by restricting sampling to surface soils. Here, we used a standard soil depth to be comparable with other studies and samples taken were either still within the O-horizon or encompassed the entire profile (rendzinas). More subtle treatment-induced effects may be detectable through the assessment of microbiological communities or microbial-driven processes (de Vries *et al.*, 2012); this remains to be determined. Changing pollutant loads (SO<sub>2</sub> and NO<sub>x</sub>) have also varied over the course of these studies at Moor House and may have affected species responses (Monteith *et al.* 2017; Rose *et al.*, 2017); clearly, they have not yet affected soil chemistry or herbage nutrition. Therefore, rewilding within the British uplands merely by reducing sheep grazing, will have very limited effect in the short term (48-62 years) of reversing ecosystem degradation caused by long-term sheep grazing.

It was also clear that the main differences in herbage quality and soil chemistry was between the differing plant communities tested, which in turn reflects their differing soil types and altitude. The altitudinal effect was presumably because of cooler temperatures and greater rainfall at higher elevations. There were no correlations detected with sheep grazing pressure and this may result the continued reduction in sheep numbers or from differential distribution patterns at each site. For example, it is feasible that as the sheep numbers drop, the grazing intensity could be maintained on

the most productive *Festuca*- and *Agrostis-Festuca* grasslands (Rawes & Welch, 1969) with a disproportionately lower pressure on the blanket bog vegetation. This remains to be tested.

In ecological terms, we speculate that the derived degraded ecosystems have a high resistance to change, and if attempts are made to restore a wider diversity of plant species then either there must be an acceptance that this will take a very long time, i.e. greater than ca. 50 years or there must be an intervention approach. The former option is an unknown and can only be addressed by much longer term studies. There latter suggests are three potential constraints to the colonization by new species, a lack of (1) propagule availability, (2) regeneration niches (*sensu* Grubb, 1977), and (3) the small size of the experimental plots (Milligan *et al.*, 2016). In terms of new colonists there has been no colonization by tree species in any of these experiments (Milligan *et al.*, 2016), although in another, larger, long-term experiment at this site (Milligan *et al.*, 2018) one small *Betula* sapling persisted for some time then died, and a few *Picea sitchensis* seedlings have been detected recently after a period of ca. 60 years grazing-free (R.H. Marrs pers. comm.). We have no information on the potential propagule banks or seed rain in these upland systems, but the combined biomass and litter present will probably be an obstacle to both to seed rain into the system and producing appropriate conditions for establishment (Lowday *et al.* 1992; Ghorbani *et al.*, 2006). Alternatives would be to develop some form of intervention approach with both propagule addition and applied disturbance to aid colonization of new species. This requires an experimental approach.

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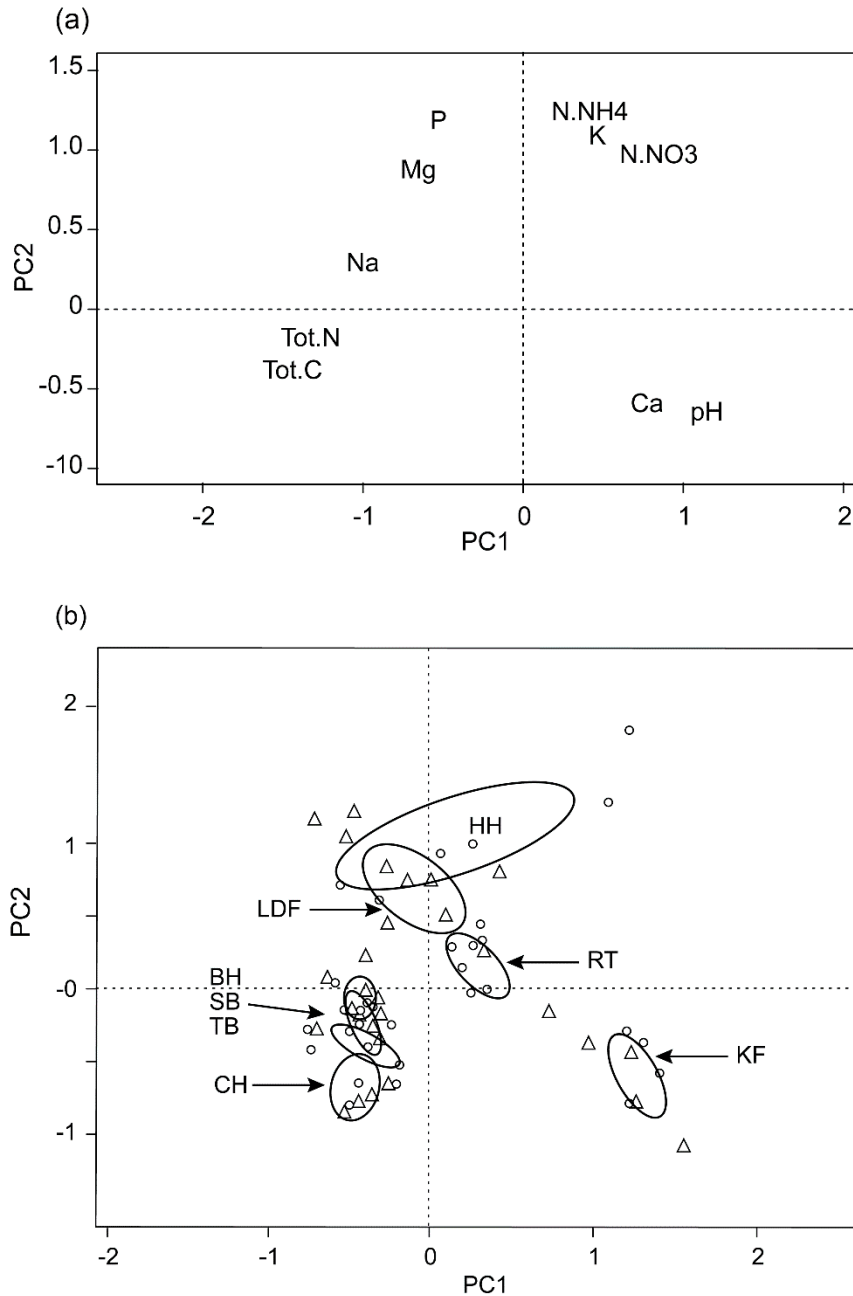


Figure 1. Principle Components Analysis of the soil chemical properties in the grazed ( $\Delta$ ) and ungrazed ( $\circ$ ) plots at the eight sites at Moor House NNR: (a) soil chemical properties, (b) all sampled quadrats and site positions described using 2D standard-deviational ellipses. Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, RT = River Tees, HH = Hard Hill, LDF = Little Dun Fell and KF = Knock Fell.

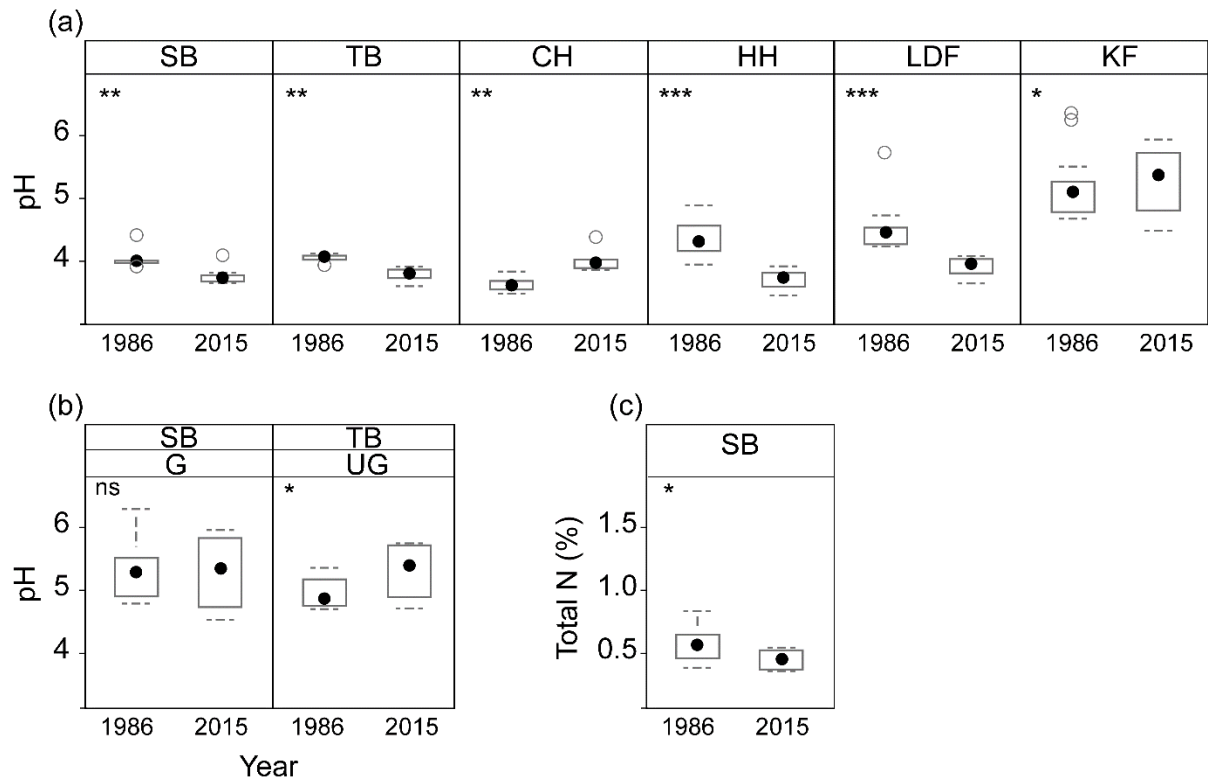


Figure 2. Significant changes in soil pH and total N in the long term grazing exclosure sites at Moor House NNR: (a) sites that showed differences in pH between years, (b) interaction between grazing treatments and time at Knock Fell, and (c) differences in total N between years at Knock Fell. Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, HH = Hard Hill, LDF = Little Dun Fell and KF = Knock Fell; Grazing treatment codes: G = sheep-grazed, UG = ungrazed; Significance codes (full data in Table S2): ns = not significant,  $P > 0.05$ ; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ .



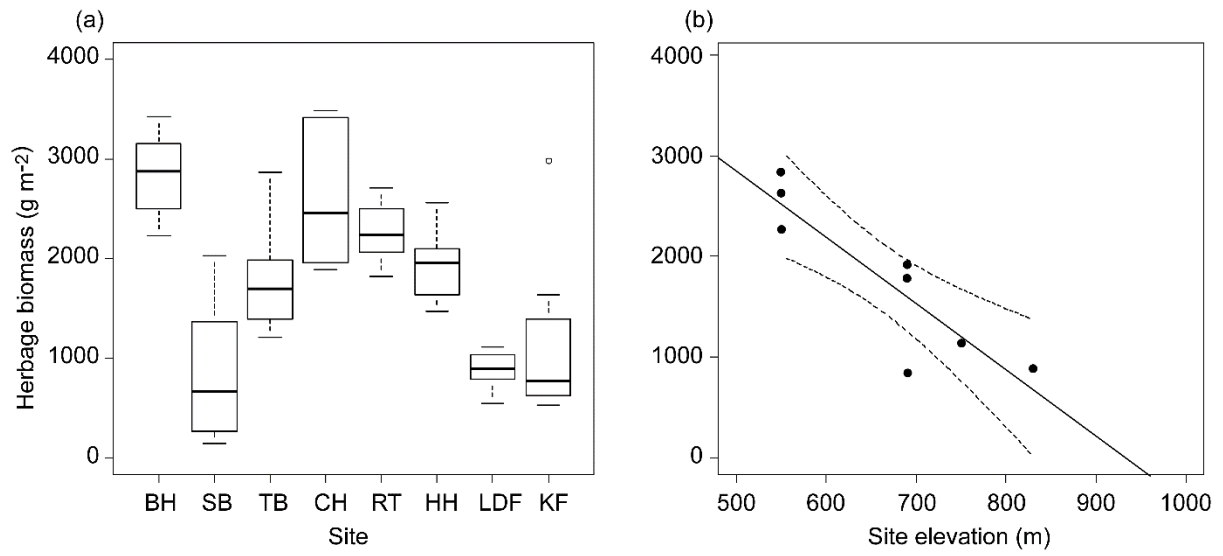


Figure 3. Herbage biomass at each of the long term grazing exclosure sites at Moor House NNR: (a) by site, and (b) with respect to elevation Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, RT = River Tees, HH = Hard Hill, LDF = Little Dun Fell and KF = Knock Fell.

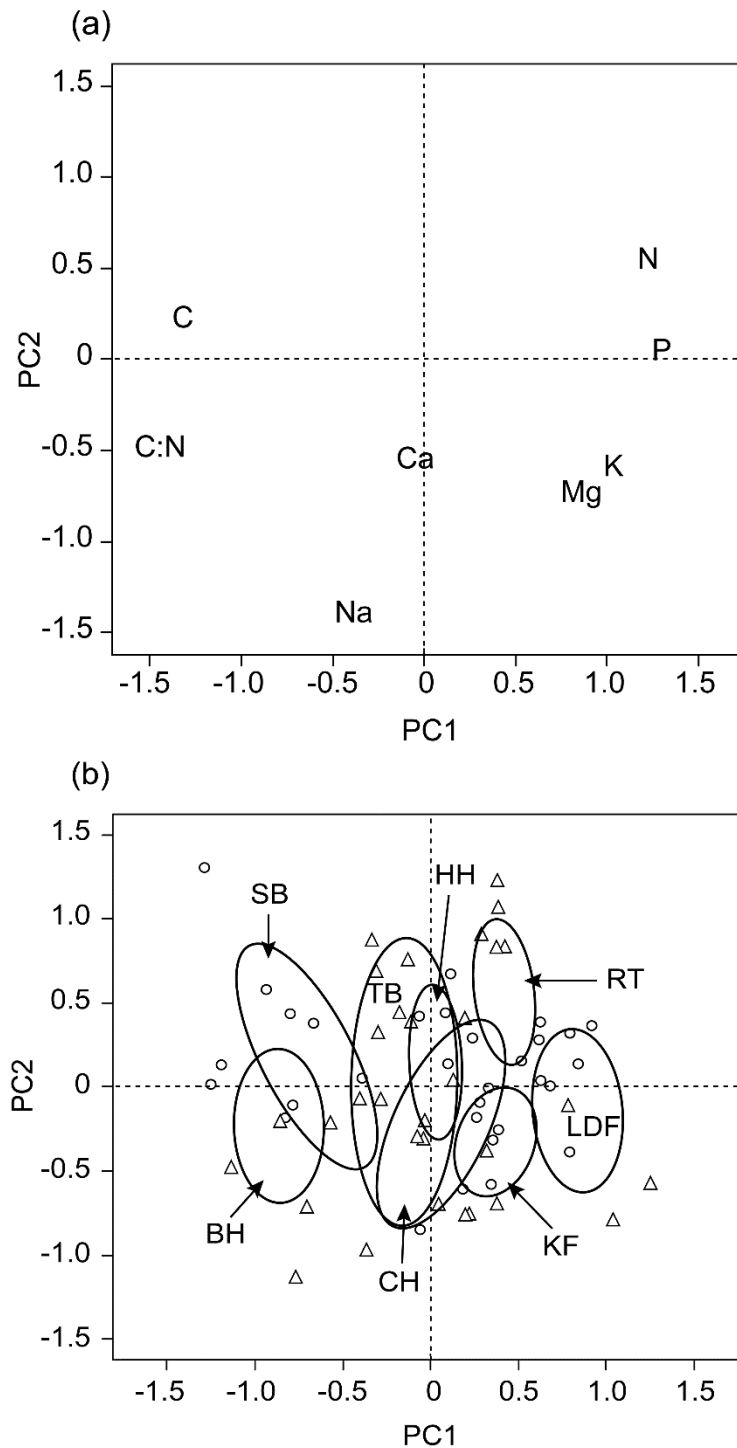


Figure 4. Principle Components Analysis of the herbage chemical properties in the grazed ( $\Delta$ ) and ungrazed ( $\circ$ ) plots at the eight sites at Moor House NNR: (a) herbage chemical properties, (b) all sampled quadrats and site positions described using 2D standard-deviational ellipses. Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, RT = River Tees, HH = Hard Hill, LDF = Little Dun Fell and KF = Knock Fell.

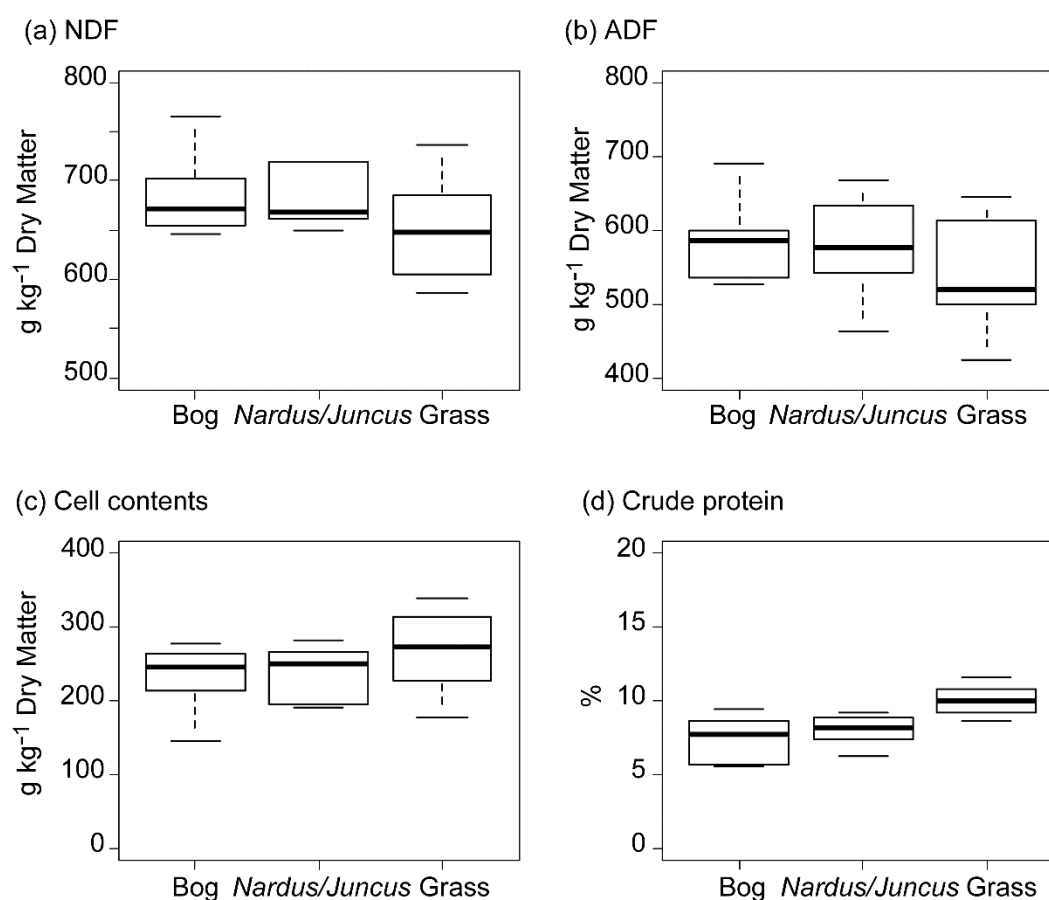
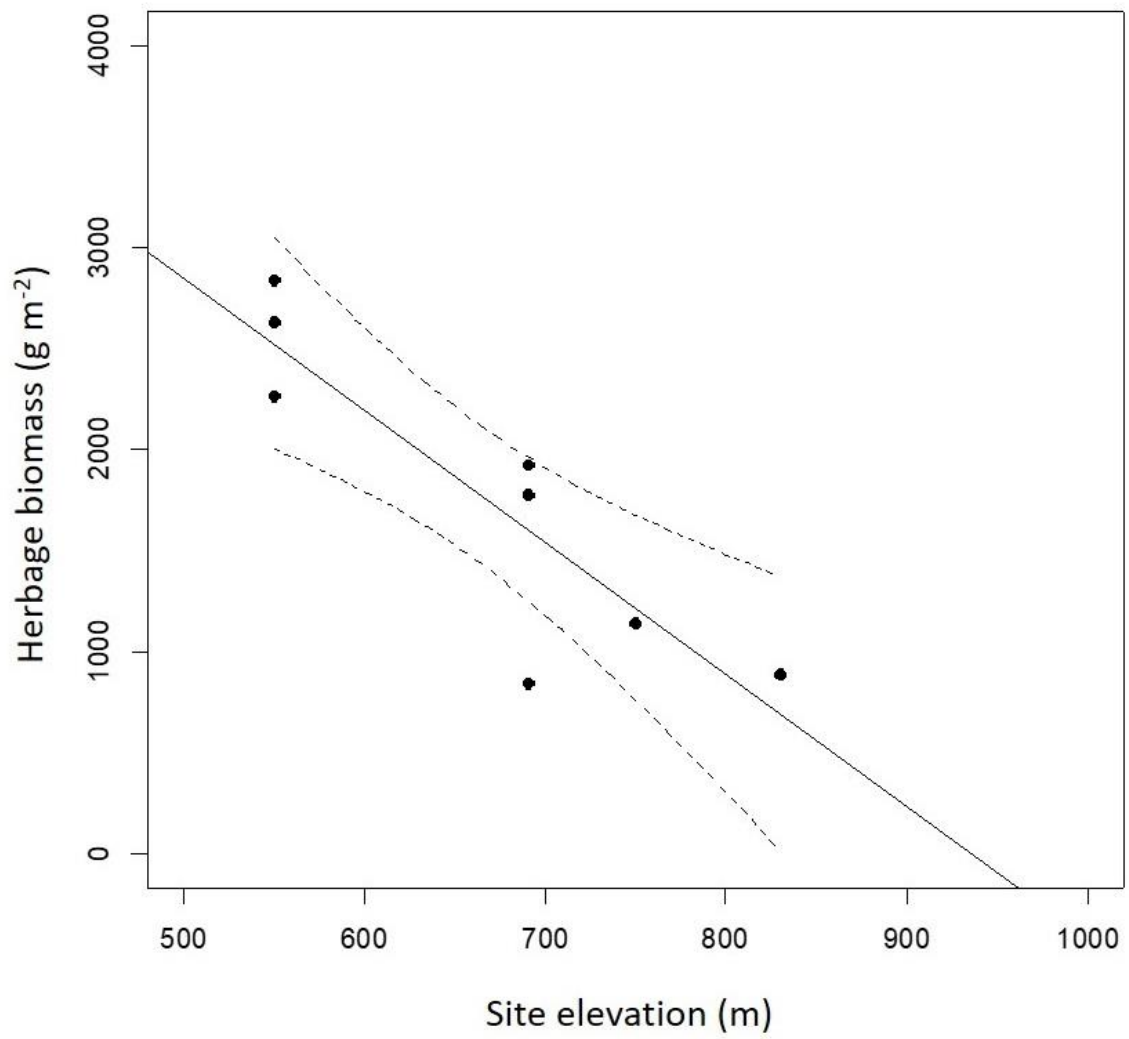


Figure 5. Dietary components of the herbage in three grouped vegetation types within the long term grazing enclosure sites at Moor House NNR: (a) NDF, (b) ADF, (c) cell contents, and (d) crude protein. P, and (e) K. Main vegetation types are denoted: Bog = *Calluna/Eriophorum*, *Nardus/Juncus* = *Juncus squarrosus/Nardus stricta* grassland, Grass = *Festuca ovina/Agrostis capillaris* grassland

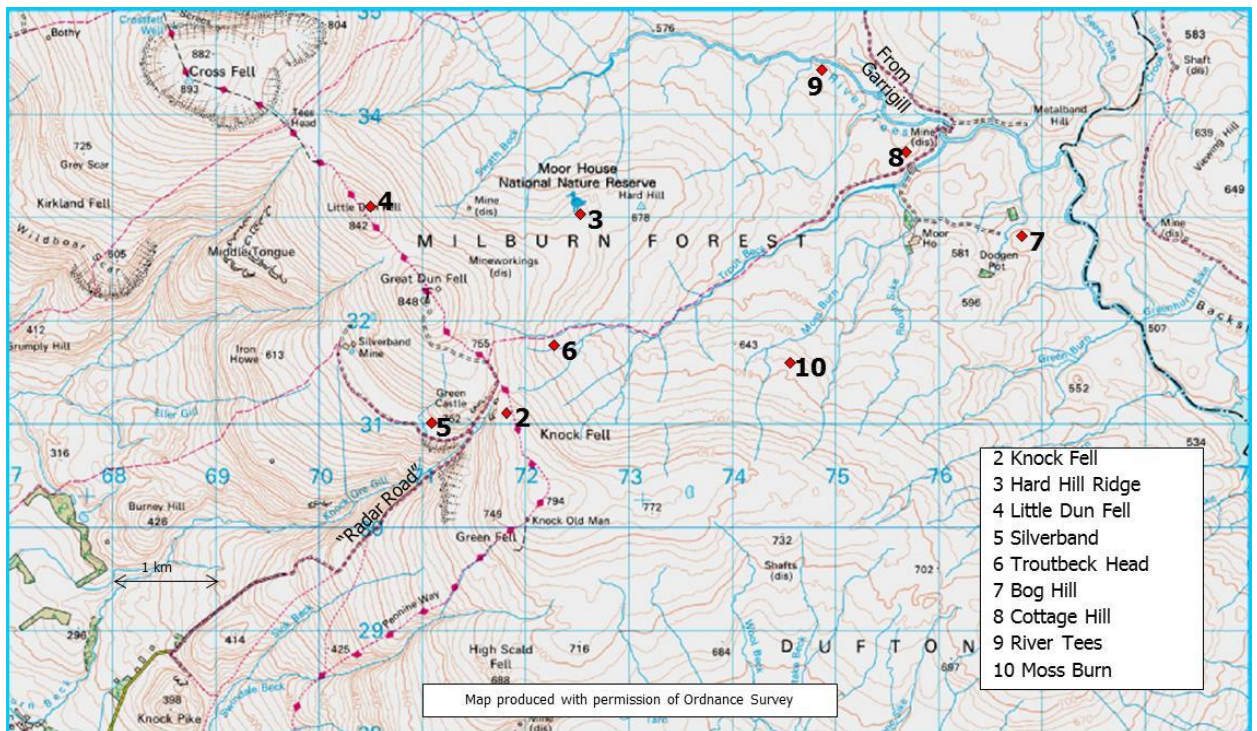


Graphical Abstract. Herbage biomass was related to elevation: presence/absence of sheep grazing had almost no effect on soil or plant nutrition.

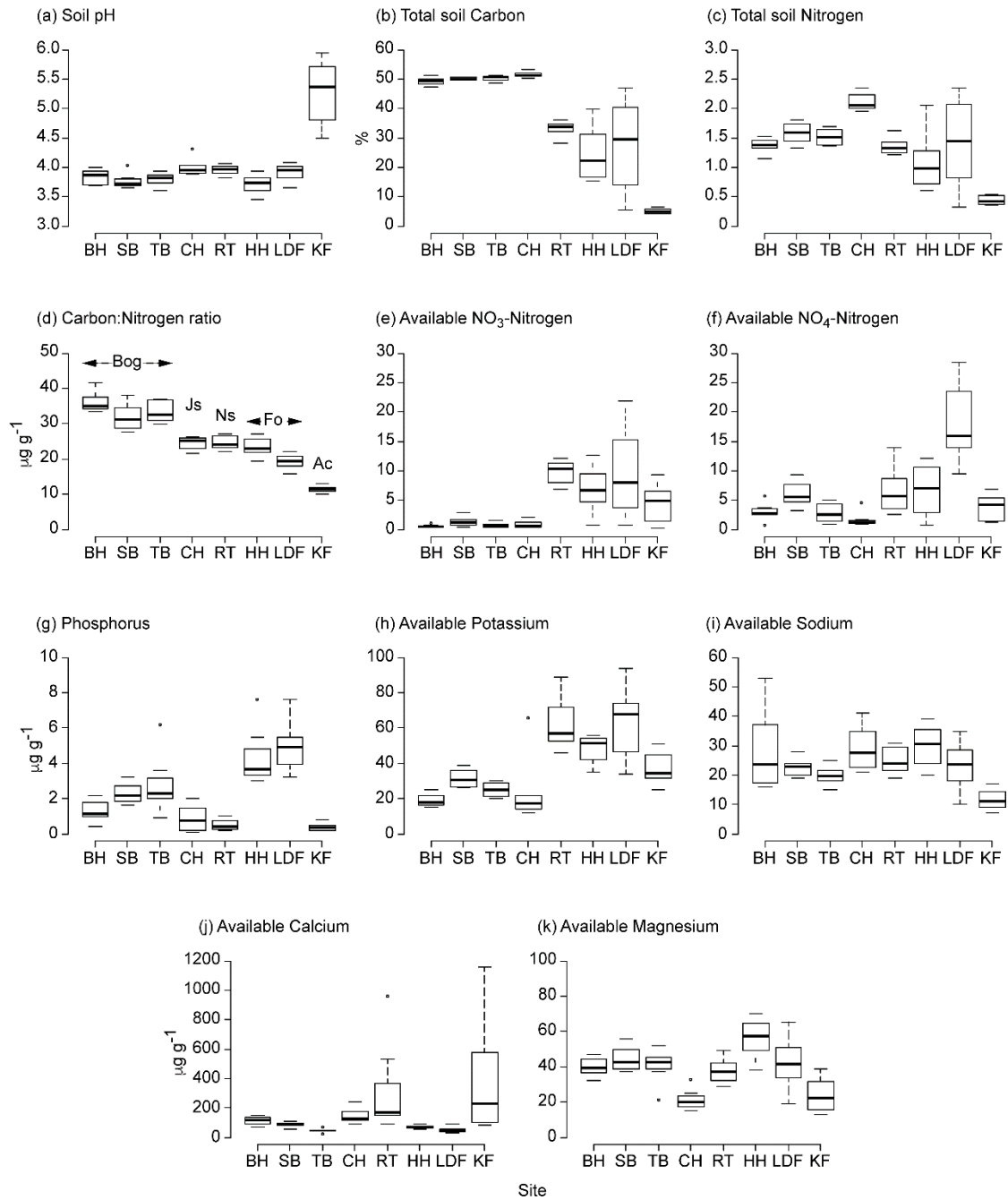
(a)



(b)



**Fig. S1.** (a) Location of Moor House NNR, and (b) a map of the Moor House site showing positions of all vegetation monitoring experiments.

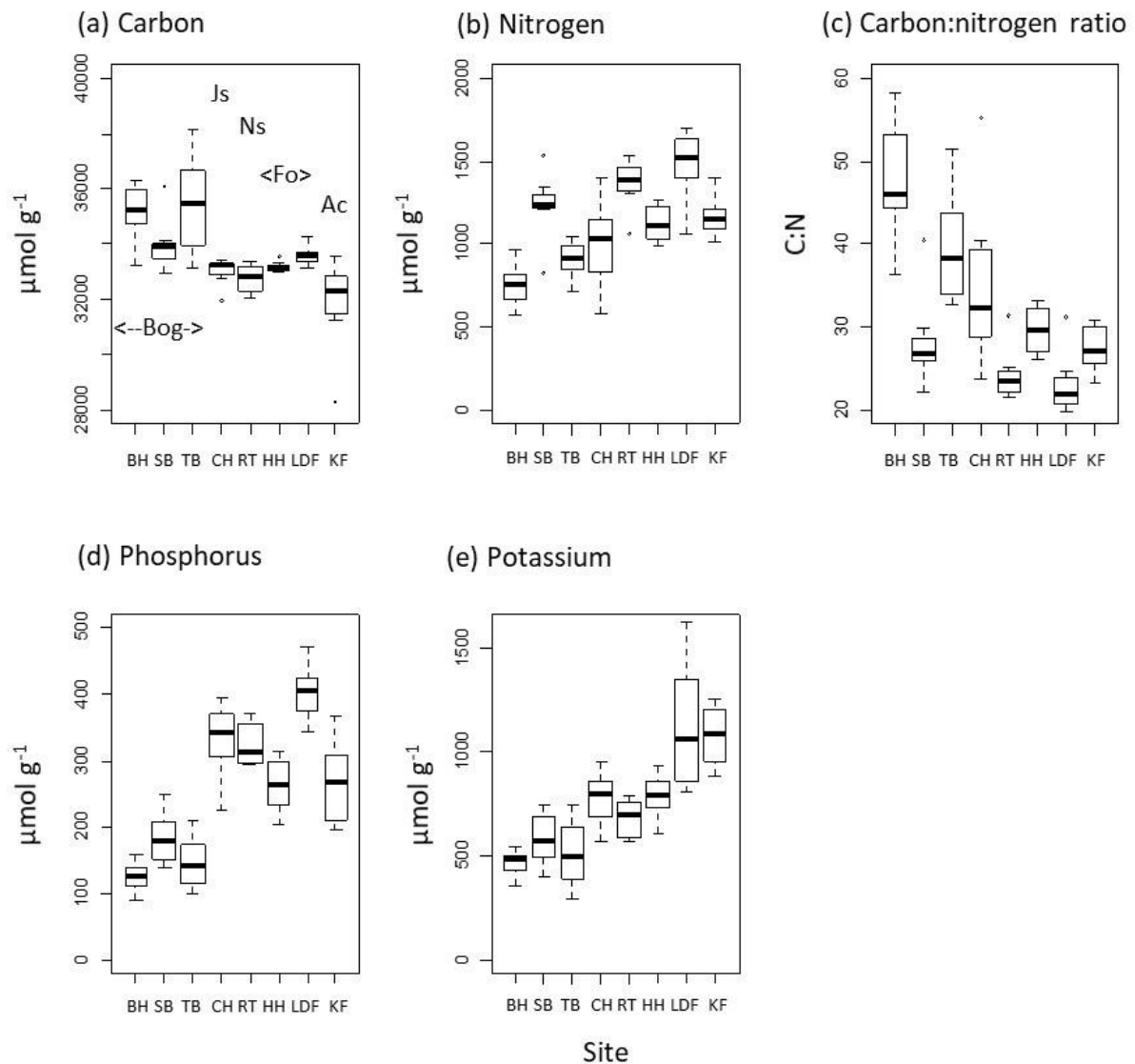


**Figure S2.** Soil chemical properties of soils from the eight study sites at Moor House NNR; as there were no significant treatment effects between ungrazed and grazed plots data for these treatments have been pooled: (a) soil pH, (b) total soil carbon, (c) total soil nitrogen, (d) soil C:N ratio, (e) available NO<sub>3</sub>-N, (f) available NH<sub>4</sub>-N, (g) available P, and exchangeable concentrations of (h) K, (i) Na, (j) Ca and (k) Mg. Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, RT = River Tees, HH = Hard Hill, LDF = Little Dun Fell and KF = Knock Fell. Main vegetation types are denoted: Bog *Calluna/Eriophorum*, Js = *Juncus squarrosus*, NS = *Nardus stricta*, Fo = *Festuca ovina* and Ac = *Agrostis capillaris*.

## Interpretation of Fig. S2

Significant differences were found between sites for all soil variables (Soil pH,  $F_{7,8} = 59.88$ ,  $P < 0.0001$ ; Total C,  $F_{7,8} = 46.09$ ,  $P < 0.0001$ ; Total N,  $F_{7,8} = 8.156$ ,  $P = 0.0041$ ; C:N,  $F_{7,8} = 33.96$ ,  $P < 0.0001$ ; Available  $\text{NO}_3\text{-N}$ ,  $F_{7,8} = 12.1$ ,  $P = 0.0011$ ; Available  $\text{NO}_3\text{-N}$ ,  $F_{7,8} = 7.292$ ,  $P = 0.0059$ ; available P,  $F_{7,8} = 20.33$ ,  $P = 0.0002$ ; exchangeable K,  $F_{7,8} = 8.737$ ,  $P = 0.0033$ ; exchangeable Na,  $F_{7,8} = 6.374$ ,  $P = 0.0091$ ; exchangeable Ca,  $F_{7,8} = 4.167$ ,  $P = 0.0315$ ; exchangeable Mg,  $F_{7,8} = 5.492$ ,  $P = 0.0143$ ).

The soil chemical properties reflected a change across the bog-grassland transition (Fig. 1). Soil pH was low (mean  $< 4.0$ ) in all sites except the Knock Fell *Agrostis-Festuca* grassland (mean  $\pm$  SE,  $5.3 \pm 0.3$ ). Total soil C was greatest in the Bog sites and Cottage Hill (*Juncus squarrosus* grassland), intermediate in the *Nardus*- and *Festuca*-dominated grassland (means all  $> 20\%$ ) and lowest in the *Agrostis-Festuca* grassland at Knock Fell ( $5.0 \pm 0.2\%$ ). Total soil N showed a similar pattern. The C:N ratio showed a clear transition from the bog sites (mean  $> 30\%$ ), through the *Juncus*-, *Nardus*- and *Festuca*-dominated grasslands (19-24%) to the lowest in the Knock Fell *Agrostis-Festuca* grassland ( $11.4 \pm 2.8\%$ ). Both available N concentrations showed similar responses, very low in the bog communities and the *Juncus*-community and greater in the *Nardus*, *Festuca* and *Agrostis-Festuca* grasslands. Available P values were low ( $< 10 \mu\text{g P g}^{-1}$ ) especially in the Knock Fell *Agrostis-Festuca* grassland with greatest concentrations found in the *Festuca*-dominated grasslands,  $4.3 \pm 0.6$  and  $4.9 \pm 0.5 \mu\text{g P g}^{-1}$  for Hard Hill and Little Dun Fell respectively; other sites were intermediate. Available cations showed variable responses. Available K was low in the bog and *Juncus*-dominated communities ( $< 35 \mu\text{g K g}^{-1}$ ) and greater in the *Nardus*, *Festuca* and *Agrostis-Festuca*-dominated communities ( $> 35 \mu\text{g K g}^{-1}$ ). Lower concentrations of Na were found in the *Agrostis-Festuca* grassland at Knock Fell ( $11.6 \pm 1.1 \mu\text{g Na g}^{-1}$ , all other sites  $> 20 \mu\text{g Na g}^{-1}$ ) and larger concentrations of Ca were found at the *Nardus* grassland at the River Tees site and the *Agrostis-Festuca* grassland at Knock Fell albeit with large variability  $300 \pm 106$  and  $383 \pm 133 \mu\text{g Ca g}^{-1}$  respectively; other sites ranged between 46-150  $\mu\text{g Ca g}^{-1}$ .

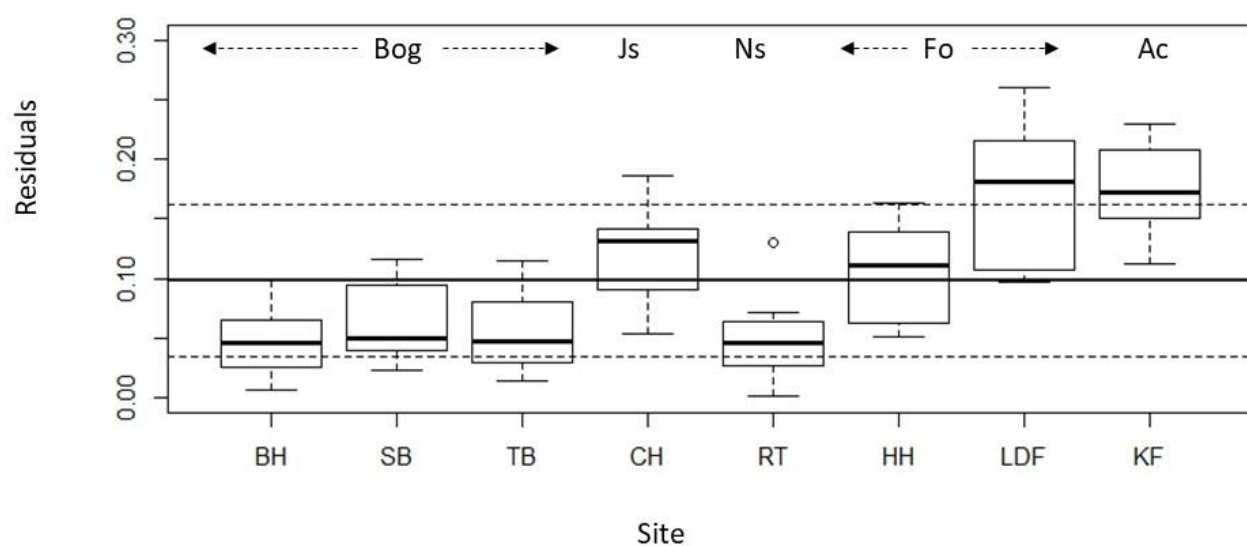


**Figure S3.** Chemical properties of the herbage from the eight sites at Moor House NNR; as there were no significant treatment effects between ungrazed and grazed plots data for these treatments have been pooled: (a) carbon, (b) nitrogen, (c) soil C:N ratio, (d) P, and (e) K. Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, RT = River Tees, HH = Hard Hill, LDF = Little Dun Fell and KF – Knock Fell. Main vegetation types are denoted: Bog = *Calluna/Eriophorum*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, Fo = *Festuca ovina* and Ac = *Agrostis capillaris*.



### Interpretation of Fig. S3

There were highly significant differences between sites for N ( $F_{7,8} = 23.84$ ,  $P < 0.0001$ ), C:N ( $F_{7,8} = 14.68$ ,  $P < 0.0001$ ), P ( $F_{7,8} = 18.06$ ,  $P < 0.0001$ ), and K ( $F_{7,8} = 8.32$ ,  $P < 0.0001$ ), a marginal difference for C ( $F_{7,8} = 4.83$ ,  $P = 0.02$ ), and no significant effects for Ca, Mg and Na ( $P > 0.05$ ). The elemental composition of the herbage showed two main responses; (1) CN, C:N ratio and K showed a changing response along the gradation from the bog communities to the *Agrostis*-*Festuca*-dominated grassland: C and C:N ratio both decreasing and N and K increasing, and (2) P showed a step response being lower in the three bog communities and greater in all the grassland ones.



**Figure S4.** Residual derived from a Procrustes Rotation Analysis of the PCA analyses of the chemical properties of the soils (Fig. 1) and herbage (Fig.4) from the eight sites at Moor House NNR. Site codes: BH = Bog Hill, SB = Silverband, TH = Troutbeck Head, CH = Cottage Hill, RT = River Tees, HH = Hard Hill, LDF = Little Dun Fell and KF = Knock Fell. Main vegetation types are denoted: Bog = *Calluna/Eriophorum*, Js = *Juncus squarrosus*, Ns = *Nardus stricta*, Fo = *Festuca ovina* and Ac = *Agrostis capillaris*. Bold vertical line indicates the overall mean.

**Table S1** Description of the eight sites each with a sheep-grazing exclosure a comparator grazed site at Moor House NNR in north-west England (data abstracted from Milligan *et al.*, 2016).

Site Name	Plant community type – Dietary fibre analysis	Site code	British National Grid reference	Elevation (m)	Year established	Vegetation type according to (Eddy <i>et al.</i> , 1969)	NVC type according to (Mean Goodness of fit)	NVC description (Rodwell, 1991, 1992)	Total area of pure stands of the vegetation types on the Moor House reserve (ha)	**Sheep Grazing Density (sheep ha <sup>-1</sup> )
Bog Hill	Bog	BH	NY 76789 32869	550	1953	<i>Calluna-Eriophorum</i>	M19 (68%)	<i>Calluna vulgaris-Eriophorum vaginatum</i> blanket mire	1169	nd
Silverband	Bog	SB	NY 71059 30975	690	1966	Eriophoretum (eroding)	M20b (71%)	<i>Eriophorum vaginatum</i> blanket and raised mire: <i>Calluna vulgaris-Cladonia</i> spp. sub-community	323	0.25
Troutbeck Head	Bog	TB	NY 72236 31760	690	1966	Eriophoretum	M20b (73%)	<i>As above</i>	419	0.5
Cottage Hill	<i>Juncus/Nardus</i>	CH	NY 75801 33641	550	1967	<i>Juncus squarrosus</i> grassland	U6b (61%)	<i>Juncus squarrosus-Festuca ovina</i> grassland: <i>Carex nigra-Calypogeia trichomanis</i> sub-community	373	1.4
River Tees	<i>Juncus/Nardus</i>	RT	NY 74796 34485	550	1967	<i>Nardus stricta</i> grassland	U5 (73%)	<i>Nardus stricta-Galium saxatile</i> grassland	416	2.8
Hard Hill	Grass	HH	NY 72576 33034	690	1954	<i>Festucetum</i>	H19a (61%)	<i>Vaccinium myrtillus-Cladonia arbuscula</i> heath: <i>Festuca ovina-Galium saxatile</i> sub-community	180	2.6
Little Dun Fell	Grass	LDF	NY 70475 33104	830	1954	<i>Festucetum</i>	H19a (63%)	<i>As above</i>	-	5.8
Knock Fell	Grass	KF	NY 71794 31267	750	1955	Limestone Agrosti-Festucetum	CG10 (55%)	<i>Festuca ovina-Agrostis capillaris-Thymus praecox</i> grassland	125	5.8

\*The total area of these communities makes up 3019 ha, i.e. 79% of the reserve area of 3842 ha, the remaining vegetation comprised predominantly re-colonising peatland, Sandstone scree and mosaics of the above vegetation classes (Eddy *et al.*, 1969).

\*\*Sheep grazing density was determined by dropping volume measurement (Rawes & Welch 1969); data were not available for Bog Hill.

**Table S2.** Results from the Generalized Linear modelling assessing effects of time; the intercept is the Cottage Hill grazed treatment in 1984. Site codes see Table S1, Ungrazed = UG and Year = 2015. Significance: ns= $P>0.05$ , \*= $P<0.05$ , \*\* =  $P<0.01$ , \*\*\*= $P<0.001$ .

Variable ( $\Delta$ AIC)	Treatment	Estimate	Standard Error	t-value	P	Significance
pH (245.1)	(Intercept)	-29.428	10.525	-2.796	0.006	**
	SiteHH	76.861	15.004	5.123	<0.001	***
	SiteKF	39.974	14.884	2.686	0.008	**
	SiteLDF	57.505	15.591	3.688	<0.001	***
	SiteRT	13.481	14.884	0.906	0.367	ns
	SiteSB	58.091	17.231	3.371	0.001	***
	SiteTB	47.044	17.231	2.730	0.007	**
	UG	15.888	14.884	1.067	0.288	ns
	Year	0.017	0.005	3.153	0.002	**
	SiteHH:UG	-14.651	21.459	-0.683	0.496	ns
	SiteKF:UG	-46.852	21.049	-2.226	0.028	*
	SiteLDF:UG	16.057	21.873	0.734	0.464	ns
	SiteRT:UG	-31.464	21.134	-1.489	0.139	ns
	SiteSB:UG	-27.882	24.369	-1.144	0.255	ns
	SiteTB:UG	-8.561	25.449	-0.336	0.737	ns
	SiteHH:Year	-0.038	0.008	-5.092	<0.001	***
	SiteKF:Year	-0.019	0.007	-2.581	0.011	*
	SiteLDF:Year	-0.029	0.008	-3.661	<0.001	***
	SiteRT:Year	-0.007	0.007	-0.908	0.366	ns
	SiteSB:Year	-0.029	0.009	-3.368	0.001	**
	SiteTB:Year	-0.023	0.009	-2.724	0.007	**
	UG:Year	-0.008	0.007	-1.070	0.287	ns
	SiteHH:UG:Year	0.007	0.011	0.680	0.498	ns
	SiteKF:UG:Year	0.023	0.011	2.213	0.029	*
	SiteLDF:UG:Year	-0.008	0.011	-0.725	0.470	ns
	SiteRT:UG:Year	0.016	0.011	1.486	0.140	ns
	SiteSB:UG:Year	0.014	0.012	1.148	0.253	ns
	SiteTB:UG:Year	0.004	0.013	0.338	0.736	ns
Tot.N (156.6)	(Intercept)	9.133	15.350	0.595	0.553	ns
	SiteHH	-39.910	21.890	-1.823	0.071	ns
	SiteKF	8.528	21.710	0.393	0.695	ns
	SiteLDF	-46.550	22.740	-2.047	0.043	*
	SiteRT	7.540	21.710	0.347	0.729	ns
	SiteSB	-4.672	25.140	-0.186	0.853	ns
	SiteTB	22.390	25.140	0.891	0.375	ns
	UG	-2.197	21.710	-0.101	0.920	ns
	Year	-0.003	0.008	-0.448	0.655	ns
	SiteHH:UG	36.380	31.300	1.162	0.247	ns
	SiteKF:UG	-12.580	30.700	-0.410	0.683	ns
	SiteLDF:UG	28.010	31.710	0.883	0.379	ns
	SiteRT:UG	-1.656	30.700	-0.054	0.957	ns
	SiteSB:UG	3.696	35.550	0.104	0.917	ns
	SiteTB:UG	-1.659	37.120	-0.045	0.964	ns

SiteHH:Year	0.019	0.011	1.754	0.082	ns
SiteKF:Year	-0.005	0.011	-0.469	0.640	ns
SiteLDF:Year	0.023	0.011	2.013	0.046	*
SiteRT:Year	-0.004	0.011	-0.385	0.701	ns
SiteSB:Year	0.002	0.013	0.155	0.877	ns
SiteTB:Year	-0.011	0.013	-0.908	0.366	ns
UG:Year	0.001	0.011	0.093	0.926	ns
SiteHH:UG:Year	-0.018	0.016	-1.145	0.255	ns
SiteKF:UG:Year	0.006	0.015	0.411	0.682	ns
SiteLDF:UG:Year	-0.014	0.016	-0.897	0.372	ns
SiteRT:UG:Year	0.001	0.015	0.063	0.950	ns
SiteSB:UG:Year	-0.002	0.018	-0.091	0.928	ns
SiteTB:UG:Year	0.001	0.019	0.044	0.965	ns